Assessment of Biodiversity at Different Stages of the Forest Cycle

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EXECUTIVE SUMMARY

OBJECTIVES

The main objectives of this project were to:

1. Assess the range of biodiversity in representative forests at key stages of the forest cycle;
2. Review possibilities for enhancement of biodiversity in plantation forests and make recommendations;
3. Assess the effectiveness of the *Forest Biodiversity Guidelines* in light of the results of this study.

STUDY DESIGN AND METHODOLOGY

We investigated variation in biodiversity between forest types and across the age cycle; identified structural, compositional and functional variables (biodiversity indicators) that are related to biodiversity variation across sites; and made recommendations for forest management practices that will maintain and/or enhance biodiversity in plantation forests.

The forest types we studied were Sitka spruce (*Picea sitchensis*), ash (*Fraxinus excelsior*), and non-intimate Sitka spruce-ash mixes. These represent the main conifer and broadleaf species currently being planted in Ireland, and non-intimate mixes of conifers and broadleaves are likely to become the dominant configuration in future afforestation.

We sampled five age classes (5, 8-15, 20-30, 35-50 and > 50 years) that represent the major structural changes that take place in forest development over the course of a commercial rotation. As forest age is only one of many factors that affect stand structure, we developed an age-independent structural type classification to summarise the structural characteristics (canopy cover, tree size and spacing) of our study sites.

We carried out surveys of vegetation, spiders, hoverflies and birds, using standard survey methods, and collected environmental and management information for all our survey sites. We constructed a Geographical Information System (GIS) containing all our survey data, along with base mapping, forest inventory details, and other relevant geographical data.

ASSEMBLAGES OF ASH AND SITKA SPRUCE PLANTATION FORESTS

Over the forest cycle, ash and Sitka spruce plantations can support diverse vegetation, spider, hoverfly and bird assemblages. These assemblages contain a large proportion of generalist species and we recorded few species of conservation importance. However, mature stands can develop a characteristic woodland flora and support forest specialist spiders and hoverflies.

The various taxonomic groups showed different trends in total species richness across the forest cycle, but highest species richness generally occurs either at the beginning or the end of the forest cycle. High species richness in the pre-thicket stage is probably associated with the persistence of species associated with the pre-planting habitats and should not necessarily be interpreted as a positive contribution by plantation forestry to biodiversity conservation. We, therefore, emphasise the importance of the mature stages for biodiversity, especially as the biodiversity of forest-associated species tends to be highest in this stage.

Forest type generally did not have a major effect on biodiversity and there were few differences in overall species richness between ash and Sitka spruce. Ash sites > 50 yr old did have distinctive vegetation, spider and hoverfly assemblages, but did not tend to have higher species richness (even of forest-associated species) compared to the mature Sitka spruce sites.

Comparison of the assemblages in the ash and Sitka spruce components of mixed sites does indicate that adding ash to a Sitka spruce plantation increases biodiversity at the plantation scale.

BIODIVERSITY INDICATORS

The best indicator of changes in biodiversity over the forest cycle is stand structural stage, although there are differences in resolution among different species groups in how they "perceive" forest structure. A fundamental distinction in forest structure is between the pre-thicket stage and structural stages post-canopy closure.

Within structural stages, we have identified a number of structural, functional and compositional biodiversity indicators for individual taxonomic groups. These should be considered as potential indicators only, until they are verified using independent data.

Comparisons of variation in species richness between the different taxonomic groups produced few significant correlations. These results suggest that use of relatively easily surveyed groups (such as vascular plants and birds) as surrogates of biodiversity for other taxonomic groups is not justified.

MANAGEMENT RECOMMENDATIONS

We have made fifteen recommendations for forest planning and management practices that will maintain and/or enhance biodiversity in plantation forests. Twelve of these recommendations will require modifications to the Forest Service's *Forest Biodiversity Guidelines*. Most of these management recommendations will benefit more than one taxonomic group. Other management recommendations are specific to particular taxonomic groups, but in no cases do we believe that the management recommendations for one group conflict with those for another group.

1 INTRODUCTION

1.1 CONTEXT

1.1.1 The concept of biodiversity

1.1.1.1 Definition and scale of biodiversity

The Convention on Biological Diversity (CBD) was originally adopted by 154 countries following the United Nations Conference on Environment and Development (UNCED) in 1992. The four main themes of this convention were:

- Conservation of biodiversity
- Sustainable development
- Education and research
- Mutual sharing of the benefits of genetic resources

In the CBD, biodiversity is defined as: "The variability among living organisms from all sources…and the ecological complexes of which they are a part, this includes diversity within species, between species and of ecosystems" (UNEP, 1992). According to this definition, biodiversity may be considered at three different levels of biological organisation: genetic diversity, species diversity and ecosystem diversity. A holistic evaluation of biodiversity over a landscape or region would ideally focus on all of these levels, but because of resource constraints, biodiversity assessments typically focus on only one level. In this report, we focus on biodiversity at the species level.

Biodiversity can be considered at several spatial scales, including local (populations or communities), landscape, national and international. In the context of forestry, the fundamental management unit at the local scale is the stand. A stand is "a contiguous group of trees sufficiently uniform in age class distribution, composition, and structure, and growing on a site of sufficiently uniform quality, to be a distinguishable unit" (Helms, 1998). As such, the analysis, discussion and recommendations on biodiversity in plantation forests in this report are largely focused on the stand scale. Plantations are often comprised of more than one stand, however, and plantations themselves are located in a landscape matrix composed of forested and unforested ecosystems. Because changes in biodiversity at the stand scale frequently affect biodiversity at larger scales, we will also consider the implications of our findings at the plantation and landscape scales where appropriate.

1.1.1.2 Measurement of biodiversity

No single standardised protocol for the assessment of biodiversity in afforestation sites or forested ecosystems exists. Assessment of species biodiversity typically includes traditional ecological inventory and census techniques (Noss, 1990; Burley & Gauld, 1994) Data obtained from inventories of biota are important in the estimation of species and habitat diversity, population densities and geographical distribution, and to provide baselines as an aid in the prediction of changes in biodiversity as an integral part of monitoring programmes. Inventories help to develop strategies for the management and conservation of species and habitats (Stork & Samways, 1995). Methods of inventory and biodiversity analysis vary widely, and there is no single protocol for the standardisation of assessment techniques. However, each assessment should use the minimum amount of proven collecting methods for each taxon and allow variation to be estimated and analysed (Coddington *et al.*, 1991). Ideally, surveys of biodiversity should be carried out on different occasions and at different times of the year (Harris & Harris, 1997) in order to obtain representative data.

Measurement of species diversity usually distinguishes two components: species richness, the number of species present in a given area, and evenness, the relative abundances of each species (Begon *et al.*, 1990; Gaston, 1996b). Diversity indices, such as the Shannon index or Simpson's index, attempt to combine richness and evenness in one statistic and have been used widely to estimate species diversity. Such indices, however, do not distinguish among species and therefore cannot identify sites with species that are considered rare at regional or national scales. Such sites may have low species richness but high biodiversity value compared to a site with higher richness of common species. Therefore, caution must be exercised in using mathematical indices, or indeed species richness or any single statistic, to assess biodiversity value. The methods we have employed to measure biodiversity are discussed in more detail in Section 2.4.

1.1.1.3 Indicators of biodiversity

Resources for biodiversity assessment are usually limited to the evaluation of only a small proportion of existing biota and landscape or structural data which may then be used as indicators of overall biodiversity. According to Hansson (2000a), "an indicator may be a species, a structure, a process or some other feature of a biological system, the occurrence of which insures the maintenance or restoration of the most important aspects of biodiversity for that system". Also, "indicators of biodiversity provide quantitative values which aid in the prediction of the impacts of changing management practices and ecological trends in the future" (Ferris & Humphrey, 1999). There have been many studies on the use of indicators in forests in recent years to aid in assessing biodiversity and to help formulate policy, management and monitoring plans (Rose, 1976; Williams & Marcot, 1991; Ferris & Humphrey, 1999; Noss, 1999; Gustafsson, 2000; Larsson *et al.*, 2000; Lindenmayer *et al.*, 2000). In order for indicators to be integrated into a management plan for sustainable forestry, it is important that they are easy to assess, repeatable, cost-effective and ecologically meaningful (Ferris & Humphrey, 1999).

Indicators of biodiversity may be divided into three hierarchical categories (Noss, 1990; Schulze, 1994):
- compositional,
- structural, and
- functional.

These categories may be used at different levels of scale (including regional, community, population and genetic scales) to ensure that Sustainable Forest Management (SFM) criteria, are met.

Compositional indicators can include types of habitats present at the regional level, particular species and their abundances at community and population levels or allelic diversity at a genetic level. Differences in indicator species abundance, for example, should be indicative of biodiversity differences in the ecosystem as a whole. Structural indicators are related to the spatial distribution of compositional elements at different hierarchical levels. Lindenmayer (2000) made a comprehensive review of structural indicators such as stand complexity, connectivity and heterogeneity (size and spatial arrangement of habitat patches) in relation to SFM. The quantity and quality of deadwood has been found to be a good structural indicator of forest ecosystem health and biodiversity, as it adds a distinct habitat to the forest ecosystem and is strongly influenced by management (Hodge & Peterken, 1998). Functional indicators can include processes such as productivity, nutrient cycling rates, disturbance regime and management practices (Noss, 1990; Hansson, 2000a).

Noss (1990) compiled a list of terrestrial biodiversity indicators at different hierarchical levels which could be used as a framework for selecting indicators for monitoring biodiversity. In doing so he warns of the importance of a holistic approach to biodiversity assessment at these different levels of scale. This point is echoed by Hansson (2000a) and Ferris and Humphrey (1999) who recommend the use of more than one type of indicator of biodiversity due to the complexities of habitat use and requirements of different species in an ecosystem. After identification of potential indicators for biodiversity, they must be rigorously validated before adoption for formal use (Noss, 1990; Lindenmayer, 1999; Noss, 1999).

In this report, we develop potential indicators for biodiversity in plantation forests. These indicators can be used as tools to assess the effectiveness of current management practices in maintaining forest biodiversity and/or to identify stands or forests of potentially high biodiversity value. In sites where the indicators suggest that current management is inadequate for biodiversity, practices can be reviewed and improved. Forest units identified as being of potentially high biodiversity can be surveyed and assessed more thoroughly and managed in such a way that biodiversity conservation and enhancement is a priority.

1.1.2 Forest biodiversity and policy development in Ireland

Following UNCED in 1992 and the adoption of the Forest Principles, the concept of SFM was developed as part of the Helsinki Pan-European Process in 1993 for the protection of Europe's forests. The principles developed during the Helsinki Process were formally adopted at the Third Ministerial Conference of Forests in Lisbon in 1998 with the aid of the Intergovernmental Panel on Forests, which was set up in 1995 to ensure that the goal of SFM was implemented successfully on a global basis. The aim of SFM is to ensure that forests are managed in accordance with best forest practices under relevant legislation and regulations. SFM addresses the full range of economic, ecological and social forest functions. It may be defined as:

> "The stewardship and use of forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfil, now and in the future, relevant ecological, economic and social functions, at local, national and global levels, and that does not cause damage to other ecosystems." (Anon., 1995)

There are currently thirty-nine countries, including the EU member states, who have signed up to the principles of SFM and have adopted the various criteria and indicators of SFM into their own strategic forestry development goals and policies (Forest Service, 2000e). In Ireland, the SFM principles are being adopted through the development of various guidelines and regulations from the Forest Service of the Department of Communications, Marine and Natural Resources, including the Irish National Forest Standard (Forest Service, 2000e), Code of Best Forest Practice (Forest Service, 2000a) and the series of Forestry Guidelines (e.g. Forest Service, 2000b).

One of the driving forces for SFM is environmental certification of forestry practices, a marketing tool which demonstrates that timber production is sustainable and not damaging to the environment. The Forest Stewardship Council (FSC) is one of the approved authorities responsible for the certification of forestry to ensure that SFM is implemented successfully, and Coillte Teoranta, the semi-state body responsible for managing over 60% of Irish forests, was awarded FSC Certification in September 2001.

Coillte are addressing SFM and biodiversity issues through forest management planning. Since 2000, Coillte has begun to use five-year management plans for each of their 36 Forest Management Units (FMU). These management units were determined using the following criteria: geographical area, similar soil type, location along major river catchments areas and administrative regions (Coillte, 2000).

The forest management unit plans address economic, social and environmental objectives (Coillte, 2000). They are to be used in the future to promote ecologically sound timber production and to aid in the diversification of tree species in Irish forests in accordance with

FSC requirements. The long-term biodiversity objectives in the plans are generally similar throughout the country, with 15% of the forest estate in each FMU managed with conservation as a priority. Ecological surveys of the estate contained within each management unit are being carried out to identify features of biodiversity importance such as habitats or species of conservation value, old woodland sites, deadwood and open space and to determine management strategies to enhance and conserve these sites.

1.1.3 Existing information on forest plantation biodiversity in Ireland

In Ireland, there are virtually no data available for evaluation of biodiversity importance outside of sites designated for conservation importance. The National Parks and Wildlife Service of the Department of the Environment, Heritage and Local Government (formerly Dúchas), is the body responsible for the gathering and dissemination of information on biodiversity in designated sites throughout the country. There is no effective national biological recording system, although proposals have been made for the establishment of a new Biological Records Centre (McGowan *et al.*, 2002). Much of the information on Ireland's biodiversity is contained in inaccessible form as unpublished manuscripts and theses, published papers in obscure journals, reports by small non-governmental organisations and poorly circulated reports by larger state or semi-state bodies. Some published papers address the avian biodiversity of plantation forests, but to date these have been restricted describing particular sites (e.g. Duffy *et al.*, 1997) or single species (e.g. Walsh *et al.*, 1999), or afforded an overview based on preliminary results (Walsh *et al.*, 2000). A recent study comparing plant and carabid beetle communities in Irish forests by Fahy and Gormally (1998) found that there is very little information available in relation to the impact of conifer plantations on terrestrial plant and invertebrate communities.

1.1.4 Need for the present study

The strategic plan for the forestry sector (Anon., 1996) calls for 20,000 ha to be planted every year until 2030. With the current trend in forest ownership, the bulk of this will be privately-owned agricultural land, which is potentially of biodiversity value. To date, very little research has been carried out on the biodiversity of forest plantations and how it changes through different stages of the forest cycle. Investigation into the ecological impacts of Sitka spruce (*Picea sitchensis*) plantations, which will account for at least 60% of the forest cover in Ireland up to 2030 (Anon., 1996), is necessary. With greater encouragement for the planting of broadleaves, research on the biodiversity of broadleaf plantations is also necessary. Given the proposed scale of planting throughout the country over the next thirty years, it is imperative that current guidelines and methods of best forest practice be assessed to ensure that SFM is being implemented successfully and that the natural heritage contained within Irish forests is conserved and enhanced.

1.2 OBJECTIVES

This project addresses the current lack of information on biodiversity in Irish plantation forestry. The overall aim is to obtain a comprehensive picture of the biodiversity of conifer and broadleaf forest plantations at different stages of development. Indicators of biodiversity will be developed as tools for monitoring and management. The research results will also be used to evaluate current forest practices affecting biodiversity and, where appropriate, to recommend changes to these practices.

Specifically, the main objectives of this project are to:

1. Assess the range of biodiversity in representative forests at key stages the forest cycle;
2. Review possibilities for enhancement of biodiversity in plantation forests and make recommendations;

3. Assess the effectiveness of the *Forest Biodiversity Guidelines* (Forest Service, 2000b) in light of the results of this study.

2 SURVEY DESIGN AND DATA ANALYSIS

2.1 SELECTION OF FOREST TYPES AND AGE CLASSES

2.1.1 Forest type

Our objective was to select forest types that would be most representative of the likely future trends in afforestation, and the range of variation that will result from these trends.

- Recent planting trends (see Figure 1) show that Sitka spruce (*Picea sitchensis*) is the dominant species being planted, and that ash (*Fraxinus excelsior*) is both the dominant broadleaved species, and possibly also the second most frequently planted species overall.
- Applications for afforestation grants on improved/enclosed land must contain a minimum of 10% broadleaves, site permitting (Forest Service, 2000d). The *Forest Biodiversity Guidelines* recommend that these broadleaves should be planted "in swathes and not as single stems within the canopy". As the majority of current afforestation involves conifers on improved/enclosed land, non-intimate mixes of conifers and broadleaves are, therefore, likely to become the dominant configuration in future afforestation.

Based upon these considerations, we selected Sitka spruce and ash as the two forest types that we would study and we decided to include non-intimate mixes of these species in the survey design.

2.1.2 Age classes

Given the time involved in studying changes in one site over the forest cycle from planting to commercial maturity, we employed a chronosequence approach where we sampled different sites at different stages of maturity. Our objective was to select age classes that would represent the major structural changes that take place in forest development over the course of a commercial rotation. Therefore, based on advice from forestry practitioners, we selected the following age classes:

- 5 years - the stage before closure of the forest canopy (Age class 1).
- 8-15 years - the stage immediately after closure of the forest canopy (Age class 2).
- 20-30 years - the middle stage of the forest rotation, when the first thinning has occurred (Age class 3).
- 35-50 years - approaching commercial maturity of Sitka spruce (Age class 4).
- > 50 years - approaching commercial maturity of ash (Age class 5).

2.1.3 Survey objectives

Following the selection of the forest types and age classes we focused the objectives of this survey on three questions:

- How does biodiversity change during the forest cycle?
- Are there differences in the biodiversity of ash and Sitka spruce plantations?
- Does the inclusion of a small area of ash influence the biodiversity of a predominantly Sitka spruce plantation?

2.2 SURVEY STRATEGY

2.2.1 Age classes

Our survey design includes three forest types (pure Sitka spruce, pure ash and Sitka spruce-ash mixes) and five age classes. Thus, there are 15 potential combinations of forest type and age class that at four sites per combination as the degree of replication would yield a total of 60 sites. Taking into account the fact that the mixed sites require double the sampling effort of pure sites (both the ash and Sitka spruce component need to be surveyed separately), the effective number of sites would be 75. As we did not have the resources for this level of sampling effort, we had to select a limited number of combinations of tree species and age class (Table 1).

For pure Sitka spruce, we included age classes 1-4, but excluded age class 5 due to the very limited availability of overmature Sitka spruce.

For pure ash, we included age classes 1, 2 and 5. There is a relatively good availability of pure ash in age classes 1 and 2, due to the recent trends of increased broadleaved planting. We included age class 5 because this represents the endpoint of the ash forest cycle when the forest will have had the maximum length of time to develop its biodiversity.

For the Sitka spruce-ash mixes, we included age classes 1, 2 and 4. There is a relatively good availability of Sitka spruce-ash mixes in age classes 1 and 2, due to the recent trends of increased broadleaf planting. We included age class 4, because this represents the endpoint of the Sitka spruce forest cycle when the forest will have had the maximum length of time to develop its biodiversity.

Table 1. Number of sites surveyed in each forest type-age class combination.

	Pure ash	Pure Sitka spruce	Sitka spruce-ash mix
Age class 1 [1]	4	4	4
Age class 2	4	4	4
Age class 3	0	4	0
Age class 4	0	8	4
Age class 5	4	0	0

[1] See Section 2.1.2 for age class definitions.

2.2.2 Geography and environment

In order to address the objectives of this survey (see Section 2.1.3), we needed to compare sites that differed in the relevant features (e.g. age), but that were otherwise similar (e.g. soil type). We were not able to find groups of matching sites that displayed the entire range of forest type-age class combinations that we wished to sample. Instead, we divided our sampling strategy into subsets that addressed components of the above objectives. Each of these subsets involves pairs or clusters of sites that were matched for geographical location, soil type, drainage and altitude. These subsets are described below, and the locations, crop species and age classes of sites are shown in Figure 2.

2.2.2.1 Geographic clusters

We selected four clusters of matching sites, each containing pure Sitka spruce sites of age classes 2-4 and a Sitka spruce-ash mix site of age class 2. These clusters allow us to compare the biodiversity of three age classes of Sitka spruce, and to investigate whether the addition of ash affects the biodiversity of Sitka spruce of age class 2.

2.2.2.2 Age class 1 pure and mixed Sitka spruce pairs

We selected four pairs of matching sites, each containing a pure Sitka spruce site and a Sitka spruce-ash mix site of age class 1. These pairs allow us to investigate whether the addition of ash affects the biodiversity of age class 1 Sitka spruce.

2.2.2.3 Age class 4 pure and mixed Sitka spruce pairs

We selected four pairs of matching sites, each containing a pure Sitka spruce site and a Sitka spruce-ash mix site of age class 4. These pairs allow us to investigate whether the addition of ash affects the biodiversity of Sitka spruce of age class 4. After field work had commenced, however, one pure Sitka spruce site (Conavalla) was found not to be a suitable match for its matching mixed site (Sunderlands) for plants or invertebrates. Thus, the pure spruce site was not surveyed for plants or invertebrates. For birds, Conavalla was a suitable match for Sunderlands and was therefore surveyed for this taxonomic group.

2.2.2.4 *Pure ash sites*

Because we found very few pure ash sites of suitable size and configuration for the purposes of our survey, controlling for variation in site conditions was frequently not possible. This means that the pure ash sites were not selected on criteria of matching geographically or environmentally any of the other sites in our survey, although, in some cases they may do so fortuitously.

2.3 SITE SELECTION

2.3.1 Desktop

We initially identified potential sites from the Coillte inventory database, using the criteria in Table 2. The main factors dictating our selection of sites were the availability of Sitka spruce-ash mixes and of pure ash sites. For example, potential *Geographic clusters* were selected by locating Sitka spruce-ash mixes of age class 2 and searching for matching pure Sitka spruce of the relevant age classes nearby. We then sent lists of potential sites to Coillte forest managers to check whether any forestry operations were planned for the sites that might interfere with our surveys. We excluded any such sites from further consideration.

Table 2. Criteria used for desktop selection of potential sites.

Feature	Criterion
Size	Minimum of 4 ha in size to allow sufficient space for the bird survey
Configuration	Minimum of 100 m width to allow sufficient space for the bird survey
History	First rotation and not planted on sites coded as old woodland in the site fertility classification of the Coillte database
Geography/ Environment	For the clustered and paired sites subsets: sites within each cluster/pair to have similar soil type, drainage and altitude, and to be geographically close to each other
Landscape position	For the pure ash and Sitka spruce sites: not adjacent to a large block of conifers (pure ash) or broadleaves (pure Sitka spruce)

2.3.2 Field

We ranked the sites in order of preference on the basis of the available information and made field visits to confirm site suitability. For example, the *Geographic clusters* were ranked according to the availability of duplicate pure Sitka spruce sites within the cluster, to allow for the possibility that any particular pure Sitka spruce site might not prove to be a good match to the Sitka spruce-ash mix. On these field visits, we checked:

- The structural development of the forest. Sites with Sitka spruce of age class 1 with a closed canopy, Sitka spruce of age class 2 with an open canopy, and poorly developed Sitka spruce of age classes 3 and 4 were excluded.
- The soil type and drainage, to determine whether they corresponded to the classification in the Coillte database.
- The adjacent land use.
- Any special features that might have affected our survey.

2.4 CHARACTERISATION OF BIODIVERSITY

2.4.1 Taxonomic groups

As with virtually all biodiversity studies, we were not able to survey all taxonomic groups that may be present in plantation forests. We therefore focused our efforts on four groups of species: plants, spiders, hoverflies and birds. These groups vary in mobility and the scales at which forest environment and management are likely to affect the number of species present and their abundances. In addition, the ecology and taxonomy of these groups is relatively well-known. Forest understorey vegetation is relatively easy to sample and provides food and structural diversity that can be exploited by dependent fauna. Vascular plants in particular are a well-known group in Ireland and have frequently been used as surrogates for total biodiversity in other countries (Ferris & Humphrey, 1999). We also surveyed bryophytes (i.e. mosses and liverworts), which are an important component of the semi-natural forest flora. Spiders represent an intermediate trophic level and therefore may have value as indicators for their invertebrate prey and their predators. Because of their small ranges, they are more responsive to changes at the stand scale than many other invertebrate groups. Spiders are found in all vertical layers of a plantation, unlike other groups of invertebrates, such as carabids, which are mostly ground dwelling. Although sampling in this study has focused on ground-dwelling spiders, our data may provide a useful comparison for other studies of plantation forests, for example an examination of forest canopies. Unlike spiders, hoverflies are quite mobile and are therefore more sensitive to conditions at the plantation and landscape scales. They are a diverse group in terms of trophic and habitat requirements, and have been used as indicators of disturbance or habitat quality (Sommagio, 1999). Individual birds range over wider areas than members of any of the other three taxa, and are therefore affected by environmental variation at the plantation and landscape scales. As with plants, birds are relatively easy to survey and include several species of conservation value. Plantation forests may be of benefit to some of these (Newton *et al.*, 1999; Walsh *et al.*, 2000), including some forest specialist species.

2.4.2 Species richness

The most basic method of measuring biodiversity is to report the total species richness of the taxonomic group being considered (Magurran, 1988; Gaston, 1996a). However, total species richness does not indicate anything about the identity of the species involved. Biodiversity conservation is concerned with maximising the biodiversity of a particular area (e.g., the European Union, the Irish state, Co. Cork). Ubiquitous and widespread species generally require little effort to ensure their conservation. However, rare, threatened and specialised species will probably require conservation of particular sites or adoption of specific conservation measures. Therefore, the focus of biodiversity conservation is on this latter group of species. In this context, simply reporting total species richness is of little interest as this does not distinguish between a site that supports rare, threatened and specialised species and a site that does not. In fact, total species richness can be misleading, as in some habitats of biodiversity conservation value (e.g., blanket bog) total species richness can increase following anthropogenic disturbance due to the invasion of widespread generalist species, masking the effect of the loss of rare, threatened and specialised species.

To address this issue, we have analysed species richness of various species groupings that are subsets of the total biota in each of the taxonomic groups. The groupings considered depend upon the properties of the particular taxonomic groups, and the availability of data, but can be classified under the following general headings: rarity/conservation status, forest use, and functional or behavioural groups. Details on the assignment of species to particular categories in these groups are provided in the methods sections of the relevant taxonomic group chapters.

Species groups reflecting rarity/conservation status included formal conservation designations (e.g. bird species defined as red and amber listed by Newton et al. (1999)), and ecological classifications that reflect conservation status (e.g. native and introduced plant species, anthropophobic hoverfly species). This is the most direct measure of importance for biodiversity conservation, as it reflects the occurrence of species that require specialised habitats or conservation measures. However, there are limitations to the use of this measure.

The availability of information on conservation status is limited and there was none available for spiders. The information that is available is almost exclusively focused on species that are rare or threatened at a national scale. Apart from birds (where widespread but declining species have been given formal conservation status), it is unlikely that a survey of the type that we carried out (focusing on sampling typical habitats) would encounter many species listed as rare or threatened at a national scale. Also, plantation forestry is unlikely to be important in the conservation of these species, as their rarity often reflects their association with specialised semi-natural habitats. Where plantation forestry may contribute is towards the conservation of species that are rare or threatened at a local or regional scale because they cannot persist in intensively farmed landscapes. These are the species that are included in our anthropophobic classification (see Speight and Castella (2001) for more details about this concept).

Forest-use species groups reflect the degree of association with, and restriction to, forest habitats. The occurrence of species that are associated with forest habitats helps to develop a characteristic forest biota and to increase the biodiversity value of a forest site in terms of its representativity (Ratcliffe, 1977). Species that show strong preferences for, or are restricted to, forest habitats are dependent upon forests for their conservation. Therefore, forests that support greater numbers of forest specialists will make a greater contribution to the conservation of the forest biota. Such forests may be particularly valuable if they are located in areas with low semi-natural forest cover, such as in many upland areas.

Functional groups are classifications of species that reflect the habitat components that they utilise (moisture and pH classifications of plants, vegetation layer classification of spiders, larval microhabitats of hoverflies, and food and nest site classifications of birds), or the ecological strategies that they use (classification of plants as competitors, ruderals and stress-tolerators, and hunting strategies of spiders). This provides information on how species are using the forest habitat, and indicates which components of the forest habitat are most important for biodiversity conservation.

2.4.3 Species diversity

A species diversity index is a combined measure of species richness and the dominance or evenness of species abundance. While species diversity has been criticised as a "non-concept" (Hurlbert, 1971), it is very widely used in studies of species assemblages, and has often been used as a measure of biodiversity (Magurran, 1988). Species evenness is a potentially useful concept when we are considering groups of potentially interacting species. In this situation, an increase in abundance in one species is likely to cause a decrease in abundance in other species. For example, in plant communities competition for light, water and/or nutrients is common. Evenness as a component of biodiversity makes intuitive sense when two hypothetical sites are considered, one of which has 99 individuals of species A and 1 individual of species B, while the other has 50 individuals of each species. The distribution of species in the latter site is more even, and therefore more diverse. The contrast between assemblages dominated by a few species and those with a greater number of more evenly distributed species is of ecological interest and is relevant to both studying the ecological processes that structure the assemblage, and assessing the biodiversity value of the assemblage.

In situations where the species assemblage is comprised of a disparate group of mainly non-interacting species, however, the ecological meaning of species diversity, or indeed of any measure of species evenness, is dubious. In such situations, the abundance of a particular species can yield information on the ecological response of this species. However, because other members of the species assemblage are not affected by the abundance of this species, the effect on overall species evenness does not tell us anything about the ecological response of the species assemblage. As an example, consider two hypothetical forest bird communities. One has 2 Nightjars and 2 Woodpigeons, the other has 20 Nightjars and 100 Woodpigeons. Because Woodpigeons and Nightjars do not interact, a measure that uses their relative abundances to produce a single index tells us nothing of interest about the ecology of the assemblages.

An additional difficulty with diversity indices is their failure to account for species identity. In some cases, higher species diversity can actually reflect lower biodiversity value. Considering the Nightjar-Woodpigeon example above, the second community is clearly of greater biodiversity conservation value due to its larger population of a threatened bird species, but it has lower evenness than the first community. This shortcoming also applies to species richness: listing the number of species present in a forest does not tell us anything about their conservation value. Analysis of the species richness of groups of conservation value, as described above, will counter this deficiency; however, the application of a similar categorisation when using species diversity indices is less straightforward.

Given the above considerations, we have focused on species richness rather than species diversity as our main measure of biodiversity. We have used species diversity as well for analysis of the vegetation assemblages. The hoverfly and bird groups contain ecologically heterogeneous groups of species that, in the main, are unlikely to interact with each other, and we have not used species diversity in these groups. The situation is less clear with spiders, but given the problems involved in interpreting abundance data from pitfall traps (see Section 5.2) we have also not used species diversity for this group.

2.5 DATA ANALYSIS

We have, as far as possible, used a common approach to analyse results from the four taxonomic groups but, inevitably, the nature of the data has necessitated modifications to this approach for particular groups. This section outlines our general approach to the data analysis. Full details of the data analyses carried out for each taxonomic group are included in the relevant sections.

2.5.1 Data organisation

We have used four main classifications for sub-dividing our samples. We have classified samples by: forest type based upon the dominant tree crop species (ash or Sitka spruce); by age class based upon the planting year (using the definitions in Section 2.1.2); by structural class based upon the structural development of the plantation (using the definitions in Section 3.3.4); and by assemblage type based upon our analyses of assemblage structure within different taxonomic groups.

2.5.2 Statistical tests

We have used standard statistical tests (t-tests, ANOVA, correlation, and their non-parametric equivalents) to analyse differences in variables between sample groups and associations between variables across samples. We have often carried out a large number of analyses on the same dataset and, therefore, have increased the risk of Type I errors (i.e., of significant results occurring by chance). However, we have generally used these analyses in an exploratory manner, and when we have obtained significant results we have investigated the form of the relationship further. Therefore, because we have not relied upon significance levels to generate the conclusions that we report, we do not consider that these conclusions have been biased by the increased risk of Type I errors.

2.5.3 Analysis of assemblage structure

We have analysed assemblage structure in each taxonomic group to investigate whether the species assemblages respond to changes in forest type, structural group, or age class, and to identify appropriate groups for further analyses.

We used global non-metric multidimensional scaling analysis (NMS) to carry out ordination analyses. We used this method rather than more conventional eigenanalysis techniques (e.g. PCA and DCA) because it has been found to be better at recovering complex gradients (Legendre & Legendre, 1998).

We used flexible-beta cluster analysis to identify clusters of samples with similar assemblages. Flexible-beta clustering is a hierarchical agglomerative clustering technique, which provides a series of solutions intermediate to nearest neighbour and farthest neighbour clustering, depending on the value assigned to the β parameter. According to Legendre and Legendre (1998), chaining is limited and space properties are conserved when using this method with $\beta = -0.25$, which was the value we employed.

We used indicator species analysis to identify species characteristic of the sample clusters. Good indicator species should be found mostly in a single cluster and should be present at most of the sites belonging to that cluster. The indicator value is 100% when a species is observed at all sites belonging to a single cluster (Legendre & Legendre, 1998). A random reallocation procedure of sites among the site groups is used to test the significance of the indicator values (Monte Carlo test).

These three methods are complementary. The ordination analysis indicates the relative similarity between samples and highlights the more important gradients operating within the data. The cluster analysis can then be used to identify the discontinuities in the assemblage structure revealed by the ordination. The indicator species analysis identifies the species that have high fidelity and constancy in the cluster groups, and helps in the interpretation of the ecological meaning of the assemblage structure.

2.5.4 Identification of indicators

2.5.4.1 Structural and functional indicators

We have attempted to identify structural and functional indicators of biodiversity by examining the relationships of biodiversity measures (Section 2.4) with habitat variables and management information. Our objective in doing this is to produce indicators that could be used by forest managers to identify sites with high biodiversity potential. Identifying such indicators will also help in determining the ecological processes that cause variation in biodiversity between sites and, therefore, suggest management practices that might enhance biodiversity.

Over the entire forest cycle, changes in biodiversity are largely driven by the major changes that occur in forest structure. At this scale, potential indicators will tend to reflect different stages in stand structure. Therefore, the stand structural types developed in Section 3.3.4, which are readily distinguished on the basis of tree species, size, canopy cover and density, will serve as biodiversity indicators over the forest cycle. We have accordingly focused on identifying indicators that are correlated with biodiversity *within* groups based on the structural types. For each of the taxonomic groups we have defined appropriate groups for these analyses based upon the number of samples available and species assemblage structure. Therefore, in some cases we have amalgamated structural types to obtain a sufficient sample size, providing there are not major differences in species assemblages. In other cases, we have sub-divided structural types where there are major differences in assemblage structure. Major differences in assemblage structure are likely to reflect variation in environmental conditions (e.g., soil type, geology, altitude, etc.) between sites, and could obscure relationships between biodiversity and forest habitat characteristics. We have examined relationships between biodiversity and habitat variables both within and between groups defined on the basis of forest structure and species assemblage.

Vegetation structure below forest canopy level is likely to be an important factor for biodiversity of some or all of the taxonomic groups. However, different taxonomic groups will perceive and interact with vegetation structure in different ways. For this reason, separate classifications of understorey vegetation structure are developed in each of the taxonomic group chapters. No vegetation layer or type will have the same name, although they may be similar, to prevent ambiguity.

2.5.4.2 Compositional indicators

Within the taxonomic groups, the measures of species richness that we report are compositional indicators of the biodiversity of that taxonomic group. A second approach to identifying compositional indicators within taxonomic groups is to identify species that tend to be associated with high biodiversity sites. In practical terms, this approach is only worthwhile if the effort involved in sampling and identifying the species indicator is significantly less than the effort required to sample and identify the entire taxonomic group. For spider and hoverflies this is not the case, therefore we have only attempted to identify species indicators for vegetation and birds. The methods used to do this are described in the relevant sections (see Sections 4.2.4.2 and 7.2.5.4). We have also highlighted the occurrence of rare species, as they and the sites in which they occur are of high biodiversity value. Note that the species identified by indicator species analyses are indicators of compositional differences in species assemblages identified by cluster analyses. They are only indicators of biodiversity if there are differences in biodiversity between the species assemblages.

Another approach is to examine whether the biodiversity of one taxonomic group provides an effective indication of the biodiversity of other taxonomic groups. In terms of sampling logistics and the availability of taxonomic expertise, vegetation and birds are easier to sample than spiders or hoverflies. Therefore, it would be useful to know whether vegetation or birds are good indicators of spider or hoverfly biodiversity. To address this, we have carried out two sets of analyses. We have examined whether patterns of assemblage structure are similar among the taxonomic groups using Mantel tests (Legendre & Legendre, 1998). This indicates whether selecting complementary sets of sites for conservation measures on the basis of their vegetation or bird assemblages will tend to capture the range of assemblage variation in spiders and hoverflies. We have also examined whether the variation between sites in species richness is similar between the taxonomic groups using correlation analyses. This indicates whether identifying sites with high vegetation or bird biodiversity will also identify sites with high spider and hoverfly biodiversity. The methodology of these analyses is described in Section 8.3.1.

3 GIS DATABASE AND DESCRIPTION OF STUDY SITES

3.1 INTRODUCTION

A Geographical Information System (GIS) is a computer system capable of capturing, storing, analysing, and displaying geographically referenced information; that is, data identified according to location. A GIS is also defined as including the procedures and spatial data that go into the system.

GIS technology can be used for scientific investigations, resource management, and development planning. For example, a GIS might allow emergency planners to calculate emergency response times in the event of a natural disaster, or a GIS might be used to find wetlands that need protection from pollution.

The strength of a GIS comes from its ability to spatially relate different information and to query this information in relation to other unrelated spatial data. Many data contain a spatial reference, placing that information at some point on the globe. A GIS can also convert existing digital information, which may not yet be in map form, into forms it can recognise and use. For example, digital satellite images or aerial photographs can be analysed to produce a map of digital information about land use and land cover. Likewise, census or hydrologic tabular data can be converted to a map-like form and serve as layers of thematic information in a GIS.

The BIOFOREST GIS was developed and managed by the Coastal and Marine Resources Centre (CMRC) according to the requirements of the researchers in the BIOFOREST project. GIS was used by researchers throughout the project for site selection in relation to their survey work. GIS facilitated the visualisation of sites by providing access to overlays of aerial photos, base maps and Ordnance Survey base data. While GIS was employed by individual researchers to aid their survey work in this fashion, a GIS database was also used, in tandem, to house and display the data generated by primary field studies, along with integrating existing base mapping, sundry data and aerial photography.

This chapter also describes the location, environment, forest structure and management of the study sites. As forest structure varied significantly within age classes, we developed a small number of stand structural types to summarise the major phases of stand development.

3.2 METHODS

3.2.1 Data acquisition

3.2.1.1 GIS datasets

CMRC provided BIOFOREST researchers with a protocol (Table 3) for the collection of data so that it could easily be incorporated into the GIS database. The protocol outlined how the data should be collected by field researchers, especially in relation to GIS compatible programs and appropriate coordinate systems.

Project specific primary data were supplied to CMRC as they become available throughout the project period (Table 4). Additional data, such as site photographs or any other relevant field data, was also submitted to CMRC for incorporation into the GIS.

Along with BIOFOREST data, a breadth of ancillary data was also collected by the CMRC, processed and made available to researchers during the project and incorporated into the GIS. Data collection involved site visits to agencies such as Coillte. Issues with data formats and the sharing of large data files had to be overcome to ensure that the relevant data could be extracted and incorporated into the BIOFOREST GIS. Table 5 outlines some of the layers that were used in the GIS database, along with the relevant data providers.

Table 3. GIS data collection protocol delivered by the CMRC to BIOFOREST researchers.

Protocol for GIS Development for the BIOFOREST Project
Steps involved: 1. Once fieldwork has commenced, the BIOFOREST team should provide CMRC with a list of proposed study sites. Once confirmed, the site boundaries should be clearly marked (e.g. on 1:50,000 Discovery Series OS paper maps), and submitted to CMRC for digitising. 2. Detailed data sets will be obtained for each of the study sites. The following types of data are to be included in the GIS: • OS vector data, including topography (roads, urban areas, rivers and lakes etc); Digital Terrain Models (DTMs), slope & aspect will be derived from contour data • Geological Survey of Ireland (GSI) terrestrial geology mapping • Teagasc soil survey data • EPA critical load mapping • Met Eireann national rainfall data • Coillte inventory data • Corine Landcover data • Countryside bird survey data • Aerial photos & satellite images where data is available • Designated areas 3. Project specific primary data are to be supplied to CMRC as and when they become available. The data should be sent to the CMRC in Microsoft Excel spreadsheet format. It will then be converted into .dbf format, which can easily be integrated into ArcView. 4. It is of utmost importance that these data are subject to QA procedures by the individuals responsible for creating the data sets. For example, check that each field is completed, and that all records are correct. Standard code names should be used for each site. 5. Additional data, such as site photographs or any other relevant field data, should also be submitted to CRC for incorporation into the GIS. Methodologies and final reports should be supplied so that text links can be made to these documents. 6. Spatial references should be provided in a standardised format. GPS should be used in the field whenever a good fix can be achieved to reduce potential errors in recording positions. All data will be displayed in Irish National Grid in the GIS. All data included in the GIS will be made available to each of the project partners through the CMRC server. Individual user accounts will be created for this purpose. The possibility of serving the data through the development of restricted ASPs (Active Server Pages) on the proposed web site will be investigated.

3.2.1.2 Environmental data

Stand structural data were recorded by the vegetation team from three 100 m^2 quadrats in each site (or site × species combination for mixed sites). Average top height of the upper planted tree canopy (which includes the young trees in age class 1 plantations) was measured using a clinometer or metre stick, as appropriate, or by eye. Percent cover of the upper tree canopy was estimated. Diameter at breast height (dbh, where height=1.3m) of a random sample of ten trees per quadrat was recorded. In some cases, there were less than ten trees in a quadrat and the mean was calculated from the trees present. The minimum distance between canopy trees in each quadrat was measured.

Aspect and slope were measured in degrees at each of the 100m^2 vegetation quadrats in the majority of sites. For some sites, aspect information was taken from Ordnance Survey (OS) maps and slope data were taken from the Coillte inventory database. In the latter, slopes greater than 18° were simply coded “18+”. Soil drainage was estimated at the vegetation quadrat and site levels according to a five-point scale, expressed as ranks in quantitative analyses: 1- poor, 2- poor to moderate, 3- moderate, 4-moderate to good, 5- good. Elevation data were taken from OS maps.

Table 4. BIOFOREST data layers, format in which they were supplied and data providers.

Data	Supply Format	Data Provider
Hoverfly trap locations	Shape	Tom Gittings
Hoverfly trapping data	Excel	Tom Gittings
Hoverfly species data	Excel	Tom Gittings
Hoverfly species richness	Excel	Tom Gittings
Hoverfly habitat data	Excel	Tom Gittings
Pitfall plot data	Shape	Anne Oxbrough
Spider species data	Excel	Anne Oxbrough
Spider species richness	Excel	Anne Oxbrough
Spider habitat data	Excel	Anne Oxbrough
Deadwood	Excel	George Smith
Vegetation plot environmental data	Excel	George Smith
Vegetation plot data	Excel	George Smith
Vegetation species codes	Excel	George Smith
Forest and vegetation structure data	Excel	George Smith
Vegetation plot locations	Excel	George Smith
Visit 1 data	Shape	Mark Wilson
Visit 2	Shape	Mark Wilson
Visit 3	Shape	Mark Wilson
Bird species	Excel	Mark Wilson
Codes (behaviour, detection % species)	Excel	Mark Wilson

Table 5. Base data layers, format in which they were supplied and data providers.

Data	Supply Format	Data Provider
Ireland	Shape	EPA
Discovery Series Mapping	Tiff	EPA
6 Inch Mapping	Tiff	Coillte
Digital Elevation Model	Grid	Landmap UK
Forestry Boundaries	Shape	Coillte
Forestry Inventory	Shape	EPA
Protected Areas	ArcInfo	Dúchas

For the majority of sites, soil type information was taken from the Coillte database. Where this information was in conflict with field notes, the latter information was used. In some age class 1 sites, a soil pit was dug to a depth of at least 50cm and soil type was identified according to the Irish Great Soil Groups (Gardiner & Radford, 1980). In all sites, a soil sample was collected for each 100m^2 quadrat; subsamples were taken from the four corners of the quadrat to a depth of 5cm, and then bulked to give one sample per plot. For age class 1 sites (inventoried by the vegetation team during 2002), bulk density was calculated from soil volume collected in the field (bulk density (g/cm^3) = dry soil weight (g)/total volume of soil (cm^3). For the remainder of sites, bulk density was calculated from loss-on-ignition data according to the method of Jeffrey (1970).

The pH of field moist soils was measured using a pH meter with a glass electrode on a soil:distilled water (1:2) suspension. The soils were then air-dried for further chemical and physical analyses. All samples were sieved through a 2mm mesh, and since less than 1g soil was required for nitrogen (N), organic carbon (C) and total phosphorus (P) analyses, sub-samples were sieved through a 0.125mm mesh. The following analyses were undertaken to characterise the chemical and physical status:

1. Total N and total organic C were analysed by elemental analysis (LECO) using flash combustion (Verardo *et al.*, 1990). The soil samples were pre-treated with sulphurous acid to remove any inorganic C.
2. Total P was extracted as orthophosphate ions into solution using microwave digestion with nitric acid. It was then quantified using a colorimetric method, with absorbance

being measured at 882nm on a spectrophotometer. Soils collected in 2002 (i.e. from the age class 1 sites) were not analysed for total P because of technical difficulties with the microwave digester.

3. Morgan's reagent was used as the extraction solution for available P and an orthophosphate determination procedure was employed as above.
4. Exchangeable calcium (Ca), magnesium (Mg) and potassium (K) were extracted using ammonium acetate at pH 7. An atomic absorption spectrophotometer was then used to determine the concentration of the metallic elements in solution (Allen, 1989).
5. Loss-on-ignition was determined.

Using soil bulk densities, soil chemical results are expressed as weight per unit of soil volume. This is appropriate in plant ecology research because roots interact with the soil matrix spatially, rather than with soil mass. In addition, results presented in terms of soil volume may readily be converted to an area basis to facilitate comparison with other studies (Boone *et al.*, 1999).

3.2.1.3 Management information

Information on the management history of the study sites was acquired from several sources, including the Coillte database, field notes and correspondence with forest managers and landowners. The quality of information available varied considerably among sites. Generally, there was less information available for older sites than for younger ones as a result of gaps in record-keeping and the attrition of personnel with first-hand knowledge of management of the sites. Information was sought on former land-use and management, including livestock densities, past fertilisation, past herbicide use, burning and turf cutting. We also requested information on ground preparation techniques prior to afforestation, fertilisation, pesticide use, manual vegetation control methods and thinning.

Ground preparation reported included ploughing, mounding, ripping and no cultivation. In some cases, the type of plough used was specified: single mouldboard, which produces one ridge of soil from the furrow, or double mouldboard, which produces a ridge of soil on both sides of the furrow. Trees are then planted on the soil ridges. Because the type of plough was not always specified, no distinction was made and the ground preparation method was simply identified as "ploughed". In mounding, drains are dug using an excavator and the soil is used to create mounds, ideally 45-60 cm wide and 15-20 cm high (Forest Service, 2000a), on which trees are planted. Ripping is typically carried out on compact soils or soils with an impermeable layer below the topsoil to improve drainage and aeration. Rather than a wide drain, a narrow channel is cut through the soil, beside which the trees are planted.

Thinning information received was particularly variable. Where line thinning (i.e. the complete removal of a row of trees) was reported, the ratio of thinned lines (e.g. 1 in 7) was occasionally specified. The intensity of selection thinning (i.e. the harvesting of selected trees in several rows) was never specified.

Intensity of mammalian herbivory was estimated for each site based on examination of the vegetation quadrats and observations in the site as a whole. Grazing intensity was ranked on a four point scale: 0- little or none, 1- light, 2- moderate, 3- heavy. Signs of human recreational usage were noted.

3.2.2 Construction of GIS database

Most of the BIOFOREST data were received by the CMRC in MS Excel format (Figure 3). Depending on the data, they were either directly imported to the GIS via .dbf files, or additional data was extracted and then imported, depending on the level of detail in each MS Excel file. Some of the data were received in shape file format, which is the native

ArcGIS format. In some instances a number of pertinent data layers were extracted from each initial dataset received so that data could be visualised in a more meaningful way. The non-BIOFOREST related data were received in a number of different formats including ArcInfo, ArcView, Tiff and grid. Processing was required on all of these datasets before they could be incorporated into the GIS. Figure 4 illustrates the data structure of the BIOFOREST database. The data structure was incorporated into the Databank in a logical sequence of levels, from the highest level (e.g. flora) to the lower level of processed and visualised information (e.g. species richness).

3.3 RESULTS

3.3.1 GIS database

The GIS database was constructed using ArcInfo, a desktop ESRI product from the new ArcGIS software range (Figure 5). The ArcInfo interface was programmatically customised so that users with a limited knowledge of GIS can access and visualise the data (Figure 6). The GIS contains a Viewer with a limited number of toolbars to allow the user access to limited functions, such as pan, zoom, query, select, measure and export. Along with the Viewer, a data DATABANK acts as a portal to access information such as tables, species codes and metadata. The metadata follows the FGDC Content Standards for Digital Geospatial Metadata (FGDC-STD-001-1998). Each of the layers in the database contains a metadata file so that users can access development data about each layer. In the case of the base data information about the source provider of that data file is also available.

The GIS database was essentially divided into three separate units:

- base data;
- flora data; and
- fauna data.

The latter two units have an array of ancillary data that can be adjoined within the GIS.

A CD or DVD (stated on the front label of the disc) containing a number of items accompanies this report. Contained on the disc are an ArcMap (.mxd) project file, a ArcReader (.pmf) project file, a link to the DATABANK and the programme, ArcReader (along with the BIOFOREST data). Accompanying these files is a link to the User Instructions, which explain how to use the CD/DVD and programmes. Shapefiles are also available so that users who do not have access to ArcMap can visualise the data on ArcView 3.*. if they require more functionality than the free ArcReader software affords.

3.3.2 Site descriptions

The 44 study sites were distributed throughout the country in regions where forestry is an important land-use or appears likely to become so in the future (Figure 2). With the exception of INCH, KILW and KESH, the study sites are owned and managed by Coillte. Each study site was identified with a unique, four-letter, alphabetic code. Site codes will be used in some figures, tables and text throughout this report, and so study site names, codes and counties are shown in Table 6, below. Site codes may also be followed with a letter in cases where only one species of a mix is being referred to: "A" indicating ash, or "S" indicating Sitka spruce. Sample units within sites may be identified in tables, figures or text in a similar fashion, using "F" to denote floristic quadrats, "P" to identify spider pitfall traps and "M" to indicate hoverfly malaise traps. These letter codes are frequently followed by numbers indicating replicate sampling units. For example, "CORRF2", refers to the second vegetation quadrat sampled in the Corracloon site, whereas "MONTM1" indicates the first malaise trap in Moneyteige.

In this and the following section, descriptions of mixed stands will consider the ash and Sitka spruce components separately to take into account probable differences in environment and management between the species blocks. With 12 Sitka spruce – ash mixes, this results in 56 study site × forest species combinations.

3.3.2.1 Climate

Climate data, such as rainfall and temperature, were not recorded in the field because of the problems posed by varying weather conditions when visiting different sites. We did not consider it worthwhile to acquire more detailed climate data from local weather stations as these are generally located in lowland areas while many of our sites, particularly Sitka spruce sites, were in mountainous terrain, where elevation and topographic effects are significant. However, our study sites were distributed so as to encompass the major climatic gradient across Ireland, i.e. from the more oceanic west to the somewhat more continental eastern part of the country (Figure 2).

Sitka spruce sites ranged in elevation from 45 m to 367 m, and ash sites ranged from 25 m to 262 m above sea level. Mean elevation of pure spruce sites was 194 m (± 23 se), whereas the mean elevation of pure ash sites was 99 m (± 19 se). When the mixed sites are considered together with pure sites, the elevation differences between the species are still apparent, although smaller. Mixed ash sites were located at a mean elevation of 134 m (± 20 se); the true elevation differences between mixed and pure ash sites are greater than the means indicate, as the pure ash mean is inflated by two atypical sites, MVAN and REEN, with considerably higher elevations than the rest.

Site aspect data, collected in degrees, were grouped by eight points of the compass (N, NE, etc.) and presented in Table 7. Although there are differences between species in the number of sites in several aspect categories, it is difficult to ascertain whether these represent substantial differences in site conditions. As an aid to comparison, aspect was transformed to a linear scale, using the equation $A' = \cos(45-A) + 1$ (Beers *et al.*, 1966), where A is the aspect in degrees and A′ is the transformed aspect. Using this transformation, SW, the driest, sunniest aspect in the northern hemisphere, receives a value of 0 and NE, the shadiest, has a value of 2 (Table 7). The intermediate aspects SE and NW are both transformed to 1. The mean transformed aspect of spruce sites, 0.91 (± 0.16 se), in fact differed little from the mean for ash sites, 0.98 (± 0.12 se).

3.3.2.2 Geology and soils

The soils on which the ash and the Sitka spruce sites were located largely reflect past and current planting patterns (Table 8). For example, brown earths underlay 37.5% of the ash sites and only 6.3% of the Sitka spruce sites, whereas 21.9% of spruce sites and none of the ash sites were on peat. Of the 12 pure ash stands, eight were on brown earths and four on gleys. Five mixed ash sites were on gleys, four on podzols, and one each on brown earth and brown podzolic soils and lithosol (Table 8). Field observations and database soil type did not agree for some sites, however, and where soil type was not ascertained in the field the mixed ash sites in particular may have been established on localised areas of better soil. Also, the Coillte database does not distinguish between podzols and peaty podzols or between gleys and peaty gleys. Therefore, the occurrence of peaty gleys and peaty podzols is probably underestimated in Table 8. Loss-on-ignition data provide a more accurate basis for comparing the organic/mineral character of soils. In half of the 12 spruce-ash mixed sites, the soil organic contents of the different species components were generally similar. In five sites, BALE, CUMM, GFIN, LURG and SINB, the soils in the Sitka spruce components were considerably more organic than the corresponding ash component; in COMM, the difference is reversed (Table 8).

Table 6. Study site codes and locations

Site Code	Site Name	County
BALE	Ballyea	Clare
BALY	Ballygiblin	Cork
BARN	Barnadown	Wexford
BEND	Beneden	Clare
BOKY	Buffanoky	Limerick
BRAC	Brackloon	Galway
CLYD	Clydaghroe	Kerry
COMM	Commeanaline	Tipperary
CONA	Conavalla	Wicklow
COOA	Coolross (mixed spruce-ash)	Tipperary
COOL	Cooltymurraghy	Galway
COON	Cooneen Hill	Tipperary
COOS	Coolross (pure Sitka spruce)	Tipperary
CORB	Corbettstown	Offaly
CORR	Corracloon	Clare
CUMM	Cummeenavrick	Kerry
DEME	Demesne	Kildare
DERR	Derrybrien East	Galway
DOOG	Dooglaun	Clare
FURY	Fuhiry	Cork
GFIN	Garrafin	Laois
GLYN	Glynn's Hill	Clare
HIGG	Higginstown	Westmeath
INCH	Inchiroe	Kerry
KDUF	Kilduffahoo	Limerick
KESH	Keshcarrigan	Leitrim
KILA	Kilalongford	Carlow
KILM	Kilmacow	Cork
KILW	Kilnamack West	Waterford
LACK	Lacken	Cork
LURG	Lurgan Great	Galway
MARY	Marymount	Laois
MOAN	Trumra (Moanathoo townland)	Laois
MONT	Moneyteige	Wicklow
MSOP	Monasop	Laois
MUNG	Mungacullin	Wicklow
MVAN	Moanvaun	Tipperary
RATH	Rathcarrick	Sligo
REEN	Reenavanna	Limerick
RINC	Rincrew	Waterford
SAGG	Derrynasaggart	Cork
SINB	Sinotts Bog	Wexford
SUNS	Sunderlands	Wicklow
UNIO	Union	Sligo

Despite these differences in soil type, ash and spruce sites did not differ in soil drainage as observed in the field. If the letter codes in Table 8 are converted to a numerical scale (Section 3.2.1.2), the mean value for ash sites is 3.8 (± 0.21 se), which differs little from the spruce site value of 3.6 (± 0.20 se). There was likewise little difference in the slope of spruce and ash sites. Spruce sites tended to be located on more steeply sloping sites than ash: mean slope of spruce sites was 8.1° (± 1.30 se) as compared with a mean of 7.4° (± 1.34 se) for ash sites. Pure ash sites, however, sloped more gently; when mixed sites are removed from the calculation, mean slope was 5.5° (± 1.85 se).

Table 7. Number of ash and Sitka spruce sites occurring in eight site aspect categories. "No Aspect" indicates that the slope of the site was 0°, and therefore aspect could not be quantified.

Aspect	Transformed Aspect	Ash	Sitka spruce
N	1.7	1	3
NE	2	4	3
E	1.7	1	5
SE	1	1	5
S	0.3	6	2
SW	0	2	4
W	0.3	3	6
NW	1	2	4
No Aspect	-	4	0

In accordance with the soil type data, soil chemistry patterns among the species and mix types reflect the practice of planting broadleaves on less acidic, more fertile sites than Sitka spruce. The median pH of pure ash sites was 5.88, whereas that of pure spruce sites was 4.47 (Figure 7a). The soil pHs of mixed sites were intermediate in value. Mean values for total organic C were highest in pure spruce sites and lowest in pure ash sites, reflecting more spruce planting on peaty soils (Figure 7b). Greater organic C content in spruce sites may also reflect greater accumulation of humus under older conifer stands than under ash stands. Total P concentrations were much lower in the pure spruce sites than in the other site types (Figure 7c); both pure and mixed spruce sites had lower concentrations of available P than ash sites (Figure 7d). Patterns in cation (Ca, Mg and K) concentrations generally mirrored those for pH: highest in pure ash and lowest in pure spruce.

Table 8. Soil type, parent material, drainage, slope (in degrees) and percent loss-on-ignition (LOI) in the top 5 cm of each study site × forest species combination. Drainage is coded as follows: P = poor, M = moderate and G = good; intermediate conditions are indicated by a combination of two letters.

Code	Species	Soil Type	Solid Geology	Drainage	Slope (°)	LOI (%)
BALE	ash	gley	sandstone	M	4.3	23.0
BALE	spruce	peat, gley	sandstone	P/M	3.7	50.1
BALY	ash	brown earth	limestone & volcanic debris	G	3.0	18.7
BARN	ash	gley	rhyolitic volcanics & slate	M	0.0	24.9
BEND	spruce	peat	sandstone	P/M	4.0	93.1
BOKY	spruce	podzol	greywacke & siltstone	P/M	4.5	30.4
BRAC	spruce	peat, gley	limestone & shale	M	1.0	45.7
CLYD	spruce	peat	sandstone	P	-	76.6
COMM	ash	podzol	greywacke & siltstone	M/G	9.3	36.8
COMM	spruce	podzol	greywacke & siltstone	G	18+	16.0
CONA	spruce	podzol	complex metamorphic[1]	-	-	-
COOA	ash	gley	limestone & shale	M	4.0	20.2
COOA	spruce	gley	limestone & shale	M	2.0	22.5
COOL	ash	gley	limestone & shale	M	0.0	17.7
COON	spruce	podzol	greywacke & siltstone	M/G	7.5	25.2
COOS	spruce	gley	sandstone & limestone	M	1.7	17.1
CORB	ash	brown earth	limestone	G	-	18.6
CORR	spruce	gley	greywacke, siltstone & shale	M/G	9.0	31.2
CUMM	ash	peaty podzol	sandstone	M	8.5	25.1
CUMM	spruce	peaty podzol	sandstone	M	-	60.3
DEME	ash	brown earth	limestone	G	0.2	11.5
DERR	spruce	peaty gley	mudstone, siltstone & conglomerate	G	8.0	62.3
DOOG	ash	gley	greywacke, siltstone & shale	M	15.0	22.5
DOOG	spruce	gley	greywacke, siltstone & shale	M	-	18.2
FURY	spruce	peat	sandstone	P/M	9.0	77.3

Code	Species	Soil Type	Solid Geology	Drainage	Slope (°)	LOI (%)
GFIN	ash	gley	sandstone & limestone	M	-	9.3
GFIN	spruce	gley	sandstone & limestone	M	-	17.4
GLYN	spruce	gley	mudstone & limestone	M	15.0	24.1
HIGG	ash	brown earth	limestone	M/G	13.3	21.2
INCH	ash	brown earth	sandstone	M	10.7	20.2
KDUF	spruce	podzol	greywacke & siltstone	M	3.0	22.3
KESH	ash	gley	limestone	M	6.3	16.5
KILA	ash	brown earth	granite	G	8.5	16.3
KILA	spruce	brown earth	granite	M/G	-	15.8
KILM	ash	brown podzolic	sandstone	G	15.7	15.7
KILM	spruce	brown podzolic	sandstone	G	7.0	12.7
KILW	ash	brown earth	limestone & shale	G	0.0	14.9
LACK	spruce	brown earth	mudstone & sandstone	M/G	9.0	15.2
LURG	ash	gley	limestone & shale	P/M	0.2	31.4
LURG	spruce	peat	limestone & shale	P/M	0.7	80.9
MARY	spruce	gley	sandstone	M/G	-	10.9
MOAN	spruce	peaty gley	sandstone & limestone	P/M	-	64.6
MONT	spruce	podzol	complex metamorphic[1]	G	15.0	29.0
MSOP	spruce	gley	sandstone	P/M	-	37.6
MUNG	spruce	brown earth	schist	G	18+	18.2
MVAN	ash	gley	greywacke & siltstone	M	6.0	25.5
RATH	ash	lithosol	limestone	G	18+	14.2
RATH	spruce	lithosol	limestone	G	12.0	13.2
REEN	ash	brown earth	greywacke & siltstone	M/G	3.0	22.0
RINC	ash	brown earth	mudstone & sandstone	G	18+	16.4
SAGG	spruce	peat	sandstone	M/G	18+	72.3
SINB	ash	podzol	slate, phyllite & schist	M	-	19.5
SINB	spruce	podzol	slate, phyllite & schist	M	3.0	32.8
SUNS	ash	podzol	slate & siltstone	G	11.7	19.4
SUNS	spruce	podzol	slate & siltstone	G	18+	21.8
UNIO	spruce	lithosol	psammite (metamorphic)	M/G	0.0	40.6

[1] Site is underlain by several types of metamorphic bedrock.

3.3.3 Site management

3.3.3.1 Pre-afforestation

Very little information was available on the ecology and management of sites prior to afforestation, with the exception of very young stands. Of the 30 site × species combinations for which the pre-afforestation land-use was known, 26 were managed as grazing land. This land-use encompasses sites with very different environmental conditions, ranging from mineral soils over limestone later afforested with ash (e.g. KILW and HIGG) to peat soils afforested with Sitka spruce (e.g. BEND and SAGG). One ash site, INCH, was partly grazed and partly under tillage and had been under arable agriculture before the 1980s. Cattle were specifically mentioned as the grazing animal before afforestation more often than sheep. Occasionally drystock were specified; there is no record of any site supporting dairy cattle prior to planting. Land-use intensity was specified in terms of livestock units (LU) in only six site × species combinations; no site supported more than 1 LU/ha.

To facilitate comparisons, the formerly grazed sites were ranked according to land-use intensity. The lowest ranking, 1, was assigned to sites that had been used for rough grazing, with no record of fertilisation or hay- or silage-making. Sites where “heather” or *Molinia* was mentioned as part of the pre-afforestation vegetation were also included in this group. A ranking of 3 was assigned to sites that were annually fertilised, cut for hay or silage or both, or were identified as "improved grassland" without further details. A ranking of 2 was given to sites that appeared to be intermediate in land-use intensity. Included in this category was BRAC, a site on gley and peat soils that had been reclaimed and heavily limed and fertilised in the past.

One ash site (the ash component of SINB), representing 7.7% of the ash sites for which data were available, was in the Grazing 1, or rough grazing, category (Figure 8). In contrast, eight (47.1%) of the Sitka spruce sites were in this category. Six spruce sites (35.3%) were in the Grazing 3 category, whereas seven (53.8%) ash sites had the same land-use intensity ranking (Figure 8).

A pure ash site (BALY) and a spruce-ash mixed site (SUNS) were occupied by scrub prior to afforestation and were not used for livestock. The abundance of rabbits at SUNS was cited as the reason for the absence of livestock and the subsequent conversion to forestry. BARN, an ash stand, was described by the forest manager as an area of old oak and ash woodland interspersed with rushy patches prior to ash planting in 1939. The site is marked as broadleaved woodland and named "Barnadown Wood" on the third edition (1921) six-inch OS map of the area. It was also formerly used as rough pasture for horses and sheep during dry weather and burned at three to five year intervals. No other sites were occupied by woodland or coniferous forestry prior to the establishment of the current stand, as far as can be ascertained. However, four ash sites (BALY, DEME, REEN and RINC), a Sitka spruce site (UNIO) and a spruce-ash mix site (RATH) were located adjacent to semi-natural or estate woodland marked on the third edition six-inch OS maps (c.f. GIS database).

The above land-use results are more representative of recently-planted sites, as more data were available for them. Therefore, these data cannot be used to elucidate any trends over time in planting and land quality. Information was available for only four ash sites planted before 1991 and six spruce sites planted before 1988. It may, however, be indicative of former planting patterns that the former use of all of these older sites was woodland, scrub or rough grazing.

3.3.3.2 Silviculture

The years in which the study sites were afforested are shown in Table 9, together with their respective age classes. Ground preparation for afforestation was primarily by mounding in ash sites (Figure 9). In Sitka spruce sites, ploughing and mounding were used with nearly equal frequency. Less intensive ground preparation methods, ripping and no cultivation, were used more frequently in ash plantations than in spruce sites (Figure 9). There was some evidence of change in ground preparation methods over time. With one exception, sites that received no preparation were planted in 1965 or before. In contrast, ripping was not carried out on any site planted prior to 1987. Ploughing was largely carried out in sites planted in the 1960s and early 1970s, but also in some later planted sites on peats or gleys. Drainage was carried out prior to afforestation or as part of planting preparation in 63% of ash sites (15 of 24) and 65% of Sitka spruce sites (22 of 34 - no information was available for 2 sites).

Data on fertilisation were only available for 16 ash sites and 14 spruce sites. Of the sites for which data were available, nine (56.3%) ash sites were unfertilised as compared with five (35.7%) spruce sites (Figure 10). NPK fertiliser was applied to three (18.8%) ash sites, but no Sitka spruce sites.

Information on herbicide use was available for 19 ash sites and 24 spruce sites. Of these, herbicide was applied to 11 (57.9%) ash sites; glyphosate only was used in five sites, glyphosate and terbuthylazine were used in one site (COOA), glyphosate and propyzamide were used in one site (COOL), terbuthylazine only was used in one site (BALE), paraquat was used in one site (SUNS) and unspecified herbicides were used in two sites. Herbicides were used in only six (25.0%) of the Sitka spruce sites for which information was available. Terbuthylazine only was used in three sites, glyphosate and terbuthylazine were used in one site (COOA), glyphosate only was used in one site (COOS) and paraquat was used in one site (SUNS). In most cases, the last herbicide application was made five years or more prior to sampling. The exceptions were: BALE and KESH were treated 1 year prior to sampling, HIGG was treated 3 years prior to sampling and KILM and KILW were treated 4 years prior to sampling.

No other use of pesticides was reported, although we assume thinned stumps would have been treated with urea to prevent *Heterobasidion annosum* butt rot as per Forest Service (2000a) guidelines.

With the exception of DEME and BARN, and some harvesting of ash for hurleys, none of the ash sites or ash components of mixed sites were thinned (Table 9). All Sitka spruce stands in age classes 3 and 4 have been at least partially thinned, with the exception of DERR (Table 9). In almost all sites for which there was information, the first thinning used the line and selection method, followed by selection-only in subsequent thinnings. In several cases, the number of thinning treatments could not be ascertained, and in others, the number of thinnings removed varied among different subcompartments that comprised the study site.

3.3.3.3 Grazing

Younger, particularly age class 1, sites were usually fenced to exclude livestock, although this did not preclude break-ins. No sites were deer- or rabbit-fenced. Grazing pressure was apparently absent or light in most sites. There was little difference in mean grazing intensity rank among pure Sitka spruce (0.7 ± 0.23 se), mixed Sitka spruce (0.4 ± 0.15 se) and mixed ash (0.4 ± 0.19 se). Four (of 20) pure spruce sites, however, experienced moderate or heavy grazing pressure as compared with one mixed ash site and no mixed spruce. Grazing intensity was higher in pure ash sites (1.3 ± 0.37 se), where five (of 12) sites were moderately or heavily grazed.

3.3.4 Stand structure

Preliminary analyses of stand structural variables, such as canopy cover and tree size, showed high variability within a given age class. Forest age is only one of many factors that affect stand structure. Other factors include environmental parameters, such as rainfall and soil chemical properties, and management factors, such as thinning regime and ground preparation. Although stand age *per se* can influence biodiversity, particularly through the operation of dispersal and colonisation mechanisms, changes in stand structure in plantation forestry would be expected to have a stronger affect on biodiversity through modification of the below-canopy environment. Accordingly, most studies of forest biodiversity focus on stand structure rather than stand age (e.g. Pitkänen, 1997; Humphrey *et al.*, 1999; Ferris *et al.*, 2000a; Humphrey *et al.*, 2002). To improve our investigations of biodiversity and structural changes over the forest cycle, we developed a small number of stand structural types to summarise the structural characteristics of our study sites.

Table 9. Study site age classes, planting years, number of thinnings received and type of thinning. "?" indicates that no information on type of thinning was available. "1+" indicates that the site was thinned at least once, but the precise number is unknown.

Site	Species	Age class	Planting Year	No. Thinnings	Thinning Type
RINC	ash	5	1920	0	-
BARN	ash	5	1939	1+	-
DEME	ash	5	1939	1+	?
BALY	ash	5	1949	0 [a]	-
MVAN	ash	2	1990	0	-
REEN	ash	2	1990	0	-
COOL	ash	2	1993	0	-
CORB	ash	2	1993	0	-
INCH	ash	1	1994	0	-
KESH	ash	1	1994	0	-
HIGG	ash	1	1997	0	-
KILW	ash	1	1997	0	-
RATH	mix	4	1954	5 [b]	line & selection
KILA	mix	4	1956, 61[c]	1+ [d]	?
SUNS	mix	4	1957	4 [a, b]	selection only
SINB	mix	4	1964	3 [b]	line & selection
GFIN	mix	2	1985	0	-
COMM	mix	2	1989	0	-
CUMM	mix	2	1991	0	-
DOOG	mix	2	1992	0	-
BALE	mix	1	1996	0	-
COOA	mix	1	1996	0	-
KILM	mix	1	1998	0	-
LURG	mix	1	1998	0	-
UNIO	Sitka spruce	4	1954	6	line & selection
CONA	Sitka spruce	4	1955-56, 58	1+	?
MONT	Sitka spruce	4	1958	1+ [e]	?
DERR	Sitka spruce	4	1962	0	-
MUNG	Sitka spruce	4	1962	1+	?
FURY	Sitka spruce	4	1963-64	3	line & selection
MSOP	Sitka spruce	4	1964	3	line & selection
COON	Sitka spruce	4	1965	3	line & selection
SAGG	Sitka spruce	3	1972	3-4 [e]	line & selection
BOKY	Sitka spruce	3	1973	1-2	line & selection
MOAN	Sitka spruce	3	1976	2	line & selection
CORR	Sitka spruce	3	1979	1 [e]	?
MARY	Sitka spruce	2	1987	0	-
CLYD	Sitka spruce	2	1988	0	-
GLYN	Sitka spruce	2	1991	0	-
KDUF	Sitka spruce	2	1991	0	-
BRAC	Sitka spruce	1	1995, 97	0	-
COOS	Sitka spruce	1	1996	0	-
LACK	Sitka spruce	1	1996	0	-
BEND	Sitka spruce	1	1996-97	0	-

[a] Some hurley ash harvested.

[b] Sitka spruce only; ash component unthinned.

[c] The ash component and part of the spruce component were planted in 1956 and the remainder of the spruce was planted in 1961.

[d] Sitka spruce only; thinning history of ash component unknown.

[e] Part of site unthinned.

The study sites were classified into stand structural types using data from three 10×10 m vegetation quadrats (Section 3.2.1.2). Sitka spruce stands and ash stands were classified separately; the spruce and ash components of mixes were classified together with the respective pure stands. The variables used in the classification were percentage tree cover, tree height, mean dbh and minimum distance between trees. Values from the three 10×10 m quadrats were averaged to produce a mean value for each site × species combination. In five sites, data were missing for one or two variables: GLYN- height, DOOG- minimum distance and dbh, and GFIN, UNIO and RINC- minimum distance. Missing values were filled with the mean from sites of the same age class.

Ward's hierarchical clustering was used as the classification methodology (Legendre & Legendre, 1998). Sites begin as separate entities and are then grouped into progressively fewer numbers of clusters (i.e. agglomerative clustering). The variables were transformed by ranging prior to clustering to place them on equivalent scales. Principal Components Analysis (PCA) ordinations were performed using the covariance matrix on the range-transformed variables as an aid to cluster delineation.

3.3.4.1 *Sitka spruce sites*

The PCA ordination (Figure 11) shows that the sites form a continuum, with marked discontinuities reflecting the three-cluster solution. The continuum summarises the forest cycle and corresponding structural changes. Axis 1 explains 73% of the variance in the structural variables and represents increasing height, dbh and spacing from left to right. Axis 2 represents 21% of the variation in the data and is most closely correlated with tree cover: high scores on Axis 2 indicate lower canopy cover. age class 1 and age class 2 sites are well-ordered along the forest cycle trajectory. The results of clustering and PCA analyses on stand structure, however, do not distinguish well between age class 3 and 4 stands.

Table 10. Allocation of Sitka spruce sites to structural types. Also shown is the age class of the site.

Site	Structural Type	Age class	Site	Structural Type	Age class
BALE	pre-thicket	1	BOKY	closed-maturing	3
BEND	pre-thicket	1	CORR	closed-maturing	3
BRAC	pre-thicket	1	SAGG	closed-maturing	3
COOA	pre-thicket	1	COON	closed-maturing	4
COOS	pre-thicket	1	DERR	closed-maturing	4
KILM	pre-thicket	1	MOAN	reopening	3
LACK	pre-thicket	1	FURY	reopening	4
LURG	pre-thicket	1	MONT	reopening	4
CLYD	thicket	2	MUNG	reopening	4
COMM	thicket	2	KILA	mature	4
CUMM	thicket	2	MSOP	mature	4
DOOG	thicket	2	RATH	mature	4
GLYN	thicket	2	SINB	mature	4
KDUF	thicket	2	SUNS	mature	4
GFIN	closed-maturing	2	UNIO	mature	4
MARY	closed-maturing	2			

In the PCA diagram (Figure 11), discontinuities in the site ordination correspond with the three-cluster solution. However, limiting structural types to three would leave a very heterogeneous middle cluster, encompassing sites with, for example, average tree heights ranging from 4 – 20 m. The groupings formed by the four- and five-cluster solutions were inspected. The latter was chosen as the basis for structural types because the five groups of sites could be clearly distinguished from each other by the means and ranges of the structural variables. CUMM was reassigned from its cluster with the age class 1 sites to the next developed stage as we considered that the structural information captured in the vegetation quadrats was not truly representative. CUMM was a heterogeneous site occupied by closed-canopy thickets of 3 m tall trees interspersed with small clearings. The final allocation of sites to structural types is shown in Table 10 and mean values for the four structural variables in each type are shown in Table 11. Note that the statistics presented in Table 11 are means and ranges of site means, the latter derived from vegetation quadrat data as discussed in Section 3.3.4 above.

Table 11. Mean (and range in brackets) canopy cover (%), tree height (m), dbh (cm) and minimum spacing between trees (m) for the five Sitka spruce structural types.

Structural Type	Cover (%)	Height (m)	DBH (cm)	Min. Spacing (m)
Pre-thicket	29.6 (11.7-43.3)	2.5 (1.4-3.8)	3.7 (1.6-7.0)	1.6 (1.0-2.0)
Thicket	80.3 (60.0-93.3)	5.9 (4.3-7.3)	12.4 (10.4-16.5)	1.9 (1.5-2.0)
Closed-maturing	86.9 (78.3-95.0)	12.7 (9.8-15.7)	19.3 (14.7-24.3)	1.7 (1.4-2.0)
Reopening	70.8 (63.3-80.0)	18.8 (16.8-20)	22.4 (21.0-24.8)	2.3 (2.0-2.8)
Mature	54.7 (40.0-60.0)	21.1 (18.3-23.0)	39.0 (31.6-44.8)	3.9 (3.0-6.0)

3.3.4.2 Ash sites

When Ward's clustering was performed on the four structural variables for the ash sites, DEME remained separate from the remainder of the older (age class 4 and 5) sites until the four-cluster stage. DEME was distinguished from the other older sites largely on the basis of much wider spacing. A cluster analysis was then performed using only three tree variables and omitting minimum distance. This simplified classification was better at forming coherent clusters of larger tree sites and also clusters of smaller tree sites, while the middle groupings were also slightly improved. We therefore decided to use the cluster analysis of sites without minimum spacing as the basis for the ash structural types.

The PCA ordination of the ash sites does not show as simple a structural pattern as was found for the Sitka spruce sites (Figure 12). Axis 1 explains 86.9% of the variation in the three structural variables and is positively correlated with all structural variables. Axis 2 explains 11.4% of the variation in the data; it is negatively correlated with cover and has small positive correlations with height and dbh. According to the ordination diagram, age class is a poorer predictor of structure for the ash sites than for the Sitka spruce sites.

Four or five structural groups were appropriate for the structural types. The classifications differ in whether the six sites with the largest trees are in one or two groups. Because the clusters in the two-group solution are readily distinguished by dbh, we decided to use the five-cluster classification as the basis for the structural types. In the ordination diagram (Figure 12), KILA is revealed as an outlier, being separated from the other sites by low canopy cover relative to other sites with trees of similar size. KILA was therefore not included in the final set of structural types. The assignment of sites to structural types is shown in Table 12 and mean values for the three structural variables are shown in Table 13. Note that the statistics presented in Table 13 are means and ranges of site means, the latter derived from vegetation quadrat data as discussed in Section 3.3.4 above.

Table 12. Allocation of ash sites to structural types. Also shown is the age class of the site. Note that KILA was not assigned to a structural type.

Site	Structural Type	Age class	Site	Structural Type	Age class
BALE	pre-thicket	1	COMM	closed-maturing	2
HIGG	pre-thicket	1	COOL	closed-maturing	2
KESH	pre-thicket	1	GFIN	closed-maturing	2
KILM	pre-thicket	1	SINB	closed-maturing	4
KILW	pre-thicket	1	SUNS	semi-mature	4
LURG	pre-thicket	1	BALY	semi-mature	5
CORB	pre-thicket	2	BARN	semi-mature	5
CUMM	pre-thicket	2	RATH	mature	4
DOOG	pre-thicket	2	DEME	mature	5
MVAN	pre-thicket	2	RINC	mature	5
REEN	pre-thicket	2	KILA	not assigned	4
COOA	pole	1			
INCH	pole	1			

Table 13. Mean (and range in brackets) canopy cover (%), tree height (m) and dbh (cm) for the five ash structural types.

Structural Type	Cover (%)	Height (m)	DBH (cm)
Pre-thicket	12.2 (5.0-21.7)	3.1 (1.3-5.0)	3.8 (0.9-9.1)
Pole	57.8 (45.0-80.0)	4.4 (3.0-6.0)	6.3 (4.8-8.9)
Closed-maturing	77.1 (70-88.3)	9.0 (6.8-11.5)	10.0 (7.8-13.85)
Semi-mature	75.6 (66.7-81.7)	18.8 (16.3-22.0)	17.3 (15.8-19.7)
Mature	72.2 (70-73.3)	21.6 (18.5-25.0)	29.1 (27.6-30.9)

3.3.4.3 *Environment and structural types*

We compared variation in environmental variables among structural types to detect any associations among them. Such associations would confound structural type and environment so that species patterns among structural types would be difficult to separate from environmental factors. We also investigated grazing intensity among structural types, but no trends were detected.

3.3.4.3.1 Sitka spruce

Mean elevation of the pre-thicket stand type (86.5 m ± 9.5 m se) was considerably lower than the more mature stand types. The next lowest elevation stand type was the mature type (165.1 m ± 33.9 m se). An F-test followed by Tukey's HSD post-hoc test showed that the differences in elevation were significant ($\alpha = 0.05$) between the pre-thicket type and the two highest elevation types, thicket and reopening.

The distribution of soil types within structural groups was relatively equable. One imbalance was the location of four out of seven closed-maturing sites on gleys or peaty gleys. These soil types, however, underlay at least part of 12 of the 32 pure and mixed spruce stands. Investigation of soil chemical and physical variables by stand type shows higher soil pH in the pre-thicket and thicket sites than in the more mature stand types (Figure 13a). Loss-on-ignition data (Figure 13b), as well as total organic carbon and total nitrogen data, indicate that soils in the pre-thicket and reopening stand types were more rich in organic matter than the others. These differences, however, are not simply reflections of differences in soil type among the sites (e.g. the four reopening sites were located on brown earth, podzol, peat and gley soils). The reopening structural type is also considerably poorer in available P than the other types (Figure 13c); the total P data, however, do not reflect this finding. Cation concentrations (e.g. exchangeable Ca, Figure 13d) follow the same general pattern as pH: greater levels in the pre-thicket or pre-thicket and thicket stand types than in the more mature types.

3.3.4.3.2 Ash

Soil drainage was better in the semi-mature (mean rank = 4.3, se = 0.67) and mature (mean = 5.0, se = 0.0) ash structural types than the less mature types (mean = 3.4, se = 0.21). In the case of the mature type, this is also associated with steeper slope on average, although the variation in slope is also high.

As with Sitka spruce, soil types are distributed among the structural types fairly equally. Soil pH varied less among sites and structural types than in the Sitka spruce stands (Figure 14a) and appeared to decline from the pre-thicket to the closed-maturing stage and then increase again. The soils of the mature stand type had a lower mean organic content than the other types (Figure 14b). Available P (Figure 14c) and exchangeable K concentrations varied among the stand types, with no obvious trends. Exchangeable Ca (Figure 14d) and Mg concentrations were lowest in the pole and closed-maturing stand types, but again, considerable variation was apparent within the stand types.

3.4 DISCUSSION

Similarities and differences among the study sites reflect several factors, including: 1) differences in site climate, fertility and management between Sitka spruce and ash plantings, 2) past and present trends in afforestation and land use, 3) changes in site environment over the forest cycle, and 4) random (i.e. not controlled by the researchers) variation among sites or groups of sites.

3.4.1 Comparison of ash and Sitka spruce sites

Ash and Sitka spruce are quite dissimilar species in evolutionary history, natural distribution and physiology, and thus naturally differ in their preferred site conditions. Ash is regarded as demanding of nutrients, especially N and P, but is relatively tolerant with regard to pH in the upper soil horizon (Joyce *et al.*, 1998). Ideal ash sites are located on limestone-derived brown earths and grey-brown podzolics that are moist but free-draining (Joyce *et al.*, 1998). Ash is one of the most frost-sensitive of native species, and can also be sensitive to wind damage (Binggeli & Rushton, 1999). Accordingly, fertile lowland sites are preferred for afforestation with ash (Forest Service, 2000a). In contrast, Sitka spruce can be grown commercially on a wide range of site types, excluding the most infertile peats and podzols, and performs best on gley soils up to about 300 m elevation (Forest Service, 2000a). Sitka spruce is therefore more frequently planted in upland sites than ash or other broadleaves.

The contrasting site preferences of ash and Sitka spruce account for many of the environmental and management differences between pure spruce and pure ash sites, including elevation, slope, soil physical and chemical characteristics and pre-afforestation land-use. Silvicultural management reflects these site differences: for example, less intensive ground preparation, less fertilisation and less thinning in ash sites. In these aspects, the pure sites used in this study are most likely typical of the wider population of ash and Sitka spruce stands in Ireland.

Given the contrast in ideal site conditions between Sitka spruce and ash, it is likely that conditions in the mixed spruce sites, mixed ash sites or both will differ from those in typical pure stands in Ireland. In this study, steeper slope, higher elevation, lower pH and Ca and perhaps lower available P in the mixed ash sites as compared with pure sites show that there are environmental differences between them that must be taken into account when interpreting the results of this study. The ash component of some of the mixed ash sites, in particular CUMM and KILA, was poorly developed, suggesting that site environment was marginal for good ash growth. Likewise, comparison of soil chemical data between pure and mixed spruce sites indicates that the latter are somewhat more fertile than the former.

3.4.2 Trends in afforestation and land use

Prior to the 1980s, the vast majority of afforestation was carried out by the state. Before then, land with agricultural potential was not purchased for planting by the Forest Service. In the 1980s, falling agricultural land prices and EU grant-aid allowed acquisition of more fertile, lowland sites by public and private foresters (OCarroll, 1995). Although pre-afforestation land-use information is sparse for older stands, the absence of improved grassland sites afforested prior to 1988 suggests that the sites used in this study reflect this pattern. Therefore, the older sites may be expected to have been more nutrient poor (and perhaps originally more species-rich) at afforestation. This may partially explain lower mean pH and cation concentrations found in the closed-maturing, reopening and mature Sitka spruce stand types.

With changes in the types of sites available for afforestation and in techniques, ground preparation methods have also changed. In this study, all but one of the uncultivated sites were afforested prior to 1965. The decreasing use of ploughing in more recently afforested sites (Forest Service, 2000a) is also reflected in the study sites.

Five pure and two mixed sites planted in 1957 or before were formerly occupied by scrub or woodland or were located adjacent to woodland. Three were Sitka spruce stands, including the spruce component of SUNS, in the mature structural type. All six semi-mature and mature ash stands fall into this category. The origins and landscape setting of these stands therefore may not be typical of the land currently available for afforestation, an increasing proportion of which is former agricultural land. This factor must be taken into account when interpreting the biodiversity of these stand structural types, particularly semi-mature and mature ash. Given that much of the older ash afforestation would have taken place in an estate woodland context, the association of the more mature ash plantations with pre-existing woodland was probably unavoidable.

3.4.3 Environmental changes over the forest cycle

Conifer plantations have been found to decrease soil pH, promote podzolisation and form deep mor-humus and litter layers (Page, 1968; Miles, 1978; Hornung, 1985; Miles, 1985). The degree of impact of plantations on soils, however, varies according to initial soil conditions (Stone, 1975; Hornung, 1985). In contrast, ash litter can increase the pH of the upper soil layer (Weibull, 2001). The effect of species modification of the sites probably accounts at least in part for declining pH and lower cation concentrations with structural maturity of Sitka spruce. Similarly, the increase in pH from closed-maturing to mature ash stands may also reflect site modification, although the data are less convincing.

3.5 CONCLUSIONS

The sites chosen for this study occupy a wide geographical area and a range of site types that is generally typical of Sitka spruce and ash plantations in Ireland. The spruce-ash mixed sites are less typical than their pure counterparts, occupying sites intermediate in elevation, slope and soil properties. As with Irish forestry as a whole, the study sites reflect the change from afforestation of mainly scrub and upland sites, to the more recent trend of planting agricultural land; they also reflect accompanying management changes. Some of the variation in soil chemistry is probably also attributable to site modification by the trees.

Sitka spruce stand structure follows a well-defined pattern of increasing tree size and spacing with canopy cover at first increasing and later reopening after thinning. The forest cycle may be best divided into five structural types: pre-thicket, thicket, closed-maturing, reopening and mature. Ash stand structure is more variable. Increase in tree size accompanies an increase and then levelling-off of canopy cover. The ash forest cycle may also be divided into five structural types: pre-thicket, pole, closed-maturing, semi-mature and mature. It is important to note that the term “mature” as used in this report does not equate with commercial maturity. Ash plantations in the mature structural type may not be ready for harvest for several years. Sitka spruce stands may reach commercial maturity by the reopening stage; therefore not all spruce stands will necessarily reach the mature structural stage.

4 VEGETATION

4.1 INTRODUCTION

4.1.1 Importance of forest flora

Field and ground layer vegetation communities present in planted forests provide habitats for dependent fauna (Humphrey *et al.*, 1999), influence regeneration of shrub and canopy layers (Parker *et al.*, 1997), and are also important contributors to site productivity (Ford & Newbould, 1977; Moore & Lee Allen, 1999). In addition to their structural and functional role, vegetation communities enhance the aesthetic environment of plantation forests. Indeed, Hill (1987) in his discussion on British plantations stated, "…a forest without wild vegetation would be a dreary prospect". At present, however, there is little information on the floristic richness of plantation forests in Ireland. The majority of studies carried out to date have been site-specific, with insufficient levels of replication (Magurran, 1988; Fahy & Gormally, 1998). For example, Fahy and Gormally (1998) compared plant communities in a semi-natural oak wood, a Sitka Spruce plantation and a clear-felled conifer plantation in Connemara, Co. Galway. They found that plant species richness was greatest in the oak woodland, whilst the clear-felled site and Sitka spruce plantation were most similar in terms of species composition. Although such studies are informative at the local scale, they emphasize the need for further research.

4.1.2 Forest cycle and plant diversity

Franklin (1982) formulated a model predicting plant diversity at different stages of the forest cycle. In this model, diversity increases to a peak before canopy closure, declines to its lowest values under closed canopy and increases again when canopies of young and mature stands reopen. Franklin's model is supported by other studies including Hill (1979) who investigated the development of plant communities in British plantations and Halpern and Spies (1995) who studied diversity in Douglas fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest. Aubert *et al.*'s (2003) study of plant diversity along a beech (*Fagus sylvatica*) silvicultural cycle in Normandy also supports Franklin's model. Whilst little is known about the status of the vegetation communities in Irish plantations, research regarding vegetation diversity in British plantations has been carried out and is ongoing. For example, the reduction of floristic richness under some conifers, such as fir and spruce species, is well documented (Hill & Jones, 1978; Hill, 1979; Wallace & Good, 1995; Fahy & Gormally, 1998; Ferris *et al.*, 2000a). Sitka spruce plantations are well known for the dense shade they cast; vascular plants decline rapidly as the Sitka spruce canopy closes and *Dryopteris dilatata* (broad buckler fern), *Galium saxatile* (heath bedstraw) and *Vaccinium myrtillus* (bilberry) are among the few species that can survive (Hill & Jones, 1978). Conifer forests can be favourable habitats for shade-tolerant bryophytes; these generally increase in number and abundance through the forest cycle (Hill & Jones, 1978; Wallace & Good, 1995); however, there is much variation in the pattern of bryophyte development between forests. Whilst spruce forests have been found to support richer bryophyte communities than pine (Humphrey *et al.*, 2002), only a limited range of bryophyte species is able to persist beneath the most economically successful Sitka spruce crops (Wallace & Good, 1995). In these forests the combination of high canopy cover, low soil moisture and high litter accumulation suppresses even bryophyte expansion (Hill, 1979).

4.1.3 Comparison of conifer and broadleaf plantations

Whether the canopy species is native or non-native, deciduous or coniferous, monoculture plantations have a widespread reputation for supporting an impoverished flora (Hunter, 1990). Various studies substantiate this reputation. Indeed, Kirby (1988) found that stands of thicket Norway spruce (*Picea abies*) in southern Britain were extremely species-poor compared with nearby semi-natural oak stands of similar age. Likewise, Magurran (1988) using a variety of diversity indices found that relict oak woodland in Banagher, Northern Ireland, was substantially more diverse than an adjacent mature stand of Sitka spruce. However, Roberts (2002) observed a higher number of vascular species in managed spruce plantations than in natural mature stands in New Brunswick, Canada. Michelsen *et al.* (1996) compared vegetation communities in eucalyptus (*Eucalyptus* spp.) plantations and adjacent natural stands. Whilst no difference in richness or biomass was found, they observed that the majority of herb species in the plantations were widespread weeds. Such research highlights the need to study vegetation richness and composition in unison, since species richness cannot necessarily be used as a surrogate for the conservation value of the ground flora.

Vegetation in plantation forests must persist from the previous flora, regenerate from the existing seedbank or colonise from forest rides and surrounding habitats (Sparks *et al.*, 1996; Buckley *et al.*, 1997; Augusto *et al.*, 2001). Where deciduous broadleaves are established on sites formerly devoted to ancient broadleaved woodland, Peterken (2001) claims that there is little change in the woodland flora. In broadleaf stands that are established in upland areas on poorer soils, woodland species such as *Anemone nemorosa* (wood anemone) and *Hyacinthoides non-scripta* (bluebell) do not generally increase (Hill, 1979) (i.e. they do not appear in places where they were not present before). The short rotation of the conifer stands and the lack of suitable refuges during the establishment and thicket stages also inhibit the establishment of woodland species (Hill, 1979). Indeed, Kirby (1988) recognises that the period of ground flora stability at the end of the crop's life is much shorter under conifer crops and is a smaller proportion of the overall rotation than under broadleaves. This reduces the time available for plants to disperse through a stand.

Conifer plantations are well known for increasing soil acidity, promoting podzolisation, and formation of deep mor-humus and litter layers (Page, 1968; Miles, 1978; Hornung, 1985; Miles, 1985). According to Hunter (1990), acidic soil, which limits nutrient availability, influences the variety of plants in conifer stands. Analyses by Ferris *et al.* (2000a) indicated that vegetation composition is closely related to soil nutrient levels in conifer plantations in Britain. Variation in community composition in Scots pine (*Pinus sylvestris*), Sitka spruce, Norway spruce and Corsican pine (*Pinus nigra* var *maritima*) forests was related to a soil fertility gradient. The gradient was defined by increasing pH, exchangeable Ca, and available N in NO_3^- form, coupled with decreases in organic matter and N in NH_4^+ form. Whilst lowland sites were dominated by species requiring high pH (e.g. *Brachypodium sylvaticum*, wood false-brome), upland forests supported calcifuge species (e.g. *Vaccinium myrtillus*).

4.1.4 Diversity indicators

Recent research on biodiversity in plantation forests has recognised the need for indicators of diversity (Noss, 1990; Ferris & Humphrey, 1999; Noss, 1999; Lindenmayer *et al.*, 2000). Vascular plants have been used as a surrogate for total biodiversity in conservation evaluation for many years due to their known relationship to edaphic and climatic factors (Ferris & Humphrey, 1999). However, according to Pharo *et al.* (2000), there is little empirical evidence that vascular plants are an appropriate umbrella group. Indeed, Jonsson and Jonsell (1999) studied the effectiveness of vascular plants, bryophytes, epiphytic lichens and wood-inhabiting fungi as potential indicators in boreal spruce forests in Sweden. They concluded that no species group could completely describe vegetation diversity. In contrast, Sætersdal *et al.* (2003) found that species richness of vascular plants was well correlated with richness of bryophytes, lichens, carabids, staphylinids, snails and polypore fungi, but not spiders, in an area of Norwegian boreal forest. They concluded that vascular plants could be used for selection of conservation areas in conjunction with an inventory of habitats known to be important for rare forest species, such as dead wood and deciduous trees. Indicator methods that take species identity into account are preferable to measures of species richness (Hunter, 1990). For example, *Vaccinium myrtillus* is considered to be a useful indicator of biodiversity in boreal Scots pine forests. This shrub is a food source for birds, mammals and moths and attracts pollinators into the forest (Ferris & Humphrey, 1999). The presence of birch in the canopy layer is also indicative of a more species-rich ground flora in British spruce forests (Ferris & Humphrey, 1999).

The relationship between stand structure and plant diversity has also been investigated, with particular emphasis on the impact of canopy cover on vegetation richness and abundance (Hill & Jones, 1978; Wallace *et al.*, 1992; Ferris *et al.*, 2000a). In a study of Sitka spruce plantations in upland Britain, tree diameter diversity was also found to correlate with plant richness (Ferris & Humphrey, 1999). Humphrey (2002) found that bryophyte richness in spruce and pine plantations was positively correlated with large diameter (> 20 cm), well-decayed logs and stumps. Pitkänen (1997; 1998) classified Scandinavian boreal stands according to their stand structure in order to determine which variables best describe vegetation diversity. Pitkänen found that tree species composition, number of canopy layers and mean diameter of trees influence plant diversity. The application of these structure-based indicators, however, has generally been neglected.

4.2 METHODS

4.2.1 Fieldwork methods

The majority of sites were inventoried between June and the end of August 2001. Age class 1 stands were surveyed during the summer of 2002. Vegetation surveys were carried out at all sites listed in Section 3.3.2 with the exception of CONA, a Sitka spruce stand that was meant to act as a control for SUNSS. This site was not an adequate match for SUNSS and therefore was not surveyed by the vegetation team. An alternative site could not be located. Three 100 m^2 quadrats were inventoried at each study site, for a total of 165 quadrats. The location of each quadrat was recorded using a Global Positioning System (GPS). The quadrats were spaced at least 50 m from the edge of the forest compartment and 50 m apart; all were located adjacent to invertebrate study areas. Floristic, structural, environmental (c.f. Section 3.2.1.2) and disturbance data were recorded in the 100 m^2 quadrats.

4.2.1.1 Floristic variables

Plant species were identified, and their cover was estimated. Species coverage was estimated to the nearest 5%, or as 1, 2 or 3% if the cover was less than 5%. If only one individual of a particular species was observed, then it was allocated 0.25%. If there was more than one individual but their coverage was less than 1%, then that species was allocated 0.5%. The plant species observed in a 4 m^2 quadrat, located within the 100 m^2, were also identified. Samples of any unidentified species were collected and stored for future identification.

4.2.1.2 Structural variables

Average height and cover of vegetation layers/growth habit groupings were estimated for the following categories:

- Canopy layer: The uppermost tree stratum; planted trees always accounted for the greatest proportion of this layer. This layer was defined by relative rather than absolute height, so that planted trees were included in this layer regardless of structural stage.
- Large shrub layer: Woody vegetation below the upper tree stratum and in the 2 - 5 m height range. Note that the potential difficulty of a large shrub stratum (e.g. *Ulex europaeus*, gorse) exceeding the height of the upper tree stratum (e.g. pre-thicket Sitka spruce) did not arise in this study.

- Subshrub layer: Woody vegetation under 2 m tall. Such vegetation includes tree seedlings and small shrubs such as *Calluna vulgaris* (heather) and *Vaccinium myrtillus*. *Rubus fruticosus* agg. (bramble) and *Rosa* species (rose spp.) are not included, nor are climbers such as *Hedera helix*.
- Bramble layer: Vegetation with a bramble growth habit, including *Rubus* and *Rosa* species.
- Graminoid layer: Grasses, rushes and sedges.
- Forb layer: Vascular herbs, not including graminoids, climbers, woody species or ferns.
- Bryophyte layer: Mosses and liverworts.

When vascular species (normally in the context of richness) are referred to in Sections 4.3, 4.4 and 4.5, it is all vascular species in the understorey vegetation (i.e. forbs, graminoids, brambles and shrubs) that are being referred to. Stand structural variables discussed in Section 3.3.4 (i.e. dbh, tree height and minimum spacing) are also referred to.

Deadwood present in the quadrat was assigned to the categories described in Table 14 and Table 15. The frequency of the different types of deadwood in the 100 m^2 quadrats was observed and the volume of deadwood within each category was calculated. The total volume of deadwood for each quadrat was also calculated. In addition, the cover of conifer needles and fine woody debris (FWD), including twigs and small branches less than 10 cm diameter, and cover of coarse woody debris (CWD), including branches and logs greater than 10 cm diameter, were recorded. The cover of dead deciduous leaves and herbaceous vegetation litter was also estimated. In addition, the percent cover of exposed mineral or organic soil was quantified.

4.2.1.3 *Disturbance variables*

At each 100 m^2 quadrat, grazing intensity was recorded based on presence of dung and evidence of trampling or damage to the vegetation. The impact of recreational use was also visually assessed (e.g. presence of pathways and/or rubbish).

Table 14. Classification of deadwood types.

Category	Deadwood
1	Rot holes in standing living trees
2	Dead branches in standing, living trees
3	Dead standing trees, intact
4	Dead standing tree, wind damaged, trunk snapped
5	Dead standing tree, wind damaged-wholly or partially rooted (but not downed)
6	Fallen deadwood (trunks and large branches mid-diameter > 7 cm)
7	Fallen deadwood (small branches and twigs, mid-diameter < 7 cm)
8	Stumps

Table 15. Deadwood decay classes applied to each deadwood type.

Category	State of decay
1	Sound (intact with very little evidence of decay)
2	Moderately decayed (crumbling in the hand), bark coming off
3	At an advanced stage of decay (moist, rotten and sometimes hollow), no bark

4.2.2 Species identification

Plant species nomenclature follows Stace (1997) for vascular plants, Smith (1978) for mosses and Smith (1990) for liverworts. Refer to Appendix 1 for a list of all plant species inventoried. No red-data (Curtis & McGough, 1988) or protected vascular plant species listed in the Flora (Protection) Order, 1999, were found at any of the sites. In addition no rare (Blockeel & Long, 1998) or protected bryophytes were inventoried.

4.2.3 Data organisation

4.2.3.1 Removal of planted species

Planted trees were not included when assessing the diversity of the forest stands (e.g. Sitka spruce, ash, Douglas fir and beech). However, natural regeneration from planted trees was included.

4.2.3.2 Designation of Unidentified Species

Those species identified only to generic level were handled so that their inclusion did not cause an overestimation of species richness. Inability to identify to species level was mostly due to lack of fruiting bodies and flowers. Generally species identified only to generic level accounted for a small proportion of plot abundance (i.e. only 1 individual). The following protocol was followed when considering these cases:

- If no other species belonging to the genera of an unidentified specimen were present within the quadrat, then the specimen was included and identified only to genus level.
- If other species belonging to the genera of an unidentified specimen were present within the quadrat, then the data were amalgamated. The entry for the unidentified species was excluded from the database, and the abundance of the most abundant species was increased accordingly. Therefore, although the estimate of species richness is more conservative, the estimate for generic abundance in the quadrat is not compromised.

4.2.3.3 Species classification

Vascular plants were classified according to native/alien status, moisture and pH requirements, affinity to woodland habitats and ecological strategy. Plants were classified as aliens if, according to Preston (2002), they were introduced to Ireland after 1500 AD (i.e. "neophytes"). The moisture, pH range and woodland affinity categories are summarised in Table 16. The classifications of species were determined using habitat and autecological information contained in Webb *et al.* (1996), Preston *et al.* (2002), Grime *et al.* (1988), Peat *et al.* (2003), Jermy *et al.* (1982) and Hubbard (1984), as well as the judgement of the authors. Ecological strategy was determined using the C-S-R model of Grime *et al.* (1988). In the C-S-R model, species are classified as competitors, stress-tolerators, ruderals or intermediates between any two or all three of these categories. Competitors and stress-tolerators both exploit habitats where disturbance is rare. However, competitors are found in habitats where resources are abundant, whilst stress-tolerators are associated with habitats where resources are scarce or conditions harsh. Ruderals are characteristically found in habitats where disturbance is common and resources plentiful, they are often weeds which have high demands for nutrients and/or intolerant of competition (Grime *et al.*, 1988). Classification is based on such life-history characteristics as mode of reproduction, nutrient requirements and size. For species not covered in Grime *et al.* (1988), plants were assigned categories using the same sources as were used in identifying species' moisture and pH requirements and woodland affinities.

Bryophytes were also classified according to their moisture requirements, favoured substrate pH and affinity to the woodland environment. Details on habitat preferences were gathered from various moss and liverwort texts (Watson, 1981; Smith, 1990; Hill *et al.*, 1991; Hill *et al.*, 1992; Hill *et al.*, 1994; Phillips, 1994; Paton, 1999; Crawford, 2002).

Table 16. Ecological classification of vascular plants and bryophytes.

Category	Classification	Definition
Moisture	Dry	Prefers dry soils/microhabitats
	Mesic	Prefers mesic soils/microhabitats
	Damp	Prefers damp soils/microhabitats
	Wet	Prefers soils/microhabitats that are waterlogged for large parts of the year
pH	Acidophilic	Prefers acidic conditions (pH < 5)
	Neutral	Prefers intermediate conditions or is not normally restricted by pH
	Basophilic	Prefers base-rich conditions (pH > 6.5)
Woodland affinity	Low	Generally not found in woodlands
	Moderate	Frequently occurring both in woodlands and in unwooded habitats
	High	Typical woodland species

4.2.4 Data analysis

4.2.4.1 Measuring biodiversity

As the 'common currency' of biodiversity measurement, species richness was examined. However, since species richness can mask patterns of species dominance or evenness (Magurran, 1988), diversity indices were also employed. Large differences in diversity will be detected by any index; therefore, it was necessary to use an index that adequately assesses subtle differences in richness and relative species abundance between sites. According to Magurran (1988) indices weighted towards species richness are more useful for detecting differences between sites than indices that emphasise dominance or evenness. However, there is no general consensus on which index is the best to use. The Shannon index (which is biased towards species richness) has been utilised in the major studies relating to Project 3.1.2. (in particular Ferris *et al*. (2000a)). Therefore, for comparison purposes, the Shannon index was employed in 3.1.2 vegetation data analyses. The Simpson's index (which is biased towards evenness) has generally been advocated as a suitable alternative to the Shannon index. Therefore, a comparison of the results generated from both indices provided a more informative study of diversity. Table 17 provides a comparison of the properties of the Shannon and Simpson's indices.

The Shannon index (H) is defined as follows (Shannon & Weaver, 1949):

$$H = -\sum_{i}^{S} p_i \log p_i \tag{1}$$

where s is species richness and p_i is the relative abundance of species i in the sample.

The Simpson's index (D) is defined as follows (Simpson, 1949):

$$D = 1 - \sum_{i}^{S} p_i^2 \tag{2}$$

where notation is as for the Shannon-Weaver index in equation 1.

Table 17. Properties of the Shannon and Simpson's diversity indices (Magurran, 1988).

Diversity Index	Properties
Shannon	Biased towards richness Sensitive to rare species Widely used in related studies (e.g. Ferris (2000a)) Attracted much criticism (e.g. "insensitive measure of species abundance distribution"; "no direct biological interpretation")
Simpson's	Biased towards evenness More responsive to dominant cover types Moderate usage in related studies

Analyses have focused on total species (all species recorded within the 100 m² quadrats), vascular plant species and bryophyte species richness and diversity.

4.2.4.2 Data analysis methods

The 'average' vegetation, structural and environmental data for each forest stand were used in preliminary NMS ordination analyses. Whilst less sensitive to heterogeneity in richness and ecological processes than the 100 m² quadrat, this larger analytical scale provides a general overview of associations between forest vegetation communities and any underlying causal factors (e.g. forest type, soil fertility and management history). The stand-scale statistics were calculated using the data from the three 100 m² quadrats to derive an overall mean. Averaging the vegetation data, rather than using the sum abundance for each species, ensures that the vegetation ordination of the study sites is influenced more by species that are present throughout the stand than those with a heterogeneous distribution. Separate NMS ordinations of the Sitka spruce and ash 100 m² quadrat data were also undertaken. Cluster and indicator species analyses were used to classify and define stands and quadrats with similar species composition. The cluster analysis approach employed was beta-flexible clustering with β set at –0.25. Visual inspection of the cluster analysis dendrogram and indicator species analysis (Dufrêne & Legendre, 1997) highlighted the most sensible cluster analysis groups. Indicator species analysis was used to identify species characteristic of the stand or quadrat clusters.

A two-level nested design ANOVA (with stand structural type as the nested factor within the main factor, canopy species) was used to identify differences in species richness between the Sitka spruce and ash stands. In addition, paired sample t-tests (or the non-parametric equivalent, Wilcoxon's signed rank test) were used when comparing the Sitka spruce and ash components of the mixed stands. The similarity in species composition between the Sitka spruce and ash components of the mixed stands was quantified using Sørensen's similarity coefficient (Sørensen, 1948). One-way ANOVA (or the non-parametric equivalent, Kruskal-Wallis test), with Tukey's HSD (or Tamhane's test for unequal variances) as the post-hoc multiple comparison test, was used to compare species richness between stand structural types and environmental groups (e.g. soil type). In order to assess the relationship between species richness and structural or environmental variables, regression and correlation analyses were employed. When several tests of significance are carried out simultaneously, the probability of a type I error becomes larger than the critical p-value. Between 20 and 30 correlations were carried out for each structural group, therefore adjusted probability values were computed according to the method proposed by Hochberg (1988). Partial correlation analyses were undertaken when assessing the relationship between richness and structural variables. In these analyses, soil fertility was the variable controlled for.

Data at the 100 m² quadrat scale, rather than the average stand data, were used when determining species as indicators of plant richness. This is due to the variation in vegetation richness between quadrats at a single site. If the average floristic data were used to derive indicators, then the selected species may be present only in the more species-impoverished quadrats. In order to identify species indicators of diversity, two main techniques were utilised. Differences in richness between and within the cluster analysis groups of the 100 m^2 quadrats were identified and the indicator species were derived. In the second approach, the NMS ordination diagram was rotated so that the relationship between species richness and axis 1 was maximised. The species that had the highest correlation coefficients with axis 1 were then investigated further as possible indicators of vegetation diversity. Statistical analyses were conducted using PC-Ord (McCune & Mefford, 1997) and SPSS (2001).

4.3 VEGETATION RESULTS

4.3.1 Ordination of forest stands

The NMS ordination of the forest stands (Figure 15) highlights the differences in vegetation composition between the early forest stages and the established stands. The stands were divided into eight main clusters (c.f. Section 4.2.4.2). All pre-thicket stands are grouped together in either cluster A or B. There are also some pole and closed-maturing ash stands located within cluster A; namely COOAA, COOL, COMMA and INCH. Likewise, CUMMS and CLYD, which are thicket Sitka spruce stands, are located within cluster B. Grassland species are the principal indicators of sites in cluster A (e.g. *Festuca rubra* (red fescue) and *Agrostis stolonifera* (creeping bent)) and heathland species (e.g. *Calluna vulgaris* and *Molinia caerula* (purple moor-grass)) are indicative of forest stands clustered within group B, where the forests are located on more organic soils. Table 18 provides an overview of the indicator species for the site clusters, together with their indicator value and significance according to the Monte Carlo test. To take an example, HIGG, a five-year old ash stand located in Co. Westmeath, is grouped within cluster A and, as shown in Figure 16a, *Holcus lanatus* (Yorkshire fog) is an important component of the ground flora. In comparison, Figure 16b highlights the abundance of wet heath species, especially *Molinia caerulea*, at BEND, a Sitka spruce stand located on organic soils in Co. Clare.

Cluster C is composed of semi-mature and mature ash stands. All are located adjacent to areas of semi-natural woodland. The species indicators for cluster C include the moss *Thamnobryum alopecurum* and also *Polystichum setiferum* (soft shield fern), *Primula vulgaris* (primrose) and *Hedera helix* (ivy). Clusters D, E and F are composed entirely of Sitka spruce stands, and represent different stages of the stand cycle. Stands within clusters D and E have on average, a higher canopy cover per 100 m^2 quadrat than the other clusters (Table 19). Whilst the stands within cluster D are in age class 2, and have not been thinned, those in cluster E are older (age classes 3 and 4) and the majority (with the exception of SAGG) have been thinned. However, the high canopy cover of the stands in cluster E suggests that the forests were inventoried primarily in unthinned areas. Vegetation richness is particularly poor in stands within cluster E (Table 19). Cluster F is composed of Sitka spruce stands that have, in general, a more open canopy and where bryophyte species are the principal significant indicators; they include *Dicranum scoparium*, *Plagiothecium undulatum*, *Campylopus paradoxus* and *Hypnum jutlandicum*. The photographs in Figure 17 highlight the difference in ground flora abundance beneath Sitka spruce crops at varying stages of the management cycle. It is evident that soil organic content and moisture status are also affecting the position of the more established forest stands in the ordination space. Figure 18 highlights the gradient in drainage and organic content between those stands grouped within clusters A and B. However, it is also apparent that BOKY, DERR, FURY, MOAN, MSOP and SAGG where there are organic soils, are grouped together in the point cloud.

Table 18. Indicator species for the Sitka spruce and ash stand clusters. The five species with the highest indication values are presented for each cluster; those values with an indication value less than 25% are excluded since Dufrêne and Legendre (1997) considered the best species indicators to be those with an indication value of more than 25%.

Cluster	Indicator species	n	Indicator value (%)	p-value
A	*Festuca rubra*	19	84	0.001**
	Agrostis stolonifera		64	0.001**
	Juncus effusus		62	0.001**
	Dactylis glomerata		61	0.004**
	Holcus lanatus		59	0.001**
B	*Calluna vulgaris*	6	98	0.001**
	Molinia caerula		98	0.001**
	Potentilla erecta		85	0.001**
	Salix cinerea		75	0.001**
	Erica tetralix		67	0.001**
C	*Thamnobryum alopecurum*	4	100	0.001**
	Polystichum setiferum		88	0.001**
	Primula vulgaris		85	0.001**
	Hedera helix		84	0.002**
	Geranium robertianum		66	0.007**
D	*Rhizomnium punctatum*	5	40	0.023*
E	*Cephalozia bicuspidata*	5	31	0.049*
F	*Dicranum scoparium*	6	93	0.001**
	Plagiothecium undulatum		81	0.003**
	Campylopus paradoxus		80	0.001**
	Hypnum jutlandicum		74	0.001**
	Polytrichum formosum		45	0.006**
G	*Rubus fruticosus agg.*	6	70	0.001**
	Pteridium aquilinum		58	0.008**
	Dryopteris affinis		48	0.037*
	Plagiothecium denticulatum		41	0.012*
	Atrichum undulatum		36	0.110
H	*Rhytidiadelphus triquetrus*	4	92	0.001**
	Athyrium filix-femina		82	0.001**
	Poa trivialis		79	0.002**
	Thuidium tamariscinum		65	0.002**
	Epilobium montanum		56	0.003**

Note. * indicates that the species indicator is significant at the $p < 0.05$ level and ** indicates significance at the $p < 0.01$ level according to the Monte Carlo test of significance.

RATHA is the only mixed ash stand of those in age class 4 to be grouped with the pure broadleaf forests in cluster C (Figure 15). Cluster G contains both Sitka spruce and ash compartments from the mixed stands where *Rubus fruticosus* agg. is the dominant plant species (Table 18). The flora in the ash compartment at SUNS is quite different from the flora in other ash stands inventoried. Although *Rubus fruticosus* agg. remains an important species at SUNSA, the entire assemblage of species is more characteristic of a Sitka spruce stand, with species including *Hypnum mammillatum*, *Dryopteris dilatata* and *Lophocolea bidentata*. Beech is an important canopy species at SUNSA, and understorey vegetation cover is low in comparison to other ash stands (Figure 19). Cluster H also contains both conifer and broadleaf stands. Although woodland species, such as *Hedera helix*, are significant components of the ground flora at DEME, the abundance of grassland species including *Poa trivialis* (rough meadow-grass) and *Agrostis stolonifera* separate DEME in the ordination space from the other pure ash forests. The indicator species for the stands in cluster H include the mosses *Rhytidiadelphus triquetrus* and *Thuidium tamariscinum* and also

Athyrium filix-femina (lady fern) and *Poa trivialis*. These species all have a moderate to high affinity for woodland habitats.

Table 19. Mean (± standard error) canopy cover and total species richness of stands within the different cluster analysis groups. There is no significant difference between clusters if designated with the same letter $^{(a, b \text{ or } c)}$.

Cluster	n	Canopy cover	Total species richness
A	19	28.9 ± 5.3 ^{a}	38.8 ± 3.4 $^{a, b}$
B	6	38.6 ± 10.6 $^{a, b}$	52.2 ± 4.6 $^{b, c}$
C	4	73.8 ± 3.1 $^{b, c}$	40.0 ± 1.8 $^{a, b, c}$
D	5	89.7 ± 1.5 ^{c}	33.0 ± 3.9 $^{a, b}$
E	5	84.7 ± 3.6 ^{c}	19.6 ± 2.4 ^{a}
F	6	67.2 ± 4.0 $^{b, c}$	43.8 ± 5.1 $^{a, b, c}$
G	6	60.6 ± 6.7 $^{b, c}$	44.2 ± 3.9 $^{a, b, c}$
H	4	63.8 ± 3.6 $^{b, c}$	63.8 ± 11.0 ^{c}

Table 20. Correlations between axes from the NMS stand ordination and structural and environmental variables. Pearson's correlation coefficient (r) is displayed.

Variable	Axis 1	Axis 2
	Pearson's r	Pearson's r
Elevation	-0.56**	-0.07
Canopy cover	-0.73**	-0.49**
Tree spacing	-0.01	-0.54**
Dbh	-0.56**	-0.72**
pH	0.67**	0.10
Exchangeable Ca	0.55**	0.15
Exchangeable K	0.56**	0.19

Note. ** indicates that the correlation coefficient is significant at the $p < 0.01$ level.

The ordination of the forest stands highlights the problems of amalgamating discrete quadrat data. Heterogeneity in vegetation composition between quadrats within a single stand means that such sites do not fit adequately into any cluster grouping. For example, whilst one of the 100 m^2 quadrats at CLYD was dominated by *Molinia caerula*, an indicator for cluster B, this species was absent at the other two quadrats. In these quadrats, ground flora cover was much lower and species composition was more comparable to the more established Sitka spruce stands. Correlations between the NMS ordination axes and various structural and environmental variables are highlighted in Table 20. These indicate that canopy cover, dbh and elevation have a negative association with axis 1, whilst pH and exchangeable Ca and K have a positive correlation. Canopy cover, tree spacing and also dbh have a negative relationship with axis 2.

4.3.2 Measuring vegetation diversity

4.3.2.1 Scale of analysis

Vegetation richness in the Sitka spruce and ash stands increases with sampling size. Whilst a total of 216 species were observed in the 4 m^2 quadrats (157 vascular plants and 59 bryophytes), 329 species were recorded in the 100 m^2 quadrats (236 vascular plants and 93 bryophytes). In general, those sites where a greater number of species were observed at the 4 m^2 scale are also more species-rich at the 100 m^2 scale (Figure 20). The equation shown in Figure 20 may be used to predict species richness of the 100 m^2 quadrat when surveying at the 4 m^2 scale. Although both quadrat sizes are able to detect species-rich stands, the 100 m^2 quadrat provides a better representation of the plant communities in the Sitka spruce and ash stands because it captures a higher number of species.

4.3.2.2 *Comparison of diversity indices*

There are positive relationships between richness and the Shannon and Simpson's indices (Figure 21a and b). However, although the correlations are statistically significant, there is considerable error associated with the scatterplots. The diversity indices are more closely correlated with each other than with species richness values (Figure 21c). The Shannon and Simpson's indices are positively correlated with one another, this correlation being strongest for the more diverse sites. The relationship between bryophyte abundance and bryophyte richness may explain some divergence between richness and the diversity indices. As illustrated in Figure 22, bryophyte cover, within the 100 m^2 quadrats, is not a good predictor of bryophyte richness. Likewise, the most abundant vascular plant communities are not necessarily the most species-rich. For example, whilst only five vascular species were observed in quadrat LACKF3 where vascular species covered approximately 105%, 31 species were found in quadrat MOANF3 where vascular species covered only 8%.

4.3.3 Trends in species richness and diversity

4.3.3.1 *Comparison of species-rich and poor stands*

UNIO, a mature Sitka spruce forest in Co. Sligo, is the most floristically rich forest. A total of 51.0 ($n = 3$, $se = 0.0$) species were recorded in each 100 m^2 quadrat and 88 species were observed in total at this forest (Figure 23). The remaining study sites all had less than 70 species in total, with the mean number of species in each 100 m^2 quadrat being 23.4 ($n = 55$, $se = 0.8$). The most species-poor forest inventoried was COON, a closed-maturing Sitka spruce forest located in Co. Tipperary. On average, only 5.7 ($n = 3$, $se = 4.7$) species were found in the 100 m^2 quadrats at COON and only 11 species were observed in total. Of the 14 forests that were found to have less than 30 species in total, ten were Sitka spruce plantations. GLYN was ranked to be the most diverse stand according to both the Shannon (mean = 2.9, $n = 3$, $se = 0.1$) and Simpson's (mean = 0.9, $n = 3$, $se = 0.02$) indices.

4.3.3.2 *Comparison of Sitka spruce and ash stands*

The majority of vascular plants and bryophytes are found in both Sitka spruce and ash forests (Figure 24). However, Sitka spruce stands provide an important habitat for bryophyte diversity, 37% of all bryophytes observed were found only in the conifer forests (Figure 24b). Tree species does not have an effect on total species richness ($F_{1, 152} = 1.95$, $p = 0.17$), when variation due to structural stage is removed from the analysis (Section 4.2.4.2). However, further analyses of the composition of the vegetation communities indicate that both vascular plant ($F_{1, 152} = 17.97$, $p < 0.001$) and bryophyte ($F_{1, 152} = 18.90$, $p < 0.001$) richness are significantly different between the Sitka spruce and ash stands. Whilst the ash stands support higher numbers of vascular species, the Sitka spruce stands support greater bryophyte species richness. Vascular plant richness is also more variable between quadrats inventoried in the Sitka spruce stands than between those in the ash (Table 21). In forests beyond the pre-thicket stage, the species richness of typical woodland vascular plants was significantly greater in ash forests (5.2 ± 0.7) than in Sitka spruce forests (3.6 ± 0.4) ($F_{1, 97} = 5.68$, $p = 0.02$). There was no significant difference in species richness of woodland bryophytes ($F_{1, 97} = 1.03$, $p = 0.31$). Variation due to structural stage was removed in these analyses.

4.3.3.3 *Mixed forests*

Within all structural and age-range groups, the Sitka spruce and ash compartments of the mixed stands do not differ in terms of average species richness per 100 m^2 quadrat or total species richness. In addition, the species richness of the Sitka spruce component of the mixed forests does not significantly differ from the species richness of the pure Sitka spruce matching stands. In the mixed stands, there were many species that occurred in either the spruce component or the ash component, but not both (Table 22). Particularly high numbers of vascular plant species were observed in the ash compartments DOOGA and GFINA (in age class 2) that were not recorded in the Sitka spruce compartments. At these sites 33 and 44 vascular species, respectively, were observed only in the ash compartment. Within each age class, however, the numbers of species confined to either the Sitka spruce or ash compartment do not significantly differ.

The plant community compositions of the ash and Sitka spruce components were more similar in age class 1 forests than in age class 2 forests. Sørensen's similarity coefficient in age class 1 forests (mean = 0.40, n = 4, se = 0.017) was significantly higher than that in age class 2 (mean = 0.30, n = 4, se = 0.013) (H = 8.0, df = 2, p = 0.018), with Sørensen's similarity coefficient measured as 0.33 (n = 4, se = 0.014) for those stands in age class 4. In age class 4 mixed sites, Sitka spruce stands generally had much higher cover of the moss *Thuidium tamariscinum* and greater abundance of such acidophilic species as *Dryopteris dilatata, Hypnum jutlandicum, Carex pilulifera, Luzula multiflora, L. sylvatica, Ilex aquifolium, Vaccinium myrtillus, Oxalis acetosella* and *Galium saxatile*, many of which did not occur in the ash component. Ash stands generally had much higher cover of ivy, *Hedera helix*, a greater diversity of grass species, such as *Holcus lanatus* and *Poa trivialis,* and greater abundance of a wide range of species, including *Pteridium aquilinum, Galium aparine, Ranunculus repens, Dryopteris affinis, Hyacinthoides non-scripta* and *Veronica chamaedrys*, some of which were not found in the spruce component.

There were also differences in structure between the ash and Sitka spruce components of the mixed stands. In age class 4 forests, bryophyte cover averaged 42.0% in the spruce stands and 27.7% in the ash stands. In age class 2 forests, mean graminoid cover was 58.0%under an ash canopy and 18.2% under spruce, and mean forb cover was 10.1% under ash and 1.4% under spruce. None of these differences, however, were statistically significant, probably due to small sample size (n = 4).

Table 21. Mean (± standard error) total, vascular plant and bryophyte richness of the 100 m^2 quadrats in the Sitka spruce and ash forests. Variability in species richness between quadrats (*CV* = coefficient of variation %) is also indicated.

Canopy species	n	Total species richness	CV	Vascular plant richness	CV	Bryophyte richness	CV
Sitka spruce	93	22.3 ± 1.2	51.1	13.0 ± 1.0	74.7	9.3 ± 0.6	58.2
Ash	72	24.9 ± 1.0	33.4	19.0 ± 0.9	37.4	5.9 ± 0.5	66.3

Table 22. Mean (± standard error) number of vascular plant and bryophyte species observed only in the Sitka spruce or ash compartment of the mixed stands.

Age class	n	Vascular plant		Bryophytes	
		Sitka spruce	Ash	Sitka spruce	Ash
1	4	12.8 ± 4.5	11.0 ± 4.2	3.8 ± 2.1	3.3 ± 1.6
2	4	9.8 ± 3.6	27.3 ± 7.3	8.0 ± 2.7	5.3 ± 0.5
4	4	19.3 ± 4.5	13.5 ± 3.9	7.8 ± 1.4	5.5 ± 2.0

4.3.4 Structural groups

4.3.4.1 Sitka spruce

Through the Sitka spruce structural cycle, total vegetation richness is highest in the pre-thicket and mature forests and lowest in the closed-maturing. Vascular plant richness exhibits a similar trend (Figure 25a), whilst bryophyte richness increases through the structural cycle (Figure 25b). Therefore, on average, the mature Sitka spruce stands support the highest number of vascular plant and bryophyte species, with an average of 33.5 (n = 18, se = 2.6) species per 100 m^2. Vascular plant richness is significantly greater in the pre-thicket and mature stages than in the thicket, closed-maturing and reopening stands ($F_{4, 88} = 24.4$, $p < 0.001$); Shannon and Simpson's diversity indices detect similar trends. Bryophyte richness is significantly lower in the pre-thicket stands than in all other stages ($F_{4, 88} = 11.0$, $p < 0.001$). The difference in bryophyte diversity between structural groups was found to be near-significant (Shannon: H = 9.3, df = 4, p = 0.06; Simpson's: H = 8.4, df = 4, p = 0.08). The abundance of vascular plants is highest at the pre-thicket stage with, on average, 85.6% (n = 25, se = 2.3) graminoid cover and 12.1% (n = 25, se = 2.7) forb cover per 100 m^2 quadrat. In the pre-thicket stands, bryophytes account for only 4.4% (n = 25, se = 2.0) coverage of the quadrat, whilst in the mature stands, they cover 55.5% (n = 18, se = 7.3).

At the pre-thicket stage, vascular species indicative of more open habitats are most abundant (Figure 26a). The number of vascular species that have a preference for woodland habitats increases through the Sitka spruce structural cycle. Although the closed-maturing and reopening stands have a lower number of woodland plants than the mature stands, woodland species account for a greater proportion of the vascular community in these forests (Figure 26b). Similar trends were found for the bryophyte flora; whilst species that have a moderate affinity for woodland habitats are present within all structural groups, bryophytes characteristic of woodland habitats increase through the structural cycle. Deadwood volume is highest in the reopening (mean = 2.3 m^3, n = 12, se = 1.2) and mature (mean = 2.3 m^3, n = 18, se = 1.0) stages of the Sitka spruce structural cycle (H = 53.8, df = 4, $p < 0.001$).

Stress-tolerant and competitive vascular plant species are important components of the ground flora throughout the structural cycle in the Sitka spruce forest, whilst ruderal species become less important as the structural cycle progresses until the mature stage is reached (Table 23). Vascular plants and bryophytes that have a preference for a mesic substrate are the most abundant species at all stages of the structural cycle, whist vascular species that prefer damp conditions are more important components at the pre-thicket and thicket stages (Table 23). Acidophilic species are also important components of the ground flora. Vascular species that prefer acidic or neutral (or are broadly tolerant) conditions are the most dominant vascular plants at all structural stages, and acidophilic bryophytes become increasingly abundant as the structural cycle progresses (Table 23).

Table 23. Composition of the ground flora at the different structural stages of the Sitka spruce cycle. The data are presented as the mean % (± standard error) of the total number of vascular species or bryophytes. There is no significant difference between structural stages if designated with the same letter $^{(a, b \text{ or } c)}$.

Sitka spruce structural stage	n	Vascular plants with ruderal life strategy	Vascular plants requiring damp substrate	Bryophytes requiring acidic substrate	Bryophytes requiring basic substrate
Pre-thicket	25	50.6 ± 3.4^{a}	43.1 ± 3.2^{a}	31.2 ± 6.6^{a}	33.6 ± 7.2^{a}
Thicket	17	$39.2 \pm 5.0^{a, b}$	$34.1 \pm 3.5^{a, b}$	41.6 ± 3.8^{a}	$16.1 \pm 2.5^{a, b}$
Closed-maturing	21	12.1 ± 4.5^{c}	11.1 ± 3.7^{c}	$48.4 \pm 4.4^{a, b}$	5.3 ± 2.0^{c}
Reopening	12	8.4 ± 4.3^{c}	15.5 ± 4.3^{c}	65.2 ± 4.3^{b}	$6.2 \pm 2.3^{b, c}$
Mature	18	31.6 ± 2.3^{b}	$21.1 \pm 2.0^{b, c}$	57.9 ± 3.6^{b}	$15.8 \pm 3.0^{a, c}$

4.3.4.2 Ash

Total vegetation richness does not differ significantly between the different structural stages of the ash cycle ($F_{4, 64} = 1.2$, $p = 0.31$); this is because vascular plant richness in the ash stands decreases through the structural cycle whilst the number of bryophytes increases (Figure 27). The pre-thicket stands have a significantly higher number of vascular plant species than the semi-mature and mature ash forests ($F_{4, 64} = 4.5$, $p = 0.003$), and the pre-thicket and pole stands have a lower number of bryophytes than the more established stages ($F_{4, 64} = 11.9$, $p < 0.001$). The diversity indices indicate that the pre-thicket stands have a significantly more diverse (Shannon: $F_{4, 64} = 7.2$, $p < 0.001$; Simpson's: $F_{4, 64} = 7.2$, $p < 0.001$) vascular plant community than the semi-mature stands. Bryophyte diversity, according to the Shannon and Simpson's indices is significantly greater in the closed-maturing and semi-mature stands than in the pre-thicket and pole stages (Shannon: $F_{4, 64} = 4.9$, $p = 0.002$; Simpson's: $F_{4, 64} = 3.4$, $p = 0.01$). The cover of bryophytes increases through the ash structural cycle. At the pre-thicket stage bryophytes cover only 1.9% (n = 32, se = 0.5) of the 100 m^2 quadrat and by the mature stage they cover 55.0% (n = 9, se = 7.5). As with the Sitka spruce stands, graminoid abundance decreases with forest maturity.

As was found for the Sitka spruce stands, the number of woodland species, both vascular plants and bryophytes, increases through the ash structural cycle. Vascular species that have a high affinity for woodland habitats account for a significantly greater proportion of the vascular plant flora in the semi-mature and mature stands than in all other stages (Table 24). Competitive and stress-tolerant strategies are the most characteristic life strategies of vascular species in the ash forests. The proportion of ruderal species is significantly lower in the semi-mature and mature ash stands than in the other stages (Table 24). Vascular plants and bryophytes that prefer mesic conditions are significant components of the vegetation communities; the number of plants that prefer damp habitats decrease as the structural cycle progresses. Acidophilic species are less important in the ash stands than in the Sitka spruce. Vascular plant species that prefer a neutral substrate (or are broadly tolerant) form the largest proportion of the vascular plant community, and bryophytes that prefer base-rich conditions are important throughout the structural cycle, particularly in the mature forests (Table 24).

Table 24. Composition of the ground flora at the different structural stages of the ash cycle. The data are presented as the mean % (± standard error) of the total number of vascular species or bryophytes. There is no significant difference between structural stages if designated with the same letter $^{(a, b \text{ or } c)}$.

Ash structural stage	n	Vascular plants with high affinity for woodland	Vascular plants with ruderal life strategy	Bryophytes requiring acidic substrate	Bryophytes requiring basic substrate
Pre-thicket	32	1.9 ± 0.7 ^{a}	58.8 ± 2.4 ^{a}	17.4 ± 3.7 ^{a}	43.8 ± 6.3 ^{a}
Pole	7	4.9 ± 1.8 ^{a}	64.6 ± 5.2 ^{a}	20.8 ± 11.0 ^{a}	53.0 ± 13.1 ^{a}
Closed-maturing	12	14.6 ± 4.6 ^{a}	56.8 ± 4.7 ^{a}	34.9 ± 5.1 ^{a}	29.6 ± 3.4 ^{a}
Semi-mature	9	51.1 ± 7.4 ^{b}	17.2 ± 4.1 ^{b}	20.0 ± 6.8 ^{a}	44.9 ± 4.7 ^{a}
Mature	9	59.3 ± 4.1 ^{b}	32.1 ± 4.4 ^{b}	15.0 ± 5.1 ^{a}	57.9 ± 3.9 ^{a}

4.3.5 Diversity indicators across the structural cycle

4.3.5.1 Structural indicators

4.3.5.1.1 Sitka spruce

Results described in Section 4.3.4.1 indicate that the structural status of the Sitka spruce stand is an important influence on species richness. Indeed, canopy cover is a key factor that separates the Sitka spruce 100 m^2 quadrats in the ordination space (Figure 28). Linear regressions indicate that there is a negative association between canopy cover and total species richness (Figure 29a). Whilst vascular plant richness is greater beneath a more open Sitka spruce canopy, bryophyte richness appears to be suppressed in the most open stands (Figure 29b). If the pre-thicket stands are excluded, then Figure 30 illustrates that dbh and minimum distance between canopy trees both positively correlate with total species-richness, whilst the quantity of needles and FWD on the forest floor has a negative association with total species richness. The negative relationship between canopy cover and total vegetation richness is also more apparent if the pre-thicket stands are excluded (Figure 29a). 100 m^2 quadrats with more than 20% forb cover or 50% bryophyte cover have at least

25 species in total (Figure 31). However, quadrats with lower forb and bryophyte coverage may be as, or more, species-rich. The relationship between graminoid cover and total richness is a unimodal one (Figure 32). Graminoid dominance only appears to occur in the pre-thicket stands. Total richness exhibits a more asymptotic relationship with graminoid cover during the thicket to mature stages.

4.3.5.1.2 Ash

In contrast to the findings of the Sitka spruce analyses, there is no significant association between total species richness and stand structure in the ash forests. Canopy cover, tree height and in particular, dbh (Figure 33) are negatively correlated with vascular plant richness and positively correlated with bryophyte richness. However, if the pre-thicket and pole stands are excluded from the analyses, these relationships become non-significant.

4.3.5.2 Environmental and management indicators

4.3.5.2.1 Sitka spruce site fertility

Associations between soil type or fertility and vegetation richness are generally not evident in analyses that encompass the data from all Sitka spruce structural groups. Although lithosols support the most species-rich communities, UNIO and RATH, both in Co. Sligo were the only forests inventoried where lithosol is the primary soil type. The average soil fertility of the different Sitka spruce structural groups is described in Section 3.3.4.3.1. Soil pH, available P and exchangeable cations (Ca, Mg and K) are lower in the closed-maturing to mature stages. This decrease in soil fertility corresponds with an increase in acidophilic species and a decline in the number of ruderal vascular plants, as described in Section 4.3.4.1 and Table 23. Application of rock phosphate as a fertiliser does not account for the significantly higher number of ruderals at the pre-thicket and thicket stages. In fact, ruderal species account for a significantly higher proportion of the vascular plant flora in unfertilised sites than in fertilised sites ($t = 3.3$, $n = 33$, $p = 0.002$). In sites where fertilisers have been applied stress-tolerant species account for a significantly higher proportion of vascular plants than in stands where fertilisers have not been applied ($t = -5.7$, $n = 33$, $p < 0.001$). This is because phosphate fertilisers have been applied primarily to forests located on nutrient-poor soils. As in the Sitka spruce stands, there are no strong associations between soil fertility and species richness in the ash stands if data from all quadrats are analysed. Again, varying structural conditions may explain the lack of significant relationships. Of note is the higher pH in the ash forests than in the Sitka spruce stands. In the Sitka spruce stands, pH ranges from 4 to 5 in the closed maturing to mature stages; however at all stages in the ash forests, pH is between 5 and 6.

4.3.5.2.2 Forest age

Species richness of woodland vascular plants at the site level increased with forest age ($r^2 = 0.53$, $n = 43$, $p < 0.0001$). Woodland bryophyte species richness also increased with forest age, but the rate of increase declined in older forests. When forest age was log-transformed, a significant linear relationship was observed ($r^2 = 0.74$, $n = 43$, $p < 0.0001$).

4.3.5.2.3 Proximity to old woodland

Regression analysis showed that the species richness of vascular plants with high affinity for woodland was negatively related to the distance (log-transformed) from site to the nearest woodland or scrub shown on third edition six-inch OS maps dating from the early 20th century. This relationship was quite strong ($r^2 = 0.73$, $n = 29$, $p < 0.0001$) (Figure 34a). Both Sitka spruce and ash sites were included in the analysis; in mixed sites, the component with the highest species richness was used rather than species richness from all six plots to eliminate any species-area effect. Pre-thicket sites were not included. Species richness of woodland bryophytes showed a similar but weaker relationship ($r^2 = 0.30$, n = 29, p = 0.002). Forest age and distance to woodland were negatively correlated, however, (r = -0.65, p < 0.0001). When partial correlation was carried out to control for the effect of forest age, the relationship between woodland vascular plant species richness and distance to woodland remained significant but weaker ($r^2 = 0.56$, p < 0.0001), but the relationship between bryophyte species richness and distance became non-significant ($r^2 = 0.03$, p = 0.36).

The area (log-transformed) of old woodland or scrub within 1 km of a site was positively related to woodland vascular plant species richness ($r^2 = 0.72$, n = 29, p < 0.0001) (Figure 34b) and woodland bryophytes ($r^2 = 0.26$, n = 29, p = 0.004). Area of old woodland was also correlated with forest age (r = 0.60, p < 0.0001). When forest age was controlled for, the relation ship between woodland vascular plant species richness and area of woodland remained significant but weaker ($r^2 = 0.57$, p < 0.0001), but the relationship between bryophyte species richness and area became non-significant ($r^2 = 0.03$, p = 0.40).

4.3.6 Diversity indicators within the structural groups

4.3.6.1 Pre-thicket forests

The abiotic environment influences the vegetation communities in the pre-thicket stands, with species composition and richness both related to soil type and fertility. Figure 35 illustrates the contrast between vegetation communities on brown earth and peat soils. Stands located on the more organic soils support communities dominated by heathland species including *Molinia caerulea* (INDVAL = 61%, n = 11, p < 0.001). In contrast, improved grassland species, including *Agrostis stolonifera* (INDVAL = 51%, n = 19, p = 0.003) and *Dactylis glomerata* (cocksfoot) (INDVAL = 68%, n = 19, p = 0.01) are important components of the ground flora on well-drained brown earth soils. Indicator species for vegetation communities on gley soils have low indicator value since these soils support species indicative of both grassland (e.g. KESH and MVAN) and heathland (e.g. BALE) communities. Indeed, when quadrats located on gley soils are excluded from the indicator species analysis, the indicator value and significance of indicators for communities on brown earth and peat soils increases. Brown earth soils have higher pH, available P and exchangeable Mg and Ca content than the other soil types, whilst the peat soils have a greater organic content (Table 25a).

Total species richness is significantly higher on peat and gley soils than on brown earths ($F_{2, 52} = 13.9$, p < 0.001) (Figure 36). Ruderal and competitive vascular plants account for a greater proportion of vascular plant richness on the brown earth soils than on the peat soils. Stress-tolerant species are more important components of the ground flora on the organic soils (Table 25b and as discussed in Section 4.3.5.2.1). Total species richness exhibits a significant negative association with pH, available P and exchangeable Ca (Table 26 and Figure 37). Figure 37 indicates that BRAC and HIGG have high species richness relative to their soil fertility; in particular the soils at these sites have very high exchangeable Ca content (Figure 37c). BRAC has been heavily limed and fertilised in the past and HIGG is on the side of an esker of limestone-rich gravel. Partial correlation analyses indicate that the relationships between structural characteristics of the pre-thicket stands and species richness may arise due to differences in the abiotic environment. For example, although graminoid cover is negatively correlated with bryophyte richness (r = -0.57, n = 51, p < 0.001), this relationship becomes much weaker when differences in soil fertility are controlled for (partial correlation coefficient = -0.30, n = 51 p = 0.048). The same is true of the relationship between bryophyte richness and bryophyte cover (partial correlation coefficient = 0.55, n = 51, p < 0.01), and of the relationship between bryophyte richness and subshrub cover (partial correlation coefficient = 0.35, n = 51, p = 0.019). These relationships are weaker than those derived from bivariate correlations, however they remain statistically significant.

Table 25. (a) Median pH (interquartile range) and mean (± standard error) organic content (loss on ignition %) and nutrient content (available P and exchangeable Ca and Mg in mg L^{-1}) of the different soil types beneath the pre-thicket forests. (b) Mean (± standard error) proportion (%) of vascular species with a competitor, stress-tolerant or ruderal life strategy. There is no significant difference between soil types if designated with the same letter $^{(a, b \text{ or } c)}$. As outliers from the dataset, BRACF1 and F2 and HIGGF1 and F2 have been excluded from these data summaries.

(a)

Soil type	n	pH*	Loss on ignition	Available P	Exchangeable Ca	Exchangeable Mg
Brown earth	19	6.1 (0.6) ^{a}	16.5 ± 1.1 ^{a}	67.8 ± 5.5 ^{a}	1612.0 ± 95 ^{a}	154.4 ± 14 ^{a}
Gley	21	5.5 (0.5) ^{b}	20.0 ± 1.2 ^{a}	32.3 ± 2.8 ^{b}	1020 ± 135 ^{b}	116.8 ± 7.1 ^{b}
Peat	11	4.6 (0.7) ^{c}	81.6 ± 4.7 ^{b}	18.6 ± 3.0 ^{c}	466.3 ± 145 ^{c}	83.4 ± 6.6 ^{b}

(b)

Soil type	n	Competitor	Stress-tolerant	Ruderal
Brown earth	19	79.7 ± 1.8 ^{a}	58.2 ± 1.9 ^{a}	64.5 ± 2.4 ^{a}
Gley	21	74.4 ± 2.7 ^{a}	75.4 ± 2.7 ^{b}	54.0 ± 2.7 ^{b}
Peat	11	58.1 ± 4.2 ^{b}	85.1 ± 2.6 ^{b}	37.6 ± 4.6 ^{c}

Note. * Since pH is measured on a log scale, median (interquartile range) soil pH is presented. Non-parametric multiple comparison tests for unequal sample sizes were applied (Zar, 1999).

Table 26. Correlation between plant species richness and soil fertility for the Sitka spruce and ash pre-thicket stands. As outliers from the dataset, BRACF1 and F2 and HIGGF1 and F2 have been excluded from these data summaries. Pearson's correlation coefficient (r) is displayed for those correlations that were significant according to p-values adjusted using Hochberg's (1988) method.

Soil variable	Total species richness		Vascular plant richness		Bryophyte richness	
	Pearson's r	p-value	Pearson's r	p-value	Pearson's r	p-value
Available P	-0.64	<0.001	-0.50	0.004	-0.58	<0.001
Bulk density	-0.28	NS	-0.07	NS	-0.55	<0.001
Exchangeable Ca	-0.62	<0.001	-0.42	NS	-0.70	<0.001
Total C	0.25	NS	0.02	NS	0.57	<0.001
Loss on ignition	0.28	NS	0.05	NS	0.56	<0.001
Total N	0.25	NS	0.04	NS	0.52	0.001
pH	-0.53	0.001	-0.33	NS	-0.66	<0.001

4.3.6.2 Other structural groups

Vegetation richness is more variable between sites within the Sitka spruce structural stages than within the ash (Table 27). Consequently, within the ash structural groups, there are few significant relationships between species richness and structural and environmental variables. Total (r = 0.86, n = 10, adjusted-p = 0.030) and vascular plant (r = 0.85, n = 10, adjusted-p = 0.048) richness were found to correlate significantly with canopy height at the closed-maturing stage of the ash structural cycle.

Table 28 highlights the significant correlations between species richness and structural and environmental variables for each Sitka spruce structural group. Pearson's correlation coefficients are displayed for those correlations that were significant according to p-values adjusted using Hochberg's (1988) method. Correlations that were significant before the p-values were adjusted are also listed; these should be investigated further as possible indicators of vegetation diversity.

Table 27. Mean (± standard error) total, vascular plant and bryophyte richness of the 100 m^2 quadrats at the different structural stages of the (a) Sitka spruce and (b) ash forests. Variability in species richness between quadrats (*CV* = coefficient of variation %) is indicated. There is no significant difference between structural stages if designated with the same letter (a, b, or c)**.**

(a)

Sitka spruce structural stage	n	Total species richness	CV	Vascular plant richness	CV	Bryophyte richness	CV
Thicket	17	20.8 ± 5.3 ^{a}	25.5	11.0 ± 1.2 ^{a}	46.8	9.8 ± 0.8 $^{a, b}$	33.6
Closed-maturing	21	12.7 ± 1.5 ^{b}	54.3	3.9 ± 1.0 ^{b}	123.9	8.9 ± 1.1 ^{a}	56.9
Reopening	12	19.4 ± 3.5 $^{a, b}$	62.6	8.3 ± 2.6 $^{a, b}$	110.9	11.2 ± 1.7 $^{a, b}$	53.4
Mature	18	33.5 ± 2.6 ^{c}	32.5	19.8 ± 2.2 ^{c}	46.9	13.7 ± 0.7 ^{b}	22.3

(b)

Ash structural stage	n	Total species richness	CV	Vascular plant richness	CV	Bryophyte richness	CV
Pole	7	20.3 ± 1.9 ^{a}	24.6	17.0 ± 2.0 ^{a}	30.6	3.3 ± 1.0 ^{a}	81.8
Closed-maturing	12	28.0 ± 3.1 ^{a}	38.0	20.1 ± 2.1 ^{a}	36.7	7.9 ± 1.1 ^{b}	46.2
Semi-mature	9	23.0 ± 2.1 ^{a}	27.2	13.7 ± 1.6 ^{a}	35.3	9.3 ± 1.4 ^{b}	46.4
Mature	9	24.4 ± 1.8 ^{a}	22.1	15.3 ± 1.5 ^{a}	28.4	9.1 ± 0.7 ^{b}	23.6

At the thicket stage of the Sitka spruce structural cycle, there are no significant indicators of species richness (Table 28). However, variables such as canopy cover and the cover of forbs and graminoids require further investigation. Table 27 indicates that floristic richness is particularly variable at the closed-maturing and reopening stages of the conifer forests. Whilst cover of forbs and brambles provides some indication of vascular plant richness at the closed-maturing stage, bryophyte richness in these forests is related to soil fertility. Small reductions or gaps in canopy cover also promote species richness at the closed-maturing stage. At MARY, a closed-maturing Sitka spruce stand located in Co. Laois, only three to five species were recorded in 100 m^2 quadrats located in areas of the forest where canopy cover was 100%. In contrast, 26 species were observed where canopy cover was reduced to 85%. Canopy cover is an important indicator of species richness within the reopening stands (Table 28 and Figure 38).

In mature stands, canopy cover is less than or equal to 65%, and not as variable as in the other structural stages. Accordingly canopy cover does not appear to account for differences in species richness and composition within the mature stands. The total volume of coarse deadwood (i.e. standing dead trees, fallen deadwood > 7cm and stumps) is significantly correlated with bryophyte species richness within this stand structural group (Table 28). In contrast to the findings from the pre-thicket forests, plant richness in the mature stands is not lower on the more fertile soils. Figure 39 illustrates the positive relationship between available P and vascular species richness in the mature stands. The soils beneath the mature Sitka spruce stands have lower available P content than those beneath the pre-thicket. Available P ranges between 5.0 and 117.1 g L^{-1} in the pre-thicket soils, and between 9.9 and 54.6 g L^{-1} in the mature. The mature Sitka spruce stands range between 37 and 47 years of age. Whilst there are no significant relationships between species richness and stand age for the mature forests, UNIO (along with RATH) is the oldest mature Sitka spruce stand and also the most species-rich.

4.3.7 Species indicators

Vascular plant species richness per 100 m^2 quadrat ranges from 0 to 39, whereas the maximum number of bryophyte species observed in any 100 m^2 quadrat is only 21. Vascular plant richness is more closely correlated with total species richness than is bryophyte richness (Figure 40). This trend was found for the majority of the Sitka spruce and ash stand structural groups. However, in closed-maturing Sitka spruce stands bryophyte species richness (r = 0.72, n = 21, $p < 0.001$) and vascular species richness (r = 0.68, n = 21, p = 0.001) are similarly correlated with total species richness. Correlation between vascular plant and bryophyte richness is generally poor. A significant correlation between vascular species and bryophyte species richness was found only in the closed-maturing ash stands (r = 0.85, n = 12, $p < 0.001$).

Analyses described in Section 4.3.6.1 indicate that heathland species (e.g. *Molinia caerulea* and *Calluna vulgaris*) are suitable indicators for species-rich communities in the pre-thicket stands, with grassland species such as *Agrostis stolonifera* indicative of the more species-poor improved grassland habitats. When excluding the quadrats inventoried in the pre-thicket stands, high *Agrostis stolonifera* cover remains associated with poor species richness in the pole to mature stages of the ash structural cycle. In terms of species indicators for the Sitka spruce stands, quadrats with more than 20% cover of *Thuidium tamariscinum* have 25 or more vascular plant and bryophyte species in total (Figure 41a). Likewise, quadrats with a 3% or greater cover of *Dryopteris dilatata* have 20 or more species (Figure 41b). If the thicket Sitka spruce stands are also excluded, then the moss *Polytrichum formosum* is present in some of the more species-rich quadrats (Figure 41c). Note that these relationships are thresholds rather than correlations: some plots with lower (or 0%) covers of the above species had species richnesses as high or higher than plots where the indicative species abundances were higher than the threshold cover (Figure 41).

The NMS ordination of the Sitka spruce 100 m^2 quadrats (excluding the pre-thicket data) is shown in Figure 42. There is some correspondence between the cluster analysis groupings of the 100 m^2 quadrats with the stand-scale clusters (Figure 15). However, heterogeneity in species composition between quadrats within a single stand means that there is also some divergence. The 100 m^2 quadrats inventoried within the thicket to mature Sitka spruce stands, can be divided into five principal groups (Figure 42). As outliers from the principal clusters, CLYDF4 and CUMMF4 and 5 have been excluded from the following analyses. Although CLYD and CUMM (F4 and 5 only) were classified as thicket stands, ground flora composition and abundance in these quadrats (i.e. high coverage of *Molinia caerulea*) is more comparable to the pre-thicket sites (i.e. cluster B in Figure 15). In addition to being floristically distinct, the cluster analysis groups of the Sitka spruce quadrats also differ in terms of species richness. The difference in canopy cover between clusters accounts for the separation of clusters A and B from clusters C, D and E (Table 31). Quadrats located within clusters A and B are the most species-rich. Cluster A contains quadrats that have a significantly higher number of species than those in clusters C, D and E (Table 31). The majority of quadrats within cluster A are located in mature Sitka spruce stands, this cluster has vascular indicators including *Rubus fruticosus* agg., *Dryopteris dilatata* and *Agrostis capillaris* (common bent) (Table 31). The total number of species observed in the quadrats within cluster A ranges between 17 and 51. Although *Rubus fruticosus* agg. is found in the more species-rich quadrats within this cluster, species richness of the quadrats is lower where cover of *Rubus fruticosus* agg. exceeds 30%.

Table 29 illustrates the difference in soil organic and nutrient content between clusters. The surface soil layer in quadrats within cluster A is less organic and has a higher total P content than the soils collected from quadrats in cluster B. Cluster B contains quadrats inventoried at the closed-maturing (e.g. DERRF1, 2 and 4), reopening (e.g. MUNGF2) and mature (e.g. MSOPF1 and 3) stages of growth. Whilst vascular species outnumber bryophytes in cluster A, bryophytes are an equally important component of the ground flora in cluster B. Vascular plant richness varies between the quadrats within this cluster. Therefore, bryophytes (e.g. *Plagiothecium undulatum, Hypnum jutlandicum* and *Dicranum scoparium*) are the principal indicators of cluster B. Quadrats grouped within cluster B are significantly more species-rich than those in clusters D and E.

Structural stage and soil fertility separate cluster C from D in the ordination space. Whilst cluster C contains quadrats primarily at the thicket stage on mineral soils, cluster D contains quadrats at the closed-maturing and reopening stages, where the surface soil layer is more organic and has a lower pH and nutrient content (e.g. exchangeable Ca) (Table 29). Canopy closure is at its maximum for quadrats located in cluster E and they are therefore grouped together because of their impoverished ground flora. According to the Monte Carlo test of significance, there are no significant indicators for clusters D or E. Although vascular plant richness is lower in cluster D, the number of bryophytes observed in quadrats within this cluster does not significantly differ from the more species-rich clusters A and B (Table 31).

The total number of plant species does not differ between the cluster analysis groups of the 100 m^2 quadrats inventoried in the ash stands (Figure 43 and Table 32). However, the number of woodland plants (both vascular and bryophyte) does differ. Indicator species for cluster A, which has the highest number of woodland species, include *Thamnobryum alopecurum*, *Polystichum setiferum*, *Hedera helix* and *Primula vulgaris* (Table 32). Cluster E also has a significantly greater number of woodland species than clusters D and C. Indicators for cluster E include *Plagiomnium undulatum*, *Thuidium tamariscinum*, *Poa trivialis* and *Rhytidiadelphus triquetrus*. Forest structure separates clusters C and D from the other clusters, with dbh being significantly greater in clusters A and B. Soil fertility also differs between clusters (Table 30); the surface soil layer in quadrats within cluster B has lower pH and lower available P and exchangeable Ca content than clusters A and E. Cluster B contains quadrats inventoried in ash compartments that were a component of the mixed forests. Species indicators for this cluster include *Rubus fruticosus* agg., *Dryopteris affinis* (scaly male fern), *Pteridium aquilinum* (bracken) and the moss *Atrichum undulatum*.

Table 28. Correlations between species richness and structural and environmental variables for each Sitka spruce structural group. Pearson's correlation coefficient (r) is displayed for those correlations that were significant according to p-values adjusted using Hochberg's (1988) method. Correlations (and the direction of the association +/-) that were significant before the p-values were adjusted are also listed; these should be investigated further as possible indicators of vegetation diversity.

Sitka spruce structural stage	Total species richness			Vascular plant richness			Bryophyte richness		
	Structural/ Environmental variable	r	p-value	Structural/ Environmental variable	r	p-value	Structural/ Environmental variable	r	p-value
Thicket	No significant correlations			No significant correlations			No significant correlations		
Other relationships	Canopy cover (-) Forb cover (+) Graminoid cover (+) Needles/FWD (-)			Forb cover (+)			Canopy cover (-) Dbh (-)		
Closed-maturing	No significant correlations			Forb cover	0.80	< 0.001	Total P	-0.73	0.004
				Bramble cover	0.75	0.002			
Other relationships	Bryophyte cover (+) Canopy cover (-) Forb cover (+) Needles/FWD (-)			Needles/FWD (-)			Bulk density (-)		
Reopening	Canopy cover	-0.84	0.015	No significant correlations			No significant correlations		
	Needles/FWD	-0.82	0.025						
Other relationships	Bryophyte cover (+)			Canopy cover (-) Bulk density (+)			Bryophyte cover (+) Needles/FWD (-)		
Mature	Available P	0.70	0.031	Available P	0.71	0.022	Total coarse deadwood	0.75	0.008
Other relationships	Ca (+) Total P (-)			Ca (+)			Loss on ignition (+)		

Table 29. Soil characteristics of the Sitka spruce 100 m^2 quadrats according to their cluster analysis groupings. Median pH (interquartile range) and mean (± standard error) organic content (loss on ignition %), total and available P and exchangeable Ca (in mg L^{-1}) is presented. There is no significant difference between clusters if designated with the same letter $^{(a\ or\ b)}$.

Cluster	n	Loss on ignition	pH*	Total P	Available P	Exchangeable Ca
A	15	20.0 ± 1.9 ^{a}	4.5 (1.1) $^{a, b}$	397.0 ± 43.4 ^{a}	28.6 ± 3.6 $^{a, b}$	305.4 ± 84.6 $^{a, b}$
B	14	39.6 ± 7.6 $^{a, b}$	4.4 (0.9) $^{a, b}$	181.4 ± 31.5 ^{b}	21.3 ± 2.4 ^{a}	404.3 ± 152 $^{a, b}$
C	14	27.5 ± 5.3 $^{a, b}$	5.2 (0.6) ^{a}	345.0 ± 52.2 ^{a}	31.9 ± 4.7 $^{a, b}$	678.5 ± 140.5 ^{a}
D	15	48.1 ± 7.6 ^{b}	4.3 (0.2) ^{b}	180.6 ± 31.1 ^{b}	20.0 ± 4.0 ^{a}	68.4 ± 21.7 ^{b}
E	7	19.2 ± 5.0 ^{a}	4.6 (1.3) ^{a}, ^{b}	268.0 ± 29.2 $^{a, b}$	43.0 ± 8.0 ^{b}	280.9 ± 95.8 $^{a, b}$

Table 30. Soil characteristics of the ash 100 m^2 quadrats according to their cluster analysis groupings. Median pH (interquartile range) and mean (± standard error) exchangeable Mg, total and available P and exchangeable Ca (in mg L^{-1}) is presented. There is no significant difference between clusters if designated with the same letter $^{(a\ or\ b)}$.

Cluster	n	pH*	Exchangeable Mg	Total P	Available P	Exchangeable Ca
A	10	6.0 (0.7) ^{a}	230.8 ± 28.5 ^{a}	514.3 ± 72.5 ^{a}	47.9 ± 4.6 $^{a, b}$	1697.4 ± 259 ^{a}
B	10	5.0 (0.8) ^{b}	89.2 ± 17.6 ^{b}	520.4 ± 44.3 ^{a}	33.2 ± 6.3 ^{b}	327.3 ± 79.6 ^{b}
C	5	5.1 (0.8) $^{a, b}$	85.1 ± 14.2 ^{b}	279.7 ± 125 $^{a, b}$	53.9 ± 7.1 $^{a, b}$	867 ± 497 $^{a, b}$
D	8	5.5 (1.0) $^{a, b}$	119.2 ± 15.9 ^{b}	199.7 ± 83.7 ^{b}	32.6 ± 8.3 ^{b}	954.9 ± 173 $^{a, b}$
E	7	5.8 (0.3) $^{a, b}$	96.2 ± 14.3 ^{b}	321.1 ± 73 $^{a, b}$	67.6 ± 4.8 ^{a}	973.0 ± 185 $^{a, b}$

Note. * Since pH is measured on a log scale, median (interquartile range) soil pH is presented. Non-parametric multiple comparison tests for unequal sample sizes were applied (Zar, 1999).

Table 31. Species indicators of the Sitka spruce 100 m^{2} quadrat clusters (excluding pre-thicket data). Mean (± standard error) total, vascular plant and bryophyte species richness and canopy cover of each cluster is presented. There is no significant difference between clusters if designated with the same letter $^{(a, b, c \text{ or } d)}$.

Cluster variables	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E
Canopy cover (%)	56.7 ± 3.1 ^{a}	64.6 ± 3.9 ^{a}	88.9 ± 2.3 ^{b}	81.0 ± 3.8 ^{b}	92.9 ± 1.8 ^{b}
Total richness	32.7 ± 2.9 ^{a}	27.2 ± 2.9 $^{a, b}$	19.4 ± 1.6 $^{b, c}$	14.0 ± 1.3 ^{c}	4.7 ± 1.1 ^{d}
Vascular plant richness	20.0 ± 2.2 ^{a}	13.3 ± 2.8 $^{a, b}$	10.4 ± 1.7 ^{b}	3.5 ± 0.9 ^{c}	2.0 ± 0.6 ^{c}
Bryophyte richness	12.7 ± 1.2 ^{a}	13.9 ± 1.2 ^{a}	9.1 ± 0.5 ^{b}	10.5 ± 0.7 $^{a, b}$	2.7 ± 0.8 ^{c}
Species indicators	*Rubus fruticosus* agg.** *Dryopteris dilatata*** *Agrostis capillaris*** *Thuidium tamariscinum***	*Plagiothecium undulatum** *Hypnum jutlandicum*** *Dicranum scoparium*** *Eurhynchium praelongum**	*Rumex acetosa*** *Brachythecium rutabulum** *Fissidens bryoides** *Poa trivialis**	No significant species indicators	No significant species indicators

Table 32. Species indicators of the ash 100 m^{2} quadrat clusters (excluding pre-thicket data). Mean (± standard error) total, bryophyte and woodland plant species richness and dbh of each cluster is presented. There is no significant difference between clusters if designated with the same letter $^{(a, b, c \text{ or } d)}$.

Cluster variables	Cluster A	Cluster B	Cluster C	Cluster D	Cluster E
Dbh (cm)	20.6 ± 3.1 ^{a}	15.3 ± 1.6 ^{a}	7.2 ± 1.3 ^{b}	7.0 ± 0.8 ^{b}	19.1 ± 3.8 $^{a, b}$
Total richness	24.2 ± 1.1 ^{a}	26.4 ± 2.8 ^{a}	19.4 ± 1.1 ^{a}	19.5 ± 2.5 ^{a}	27.6 ± 4.6 ^{a}
Bryophyte richness	7.8 ± 0.5 $^{a, d}$	11.1 ± 1.1 ^{b}	4.4 ± 0.8 $^{a, c}$	3.5 ± 0.8 ^{c}	9.6 ± 0.9 $^{b, d}$
Woodland plant richness	14.7 ± 1.0 ^{a}	10.0 ± 1.6 ^{a}	1.8 ± 0.4 ^{b}	1.8 ± 0.4 ^{b}	11.9 ± 1.7 ^{a}
Species indicators	*Thamnobryum alopecurum*** *Polystichum setiferum*** *Hedera helix*** *Primula vulgaris***	*Rubus fruticosus* agg.** *Dryopteris affinis*** *Pteridium aquilinum** *Atrichum undulatum**	*Anthoxanthum odoratum*** *Holcus lanatus*** *Stellaria graminea*** *Potentilla erecta***	*Agrostis stolonifera*** *Rumex acetosa***	*Plagiomnium undulatum*** *Thuidium tamariscinum** *Poa trivialis** *Rhytidiadelphus triquetrus***

Note. * indicates that the species indicator is significant at the $p < 0.05$ level and ** indicates significance at the $p < 0.01$ level according to the Monte Carlo test of significance.

4.4 DISCUSSION

4.4.1 Overview of results

Ground flora composition and diversity in the Sitka spruce and ash plantations is dependent on forest type and structure, as well as on site fertility and history. At the pre-thicket stage, the trees have a minimal impact on the vegetation communities. Canopy closure has not occurred in these stands and species indicative of the original habitat type remain abundant. Therefore, at this stage, environment and management histories are influential factors. With the progression of the forest cycle, the differential impact of the Sitka spruce and ash canopies becomes apparent. At the thicket, closed-maturing and reopening stages of the Sitka spruce structural cycle, the number of vascular species is heavily depleted, particularly in forests yet to be thinned. This accords with related literature where the detrimental effect of canopy closure on vascular species is documented (Hill & Jones, 1978; Hill, 1979; Wallace & Good, 1995; Fahy & Gormally, 1998; Ferris *et al.*, 2000a). In comparison to Sitka spruce, the ash canopy does not have such a negative impact on the number of vascular species in the ground flora. Consequently, vascular plant richness is less variable between quadrats inventoried in the ash forests than between those in the Sitka spruce. The majority of ash stands inventoried are located on brown earth and gley soils, and species that prefer a neutral substrate or are broadly tolerant make up the largest proportion of the flora. In contrast, acidophilic vascular plants and bryophytes dominate the vegetation communities in the conifer stands. Acidophilic bryophytes become increasingly dominant beneath the Sitka spruce canopy as soil pH decreases with increasing structural maturity. The surface soil layer beneath Sitka spruce has greater acidity than that beneath the ash. This is probably due in part to the acidic nature of the conifer litter and its accumulation, forming a deep humus layer (Miles, 1978; Hornung, 1985). Weibull (2001) proposed that differences in throughfall chemistry between spruce and broadleaf stands can also have consequences for bryophyte species composition.

In both the Sitka spruce and ash forests, the numbers of species that have a preference for woodland habitats increase through the structural cycle. Humphrey *et al.* (2001) found a similar trend in their study of conifer and broadleaf plantations in Britain. The dominance of woodland species in the mature stages of the plantation cycle is at the expense of species indicative of the original habitat. Whilst species that have a preference for open habitats dominate at the pre-thicket stage in the Sitka spruce structural cycle, they account for only a small proportion of the ground flora community at the mature stage. Although the original grassland or heathland communities are retained in the pre-thicket stands, the bryophyte flora is at its poorest at this stage. In both the Sitka spruce and ash stands, the mature forests support the most abundant and species-rich bryophyte assemblages. Whilst higher numbers of vascular species were observed in the ash forests, the conifer forests are an important habitat for bryophyte diversity, also observed by Hill (1979).

These findings indicate that the different forest types and stages of the forest cycle support different forms of vegetation diversity. Neither Sitka spruce nor ash stands necessarily support the 'best' vegetation communities. In the mixed stands, the proximity of ash does not appear to augment the plant species richness of the Sitka spruce component. However, the floristic and structural differences between the ash and Sitka spruce stands suggest that plantations that contain both broadleaf and conifer stands will be more diverse than plantations dominated only by conifers. As observed in this project, Kirby (1988) found that plantations of a mixture of oak and spruce allow more ground flora survival in the thicket stage of the crop than pure coniferous stands. The negative effect that the Sitka spruce canopy can have on botanical diversity has been confirmed and quantified. However, of all forests inventoried, the most species-rich was a Sitka spruce stand, namely Union (UNIO), located in Co. Sligo. Ground flora richness has been promoted at Union forest by low canopy cover (between 50 and 65%), fertile soils (in comparison to other mature Sitka spruce stands) and close proximity to old oak woodland. Therefore, if the management and environmental conditions suit, conifer forests are able to support a species-rich ground flora.

4.4.2 Vegetation composition

While we have found that Sitka spruce and ash plantations are not necessarily "ecological deserts", neither are they refugia of high biodiversity. None of the Sitka spruce or ash stands surveyed support vegetation communities of particularly high conservation value. No red-data or protected vascular plant species or rare/protected bryophytes were found at any of the sites. In addition, plant species indicative of ancient woodlands according to Praeger (1934) (e.g. *Lathraea squamaria* (toothwort), *Milium effusum* (millet-grass) and *Pyrola media* (intermediate wintergreen)) have not been observed. The absence of 'old forest' species is not surprising since they are uncommon or rare in present-day semi-natural woodlands (Kelly & Kirby, 1982).

Of the species listed by Ellenberg (1988) as characteristic associates of coniferous woodland in Central Europe, the moss *Hylocomium splendens* was the only species recorded in the Sitka spruce stands. This species has however too wide an ecological range to be ranked as a specialist species (Kelly & Connolly, 2000). The moss *Ptilium crista-castrensis* is also listed by Ellenberg (1988) and is associated with semi-natural Scots pine woodland in Scotland (Rodwell, 1991). Though rare, *Ptilium crista-castrensis* is also found in Ireland, but was not observed at any of the Sitka spruce forests inventoried. Of the species listed by Rodwell (1991) as constant in the flora of Caledonian Scots pine forests, the mosses *Dicranum scoparium* and *Plagiothecium undulatum* appear in our own analyses as species indicators for the Sitka spruce quadrats grouped within cluster B (Figure 42 and Table 31). Therefore, there is some correspondence between the flora of the Sitka spruce stands surveyed in this project and semi-natural Scots pine forests in Britain.

Kelly and Kirby (1982) detailed the vegetation composition of Irish native woodlands on free-draining soils over limestone. Of the quadrats inventoried in the plantation ash stands, those grouped within cluster A (Figure 43 and Table 32) support a flora most similar to the Corylo-Fraxinetum association that Kelly and Kirby describe. The pleurocarpous mosses observed in these semi-mature and mature ash stands concur with the suite of mosses that are characteristic of the Corylo-Fraxinetum association, these being *Eurhynchium striatum*, *Thamnobryum alopecurum* and *Thuidium tamariscinum*. *Polystichum setiferum* and *Primula vulgaris*, species indicators for these ash stands, are also characteristic of Corylo-Fraxinetum woodlands. However, other species listed by Kelly and Kirby to be constant species in the flora of native woodlands over limestone are absent or not consistently present in the plantation ash flora (e.g. *Circaea lutetiana* (enchanter's nightshade) was not found). Kelly and Kirby recorded an average of 18.2 (n = 5, se = 4.5) herb species in 200 m^2 quadrats inventoried in Corylo-Fraxinetum typicum subassociation woodlands in the west of Ireland. In comparison to other subassociations, the flora in Corylo-Fraxinetum typicum woodlands is typically species-poor. This is because the flora is often dominated by *Hedera helix*, which can reduce herb and moss diversity through competitive exclusion (Kelly & Kirby, 1982). *Hedera helix* was abundant in the majority of quadrats inventoried in the ash plantations that are grouped within cluster A. If the total number of herb species recorded in two 100 m^2 quadrats from each ash plantation in cluster A is calculated, then the average number of herb species recorded per 200 m^2 was 16.0 (n = 4, se = 1.8). Therefore, herb species richness of the ash plantations is similar to Corylo-Fraxinetum typicum semi-natural woodlands surveyed by Kelly and Kirby, however these woodlands are species-poor compared with the majority of Corylo-Fraxinetum association woods.

Perhaps the most appropriate type of semi-natural Irish woodland for comparison with Sitka spruce plantations would be woodlands of sessile oak (*Quercus petraea*) and downy birch (*Betula pubescens*) on acid soils, the Blechno-Quercetum association (Kelly & Moore, 1975). Acidophilous oak woodland typically occurs on soils of low fertility in moist upland situations. Although they typically support vascular plant floras of limited species richness, the bryophyte floras are often rich (Kelly & Moore, 1975; Kelly, 1981), and their high conservation value is recognised by inclusion in the EU Habitats Directive (European Commission, 1999). Kelly and Moore (1975) list 21 vascular plant and bryophyte species that are characteristic of the Blechno-Quercetum association in Ireland. Of these, 17 occur in one or more 100m^2 Sitka spruce plots in the thicket and post-thicket stages. The floras of Sitka spruce clusters A and B (Table 31 and Figure 43), which are comprised mainly of reopening and mature stands, are the most similar to that of semi-natural sessile oak woodlands. In cluster A, 14 characteristic sessile oak woodland species occurred, and each plot contained an average of 4.3 of these species. Cluster B supported 15 characteristic Blechno-Quercetum species, with an average of 4.7 of these species per plot. The flora of cluster D (Table 31 and Figure 43), made up of closed-maturing and reopening stands on organic-rich, acid soils, also included more than half (12) of the characteristic sessile oak woodland species given by Kelly and Moore (1975), and each plot averaged 3.9 of these species.

The plot averages above suggest that while the more mature Sitka spruce stands have some floral affinities to sessile oak woodland, characteristic Blechno-Quercetum species are found rather sparsely in spruce stands. Kelly and Moore (1975) found eight characteristic species occurring in more than 60% of the relevés they sampled or reviewed. Of these, only two occurred in more than 60% of the plots in one or more cluster groups. *Blechnum spicant* (hard fern) was found in 67% of the plots in cluster A, and the moss *Plagiothecium undulatum* was found in 93% and 80% of the plots in the bryophyte-rich clusters B and D, respectively. One species, the liverwort *Saccogyna viticulosa*, was not encountered at all in this study. The remaining five species, *Luzula sylvatica* (great woodrush), *Vaccinium myrtillus* (bilberry, fraochán), the moss *Isopterygium elegans*, the moss *Rhytidiadelphus loreus* and the liverwort *Calypogeia muellerana*, were found in at least 25% of the plots in one or more of the clusters A, B or D. With the exception of the moss *Plagiothecium undulatum*, none of the characteristic sessile oak woodland species occurred with sufficient frequency and fidelity to be considered as indicator species for clusters A or B (Table 31). The rest of the indicator species for these Sitka spruce plantation communities are frequently found in Blechno-Quercetum woodlands, but also commonly occur in other types of woodland communities, and are therefore are not characteristic of sessile oak woodlands (i.e. they are "companion species" in phytosociological terms).

4.4.3 Effects of site history and surrounding land use

Previous and adjacent land-use are important influences on ground flora composition and diversity in the Sitka spruce and ash stands. Old woodland or scrub in the landscape can act as source populations for vascular plant species typically found in forest communities (Figure 34). Hedgerows may serve a similar role, although we were not able to estimate abundance of hedgerows near our study sites. The availability of source populations and receptor site conditions may permit establishment of typical woodland species, given sufficient time. For example, the semi-mature and mature pure ash forests (and also the ash component of RATH) were established on fertile, lowland soils, and all are located in close proximity to old woodland (though BARN was the only forest to be established on an area formerly occupied by woodland). The higher numbers of woodland species in these stands are due in part to forest age and proximity to old woodland. It appears that forest age is a more important factor for woodland bryophytes, whereas proximity to old woodland may be more important for woodland vascular plants (Sections 4.3.5.2.2 & **Error! Reference source not found.**), many species of which have limited dispersal capabilities.

Given enough time, will ash plantations develop similar floras, despite differences in site and landscape characteristics? The answer to this question is important, given increasing afforestation of agricultural lowland areas, often not in close proximity to significant amounts of semi-natural woodland. In contrast to the pure ash forests, the majority of the mixed ash stands (in age class 4) were established on sites with poorer podzolic soils, at higher elevations and with less old woodland present in the nearby landscape. The ash compartments of the mixed stands are more similar, in terms of species composition, to the Sitka spruce sites than to the pure ash forests (Figure 15). Therefore, the differences in composition between the pure and mixed ash stands suggest that greenfield plantations may not develop the woodland floras found in the pure ash forests. The Sitka spruce and ash compartments of RATH are both adjacent to semi-natural woodland. Whilst RATHA has a comparable ground flora to the pure ash forests, RATHS is separated from these stands in the ordination space (Figure 15). Its ground flora is more comparable to UNIO, the only other Sitka spruce stand located near to semi-natural woodland. Therefore, the data suggest that whilst the ash and Sitka spruce compartments of mixed stands develop similar floras on upland poorer soils (as Hill (1979) also found), there is less similarity when they are established on more fertile lowland soils in wooded areas. However, further research is required to validate this finding since other studies have observed the spread of woodland species from deciduous woods into adjacent conifer stands (Hill & Jones, 1978). According to Hansson (2000b), low levels of competition and available substrate enabled woodland herbs and trees to spread from oak-hazel woods into adjacent conifer plantations in Sweden.

4.4.4 Biodiversity indicators

4.4.4.1 Structural indicators

The structure of the Sitka spruce and ash plantations is an important determinant of vegetation abundance, composition and richness. The low canopy cover at the pre-thicket stage ensures that all pre-thicket stands support an abundant ground flora. However, well-developed ground floras are not necessarily associated with species richness. According to Fossitt (2000) improved grasslands are typically species-poor. Indeed, species richness in forests planted on improved grasslands (e.g. KILM) is suppressed by graminoid dominance. *Agrostis stolonifera* was particularly associated with the more species-poor quadrats. *Agrostis stolonifera* is a fast-growing perennial grass of mesic habitats, and forms extensive clonal patches by means of long stolons (Grime *et al.*, 1988). Gremmen *et al*. (1998) recorded the invasion of *Agrostis stolonifera* at sub-Antarctic Marion Island and found that communities dominated by the grass contained significantly fewer plant species than those without it. The structure of the forest at the pre-thicket stage has some value as a diversity indicator, but structural differences between the pre-thicket stands largely arise due to differences in the abiotic environment. The presence of subshrubs (e.g. *Calluna vulgaris* and *Erica tetralix* (cross-leaved heath)) is indicative of the more bryophyte-rich heathland communities, whilst bryophyte richness decreases with increased graminoid cover.

After canopy closure, small-scale differences in tree cover within and between Sitka spruce stands have a dramatic impact on ground flora abundance and diversity. Canopy cover is negatively correlated with species richness in thicket, closed-maturing and especially in reopening Sitka spruce stands. Small gaps within the thicket stands have allowed shade-intolerant species to persist or to recolonise from the seedbank. At KDUF, grasses such as *Holcus lanatus* are present in numerous small open spaces. The contribution that open spaces make to the diversity of plantation forests is widely accepted and advocated

(Iremonger, 1999), and will be investigated in more detail in further BIOFOREST project research. The most species-impoverished stands are associated with the highest canopy cover. Indeed, in quadrats where there was complete canopy closure, it was not unusual to observe only one vascular species (this was often a single *Hedera helix* seedling; e.g. COONF2 and MONTF2). Mature stands have a more open canopy and are characterized by higher dbh and distance between canopy trees. These forests have an abundant and relatively species-rich flora, and are also aesthetically pleasing due to the establishment of species such as *Digitalis purpurea* (foxglove), *Dryopteris dilatata* and *Oxalis acetosella* (wood sorrel) (e.g. MSOP). Assessing ground flora diversity solely by vegetation coverage is not a reliable or recommended technique. However, in the closed-maturing Sitka spruce stands, vascular plant richness increases with forb cover. In addition, in all Sitka spruce stands inventoried, 100 m^2 quadrats with more than 20% forb cover or 50% bryophyte cover have at least 25 species in total. However, some quadrats with lower forb or bryophyte coverage are just as species-rich.

Unlike vascular species richness, the number of bryophytes in the Sitka spruce stands does not increase when canopy cover falls below 80%. The asymptotic relationship between canopy cover and bryophyte species richness may be due to competition between bryophyte and vascular species in open stands. The small stature of bryophytes puts them at a disadvantage when competing with vascular plants for space and light (Richards, 1984). Investigation of over-mature Sitka spruce stands would reveal whether lengthening the management cycle enables more bryophyte species to establish. Halpern and Spies (1995) warned that plantation forestry conducted over conventionally short rotations, which precludes the development of old-growth attributes, might result in long-term loss of diversity. One such old-growth attribute is the accumulation of large-diameter deadwood (Humphrey, 2004). Deadwood provides an important habitat for epixylic bryophytes, as has been found for mature spruce stands in this study and in Sitka spruce plantations in Britain (Humphrey *et al.*, 2002). Humphrey *et al.* (2002) found that stumps and fallen logs > 20 cm diameter at or beyond the decay stage where bark is gone and sapwood is beginning to degrade provide a better substrate for bryophytes than smaller, less decayed deadwood.

Whilst ground flora composition varies between the ash structural stages, the total number of species does not. Vascular species richness decreases as the ash plantations mature, but the number of bryophytes is highest in the semi-mature and mature ash stands. Within the structural groups, richness is more variable between Sitka spruce sites than between ash sites. Consequently, within the ash structural groups, there are few significant relationships between species richness and structural and environmental variables. It is important to note the possible influence of other canopy species in the ash forests on ground flora composition and diversity. For example, beech was an important canopy species in the ash compartment at SUNS. This species casts a heavy shade (Kirby, 1988) and therefore may account for the lower number of vascular and the higher number of bryophyte species at this site.

4.4.4.2 *Environmental and management indicators*

The influence of environment and management histories on ground flora composition and diversity is apparent in the pre-thicket forests. Stands planted on improved grasslands support low numbers of ground flora species. Whilst canopy closure will cause a loss in light-demanding species from improved grasslands, it poses a threat to a greater diversity of species in heathland habitats. The more nutrient-rich brown-earth soils support fewer species than gley and peat soils, in which resources are more limiting. These findings are in accord with Tilman's (1982) 'paradox of enrichment'. According to Tilman (1982) species richness on fertile soils is limited by dominance of a small number of vigorous species. Tilman (1982) proposed that species richness is at its greatest when there is small-scale heterogeneity in the distribution of limiting resources; this is because a greater number of specialist species will occupy the habitat. In contrast to the findings from the pre-thicket forests, vascular plant richness in the mature stands increases with available P. This may be attributed to the overall lower fertility of the soils in the mature stands than the pre-thicket soils.

NMS ordinations suggest that soil type and fertility are important influences on floristic composition under Sitka spruce and ash (Figure 42 and Figure 43). For example, organic content of the surface soil layer is important in terms of the location of the Sitka spruce quadrats in the ordination space. Although the relationship was not quantified, personal observations suggest that drains in the pre-thicket and thicket stands are an important additional habitat for bryophyte species (e.g. *Pellia epiphylla*). Thinning is an essential management practice that promotes plant diversity in conifer forests (Iremonger, 1999). It allows shade-limited species to recolonise from the seedbank or invade from surrounding habitats. Thinned Sitka spruce stands also have greater aesthetic appeal. Thinning, in addition to windthrow, is an important contributor to the volume of deadwood in a stand, in the form of stumps and felled trees. The negative relationship between canopy cover and species richness in the Sitka spruce stands suggests that thinning has promoted vegetation diversity.

4.4.4.3 Species indicators

Vascular plant species richness is more closely correlated with total species richness than bryophyte species richness is. Therefore, vascular species richness may generally be used as a surrogate for total plant species richness in the Sitka spruce and ash forests. However, vascular richness may not be used as a surrogate for bryophyte richness (and vice versa) since the association between them is poor. Mature Sitka spruce stands support relatively high numbers of vascular and bryophyte species, but vascular species greatly outnumber bryophytes at the pre-thicket stage. Bryophytes are the dominant flora in Sitka spruce stands where canopy closure has shaded out the majority of vascular species. Indeed, in closed-maturing Sitka spruce stands, bryophyte richness is a good indicator of overall plant richness. Although bryophyte richness does not compensate for the number of vascular species lost in such forests (i.e. total vegetation richness is lower), bryophytes are important components of the ground flora and should not be overlooked. The soft green carpet of mosses also takes the 'bare look' off many maturing plantations.

The indicator species of the more species-rich Sitka spruce forests (clusters A and B in Figure 42 and Table 31) are, with some botanical experience, relatively straightforward to identify. Whilst *Rubus fruticosus* agg. (bramble) is easily recognised, botanical training would be required to identify different fern (*Dryopteris dilatata*, broad buckler fern) and grass species (*Agrostis capillaris*, common bent). With some experience in bryology, *Plagiothecium undulatum*, *Hypnum jutlandicum* and *Dicranum scoparium* would be recognised with ease. Careful observation and experience in bryophyte identification would be required to identify the moss and liverwort indicators for clusters C. Caution must be applied when using *Rubus fruticosus* agg. as an indicator of richness in Sitka spruce forests; the most species-rich sites within cluster A had a lower coverage of *Rubus fruticosus* agg. Indeed, at Avondale Forest Park, Co. Wicklow, dominance of *Rubus fruticosus* agg. has lead to a generally species-poor flora in an overmature Sitka spruce stand (personal observation). No significant species indicators were found for the Sitka spruce quadrats in Cluster D (Figure 42 and Table 31). Although vascular plant richness was found to be lower in the Sitka spruce quadrats grouped within cluster D, bryophyte richness does not significantly differ from the quadrats in the more species-rich clusters A and B. Therefore, alternative indicators are required for sites that are poor in vascular plants, but still support a bryophyte-rich community. These results suggest that species indicators should not be used in isolation when assessing the biodiversity of Sitka spruce or ash stands.

The moss *Thamnobryum alopecurum* and also *Polystichum setiferum* (soft shield fern), *Hedera helix* (ivy) and *Primula vulgaris* (primrose) are found in ash stands that support the most species-rich woodland flora and a flora most similar to semi-natural woodland (i.e. cluster A in Figure 43 and Table 32). Some botanical experience would be required to identify the indicator species for the more botanically interesting ash stands.

4.5 CONCLUSIONS

4.5.1 General conclusions

- Sitka spruce plantations can have a negative impact on ground flora diversity, especially during periods of canopy closure. However, if managed appropriately, Sitka spruce forests can also be species-rich and aesthetically pleasing. Of all stages in the Sitka spruce structural cycle, the mature stands support the richest communities of both vascular plants and bryophytes. It is important to note, however, that not all spruce stands may reach the mature structural stage, which is not equivalent to commercial maturity. Sitka spruce forests are important habitats for bryophyte diversity as they support more specialist species than the ash stands.
- Ash has a less variable impact on ground flora diversity than Sitka spruce. At no stage in the forest cycle are the vegetation communities beneath the broadleaf canopy as species-impoverished as the communities beneath the closed-maturing Sitka spruce stands. In addition, the ash stands support higher numbers of vascular species than Sitka spruce. Whilst the early stages of the ash structural cycle support high numbers of vascular species, the semi-mature and mature stages are more favourable habitats for bryophyte diversity. Therefore, total plant species richness does not vary with the structural stages of the ash stand.
- Different forest types and stages of the forest cycle support different forms of vegetation diversity. The early stages of the forest cycle support persisting species from the original habitat and also many ruderal vascular plants. In contrast, the later stages support a more characteristic woodland flora.
- Where an ash compartment is located adjacent to Sitka spruce, it does not appear to promote ground flora diversity in the conifer stand. However, the broadleaf-conifer mix enhances overall species and structural diversity at the plantation scale.
- Previous and adjacent land use are important influences on ground flora composition and diversity. Proximity and abundance of old semi-natural woodland and scrub in the landscape increases the species richness of typical woodland plants. In particular, ash forests originating from or adjacent to old woodland or scrub had developed a flora most similar to that of old semi-natural woodland.

4.5.2 Biodiversity indicators

- Careful botanical inventories are required to locate and identify species of conservation value. Therefore, for an accurate assessment of ground flora diversity and composition, there is no short cut.
- The role of environmental variables (e.g. soil type) in shaping community composition and diversity is evident within the pre-thicket stands. Stands established on gley and peat soils are more species-rich than those established on fertile brown earth soils. Heathland communities support higher numbers of species than improved grasslands. Data from the pre-thicket inventories indicate that the most abundant ground floras are not necessarily the most species-rich. Indeed, assessing ground flora diversity solely by coverage of the lower structural layers (e.g. graminoids) is not a reliable or recommended technique.

- The structure of Sitka spruce stands provides an indication of ground flora diversity. In thicket, closed-maturing and especially reopening stands, canopy cover is negatively associated with species-richness. In mature forests, where there is generally a more open canopy, the most species-rich stands are located on more fertile soils. Also in mature forests, bryophyte diversity is increased by the retention of large diameter deadwood.
- Within the ash structural groups, there are few significant relationships between species richness and structural and environmental variables.
- In terms of species indicators, measuring only vascular species richness will distinguish between species-poor and species-rich forests. However, there is a risk that this method will overlook habitats that are important for bryophyte diversity. Some botanical experience will be required in order to correctly identify the indicator species proposed in Section 4.3.7. No one type of indicator, including species indicators, should be used in isolation when assessing the diversity of a Sitka spruce or ash stand.
- When assessing ground flora diversity, it is recommended that the structural, environmental and management status (e.g. thinning history, previous land use, location) of the stand and the composition of the ground flora be studied in unison.

4.5.3 Management recommendations

- Differences in ground flora diversity between sites at the pre-thicket stage suggest that fewer species will be lost if plantations are established on improved grasslands or other communities of low biodiversity value. The higher species-richness of heathland communities means that afforestation poses a threat to a greater diversity of species in these habitats. Further BIOFOREST research (Project 3.1.1, Biodiversity of Afforestation Sites) will provide more information on biodiversity of pre-afforestation habitats.
- At the thicket stage of the Sitka spruce structural cycle, even small gaps in the canopy enable vegetation persistence. Such small (c. 400 m^2) gaps should be scattered throughout Sitka spruce plantations at the establishment stage. Larger gaps also provide a refuge for species until they are able to recolonise during the more open phases of the forest cycle.
- Thinning is an essential management practice that promotes ground flora diversity in Sitka spruce forests. Thinning of Sitka spruce forests should be conducted at an early stage and with sufficient intensity at the first and subsequent treatments so that the growth of surrounding trees will not bring about complete canopy closure. Although wide implementation of this recommendation would have the significant biodiversity benefits, it is contrary to current silvicultural best practice. Accordingly, rigorous thinning may be best limited to certain areas within forests, especially where windthrow is a risk.
- Differences in ground flora between forest types and stages indicate that a plantation that contains a variety of species and structural classes will be more diverse. Therefore, plantings should incorporate a mixture of canopy species, and structural variation should be promoted by diversifying stand ages within a plantation.
- Mature forest is a particularly important stage in the Sitka spruce cycle. Mature Sitka spruce stands have high vascular and bryophyte richness and woodland species account for a high proportion of the flora. Therefore, the retention of some Sitka spruce forests past conventional maturity date is recommended.

- The creation and retention of large diameter deadwood should be encouraged. During thinning, harvesting and similar operations, such as salvaging windthrown timber, standing dead trees should be retained and a number of large diameter logs should be left on site.
- It is also recommended that where possible and where not in conflict with other conservation objectives, plantations be established in close proximity to semi-natural woodland. This will facilitate the establishment of woodland species in plantations. If possible, such plantations should be established and managed under the *Native Woodland Scheme* (Forest Service, 2001). A somewhat less desirable alternative would be a conventionally managed plantation comprised of the same species as occur in the adjacent woodland. The biodiversity of plantations of exotic species may also benefit from location near woodland, such as UNIO in this study, but shade-tolerant species potentially able to invade should never be planted near native woodland. Such species would include sycamore, beech, western hemlock, fir species and western red cedar.

4.5.4 Modifications to the *Forest Biodiversity Guidelines*

These proposals (Section 4.5.3) are generally in accord with the recommendations in the *Forest Biodiversity Guidelines* (Forest Service, 2000b). This research supports the requirement for open spaces as part of the Area for Biodiversity Enhancement (ABE) and the recommendation for tree species, structural and age class diversity in plantation forests. This research also supports the recommendation for retention of deadwood, but the *Guidelines* should be modified to specify that the deadwood should be greater than 7 cm diameter, and preferably greater than 20 cm. The *Guidelines* should be modified to reflect other recommendations above, such as more intensive thinning, inclusion of several small gaps and the placement of plantations near pre-existing woodland.

In addition, the *Guidelines* should recommend the use of improved grassland, arable land or other habitats of low conservation value for afforestation. Guidance on the recognition of important habitats for vegetation diversity should be provided. The following indicators of biodiversity in pre-thicket stands can be used as part of site assessment prior to afforestation: presence of *Molinia caerulea* (purple moor-grass), *Calluna vulgaris* (heather) or *Erica tetralix* (cross-leaved heath); absence of *Agrostis stolonifera* (creeping bent); high cover of subshrubs or bryophytes and low cover of competitive graminoids; low soil pH, available P or exchangeable Ca and high soil organic content. At sites with good values for more than one of these indicators, a more thorough floristic inventory should then be carried out.

5 SPIDERS

5.1 INTRODUCTION

In most terrestrial ecosystems, spiders are the most common predators (Dippenaar-Schoeman & Jocque, 1997) with around 40 000 named species (Marc *et al.*, 1999) in over 100 families world-wide.

Spiders have been used for many years in ecological studies to investigate differences in habitat and disturbance (Williams, 1962; Uetz, 1979; Coyle, 1981; Curry & Momen, 1988; Downie *et al.*, 1996; Docherty & Leather, 1997). More recently, interest has focussed on their use as 'bioindicators' and their ability for pest limitation (Marc & Canard, 1997; Marc *et al.*, 1999; Gravesen, 2000). Paoletti (1999) defined a bioindicator as a "species or species assemblage that is particularly well matched to specific features of the landscape and/or reacts to impacts and changes". A bioindicator is an efficient method of detecting changes in an environment. It is rarely possible to sample the effects of impacts and changes on all taxa of a particular habitat; thus a 'good' bioindicator should reflect the changes of other taxa.

It has widely been agreed that the main influence on spider community composition is vegetation structure (Greenstone, 1984; Clausen, 1986; Dennis *et al.*, 1998; McNett & Rypstra, 2000). Several studies have shown that the influence of vegetation structure and not the floral species present is a more important determining factor in spider communities (Clausen, 1986; Dennis *et al.*, 2001). Vegetation structure not only provides web attachment points and affects prey abundances but also provides protection from predators and suitable microclimates. Other aspects of habitat structure are also important. Uetz (1979) noted a positive influence of deep leaf litter layers on spider species richness.

Within a microhabitat spiders can utilise many different niches. This is facilitated by two main factors: differences in behavioural strategies and differences in body size. Uetz (1999) used information on species' foraging behaviour and habitat usage to classify the families into the following guilds: foliage runners, ground runners, ambushers, sheet web builders, orb web weavers and space web weavers. These behavioural strategies have allowed spiders to fill a wide range of niches within forests. Spiders may be found living in the gaps in coarse soil, in leaf litter and ground vegetation, in the upper field layer, and also in the crevices of tree trunks and in the canopy. Species exhibiting these different strategies are able to avoid interspecific competition. Interspecific competition between spiders is further reduced by the fact that some species are nocturnally active while others are diurnal. For example two spiders which have similar body sizes and are therefore likely to handle similar prey are the active hunters *Pardosa nigriceps* and *Clubiona compta*. Both are usually found on tall vegetation and bushes (McFerran, 1997), but while *P. nigriceps* is a diurnal hunter, *C. compta* is nocturnal.

Spiders also exhibit a wide range of body sizes. This further reduces niche overlap by allowing them to take advantage of the same microhabitats by utilising different ranges of prey sizes (Enders, 1975). For example the Linyphiid *Lepthyphantes tenebricola* builds a small sheet web to ensnare prey whereas the Lycosid *Trochosa ruricola* is a nocturnal active hunter. Both are often found living close to the forest floor (Roberts, 1993). Not only do they exhibit different hunting strategies, but as *T. ruricola* is over five times the body length of *L. tenebricola,* the Linyphiid favours much smaller prey (Enders, 1975). Other invertebrate groups have also been used as bioindicators. Carabids are frequently used in studies to assess environmental variation. However unlike spiders the primary influence on their communities are ground cover attributes such as litter quality (Niemelä *et al.*, 1996). Spiders inhabit many vertical planes within an ecosystem, from the forest floor, to the herb layer, understorey and canopy layer. Other widely used groups such as Carabids are largely ground dwelling and so do not give scope for assessing environmental variations along a vertical plane.

Spiders are used as indicators of invertebrate biodiversity for several reasons:

1. They are primarily affected by vegetation structure, a factor that changes with habitat and disturbance.
2. They occupy an important place in terrestrial food webs. As both predators and prey they are important in the regulation of invertebrate populations and as a food source for higher organisms. Thus information on these other groups can be inferred from spider assemblages.
3. They are a relatively well known group of invertebrates in terms of ecology and taxonomy, especially in northern temperate Europe.
4. They are relatively immobile and are therefore better suited to indicating changes over small areas than more mobile taxa

5.2 METHODOLOGY

Pitfall traps have been used in many previous studies to sample active ground dwelling spiders, for example Curtis (1980), Downie (1996), Docherty (1997). Pitfall trapping is a quantitative technique whereby trapping effort can be measured by the number of traps set and the duration of trapping interval. Qualitative methods such as sweep netting or timed hand searches can add useful information to species inventories but their time-consuming and weather-dependent nature makes them ill suited to large scale studies.

Pitfalls can be used across a wide range of habitats, as they are not dependent on a particular type of vegetation structure being present (as are beating and sweep netting, for example). Thus they are ideally used in a study with many sites, that includes major variation in the type of vegetation present. However, despite these advantages the results derived from pitfall traps must be treated with caution.

The trapping ability of pitfalls is affected by three factors: species activity, species behaviour and species density. If these remain constant across sites then pitfall catches can be reliably compared (Downie *et al.*, 1996). The efficiency of a trap is based on the activity of the invertebrates moving around the trap. The more active a species the more likely it is to be caught in a trap, and so pitfall traps can only give reliable information about the active ground dwelling species which come into contact with the trap. Thus, a lack of sedentary species caught does not indicate that they are not present. Should traps be placed in an area of dense ground vegetation cover (for example a meadow), the invertebrates around the trap are more likely to be obstructed from coming into contact with the trap than in an area with less vegetation (for example a forest floor). Several studies have found a strong effect of the vegetation structure surrounding a trap, and cast doubt on the validity of using absolute and relative abundance data (Topping & Sunderland, 1992; Melbourne, 1999).

Curtis (1980) concluded that although great caution is needed when interpreting pitfall data, the high number of species sampled argue in favour of their use. Vegetation structure varies widely between many of the sites used in this study. It was therefore decided that spider abundance data would not be comparable between all of the sites. All analyses were therefore based on species presence-absence data.

5.2.1 Sampling protocol

At each site pitfalls traps were set in 4m x 4m plots. Within each site, plots were spaced approximately 50 metres apart in order to increase the likelihood of sampling rare species, and to ensure statistical independence (Digweed *et al.*, 1995). Each plot consisted of five pitfalls, with four placed at each corner of the plot and the fifth in the centre. In each site five plots were established, with the exception of the mix sites which had two plots in the ash stand and five plots in the Sitka spruce stand. This gives a total trapping effort of 25 traps at each site and 35 at each mix site.

Traps were constructed from plastic cups (9 cm depth by 7 cm diameter). A knife was used to cut drainage slits at two locations on the cup, each around 1 cm from the top. Each trap was filled with ethylene glycol (a killing and preserving agent) to a depth of approximately 2cm. A bulb corer approximately the same size as the cup was used to make a hole in the ground. The plastic cup was placed into this hole so that the top edge of the cup was flush with the soil surface.

The majority of sites were sampled between mid June and mid August 2001; the four young ash and mix sites being sampled between mid June and mid August 2002.

Traps were set during two weeks from mid to late May and were left in the ground for approximately nine weeks. This allowed for seasonal variations in the activities of different species during the field season, and for a more precise measure of the species present (Curtis, 1980). Traps were changed three times within this period, with approximately three weeks between each trapping interval, so that a total of 15 traps were collected for each plot.

Due to time constraints, trapping in the mature ash sites (RINC, DEME, BALY and BARN) did not begin until the end of June, and ran for three trapping intervals until the end of August. Three pure Sitka spruce sites (UNIO, MONT and MUNG) were not sampled until the end of July, and ran for two trapping intervals, ending in mid August.

5.2.2 Environmental variables

A one metre squared quadrat was used to record vegetation cover at each trap. Vegetation was classified into the following categories: Ground layer vegetation (<10 cm); lower field layer (>10 cm – 50 cm); and upper field layer (>50 cm - 200 cm). Percentage abundance cover of each vegetation layer was estimated using the Braun-Blaunquet scale (Mueller-Dombois & Ellenberg, 1974). The Braun-Blanquet scale involves giving numerical rankings to a range of percentages (+ = <1% cover; 1 = 1 - 5%; 2 = 6 - 25%; 3 = 26 - 50%; 4 = 51 - 75%; 5 = 76 - 100%). For the quantitative analyses, the appropriate median percent cover value was substituted for the Braun-Blaunquet was taken for each point and divided by 100. A mean was then calculated for each plot. Ground cover of rocks, twigs and bare soil was also recorded in each quadrat.

Litter depth was measured at two random locations in each plot and from this a mean was calculated. Two soil samples were taken from different sides of each plot. A bulb corer was used to extract the top layer of substrate (both soil and litter) to a depth of 15cm. Soil moisture and organic content of soil were calculated (for soil methodology see Grimshaw (1989) Note that soil moisture is only fully comparable within sites as soil was collected on different days with varying weather conditions.

Percentage cover of deadwood and its condition was also estimated in each plot using the methodology described in Section 4.2.1.2.

Environmental variables were measured between mid July and mid August for both 2001 and 2002 field seasons.

5.2.3 Species classification

The available literature on spiders in Ireland was used wherever possible to classify species into the following habitat preferences: forest, open or generalists (see Appendix 2). One species, *Lepthyphantes nebulosus* was classified as 'other', normally being associated with houses and other man made structures. For a few species, literature was not available on their ecology in Ireland, so information from UK sources was used. The spider species identified were divided into two functional groups: web dwellers and active hunters. The Web dwellers include web araneophages (species which inhabit the webs of other spiders and hunt them as prey), orb web, retreat web, scaffold web and sheet web weavers The active hunters consists of ambush, diurnal active and nocturnal active hunters (see Appendix 2).

Spiders were identified to species level. Due to the inaccuracy of identifying juveniles they were excluded from analyses. Nomenclature follows (Roberts, 1993).

5.2.4 Data Analysis

MONT was excluded from analysis as the traps at this site yielded insufficient data due to the fact that they were tampered with. UNIO and MUNG were only included in pairwise analyses with the Sitka spruce mix sites as they had a lower sampling effort than the other sites. SUNS was excluded from analyses involving habitat variables, as these data were not collected.

5.2.4.1 Analyses of assemblage structure

We carried out analyses on all the sites, and on sub-groups of particular structural classes. For ordinations, data for each plot were calculated by combining species data from the five pitfall traps in a plot over the three sampling periods. We used global non-metric multidimensional scaling analysis (NMS; see Section 2.5.3), flexible-beta cluster analysis (with $\beta = -0.25$) and indicator species analysis for examining assemblage structure. All analyses were carried out using PC-Ord (McCune & Mefford, 1997). For the NMS and cluster analyses we used the Sørensen (also known as Bray & Curtis) distance measures. The parameter set-up that we used for the NMS analyses is shown in Table 33. Where the NMS analysis produced a solution with more than two axes, the axes that explain the highest percent of variance in distance matrix were used for graphical representation of the results. We examined the correlations of potentially relevant environmental variables with the ordination axes.

Table 33. Standard parameter set-up used for NMS.

Parameter	Value used
Number of axes	6
Number of runs with real data	20
Stability criterion	0.001
Iterations to evaluate stability	10
Maximum number of iterations	250
Step down in dimensionality	Yes
Initial step length	0.20
Starting coordinates	Random
Number of runs of Monte Carlo test	50

We compared the similarity of species assemblages in the ash and Sitka spruce components of the mix sites by calculating pairwise Sørensen similarity coefficients between all possible combinations of plots within these sites (Sørensen, 1948). We then compared the mean similarity between ash-Sitka spruce pairs with that of Sitka spruce-Sitka spruce pairs. We used a two-way factorial ANOVA, with the pair type as a fixed factor and site as a random factor, to test these comparisons within each age class.

5.2.4.2 Trends in species richness between forest types and across the age cycle

We used a two-level nested design ANOVA (with stand structural type as the nested factor within the main factor, canopy species) to identify differences in species richness between the Sitka spruce and ash stands. Plot data were used as the sampling units. We used this design, rather than a full factorial design, because structural groups in Sitka spruce and ash are not directly comparable. Where the assumptions of normality and homogeneity of variance were violated, this is recorded in the text.

We used paired t-tests to analyse differences in total species richness between: the Sitka spruce (two plots adjacent to the ash) and ash compartments of the mixed stands; the mixed sites (two ash plots and three adjacent spruce plots) and the matching pure Sitka spruce sites; and the Sitka spruce component of the mixed sites and the matching pure Sitka spruce sites. To correct for differences in sampling effort the same number of plots were used for these comparisons. These analyses were all carried out separately for the various age classes sampled (age classes 1, 2 and 4). We did not use the structural groups for these analyses because the paired samples did not always fall within the same structural groups.

We used one-way ANOVA with Tukey HSD (or Kruskal -Wallis test, hereafter known as H, when variances were not homogeneous) to compare species richness between structural and cluster groups within each forest type (Sitka spruce and ash). Plot data were used. We carried out the above analyses on total species richness, and on the species richness of relevant species groups. These analyses were carried out using SPSS (2001)

5.2.4.3 Relationships between spider species richness and habitat variables

We investigated relationships within the following groups that were identified using cluster analysis and NMS ordination in Section 5.3.1 and 5.3.1.2 below: pre-thicket mix; pure pre-thicket ash/ pre-thicket spruce mix; mature ash; mid/mature spruce; open thicket/ open mature spruce. We used these cluster groups, rather than the structural groups, to avoid major differences in assemblage structure within structural groups obscuring relationships between biodiversity and forest habitat characteristics.

We used correlation analyses to investigate relationships between species richness and environmental variables, and only carried out analyses where there could be a potentially meaningful ecological relationship. Where we found significant relationships we investigated the form of the relationship in more detail, examining the ecological characteristics of the species and sites involved. In tests where multiple correlations are carried out there is an increased probability of making a Type 1 error. Bonferroni corrections can account for this error by means of adjusting the significance level by correcting for the number of tests. However it is often inadvisable to carry out Bonferroni correlations when only a relatively low number of correlations are being carried out (Table 34) as the significance of real relationships may be lost. Therefore all significant relationships were viewed with caution if the correlation did not appear to be ecologically meaningful. For all correlation analyses we also carried out partial analyses with organic content area as the covariable. Organic content of soil may vary between sites and reflect differences in the nature of the soil unrelated to forestry cover. The environmental variables used for each group are shown in Table 34. All analyses were carried out using SPSS (2001).

Table 34. Environmental variables used in correlations with species richness for each cluster group

Cluster group	Ground layer	Lower field layer	Upper field layer	Canopy cover	Needle litter cover
Pre-thicket mix	√	√	√	√	
Pure pre-thicket ash/ pre-thicket spruce mix	√	√	√	√	
Mature ash	√	√	√	√	
Mid/mature spruce	√	√	√	√	√
Open thicket/ open mature spruce.	√	√	√	√	√

Cluster group	Leaf litter cover	Soil cover	Twig cover	Dead wood cover	Litter depth	Organic content
Pre-thicket mix						√
Pure pre-thicket ash/ pre-thicket spruce mix	√	√	√	√		√
Mature ash	√	√	√	√		√
Mid/mature spruce	√	√	√	√	√	√
Open thicket/ open mature spruce.	√	√	√	√	√	√

5.2.4.4 *Analyses of habitat variables*

We carried out analyses on the habitat variables collected for all sites. We used NMS to compare the ordination of sites using environmental variables with the ordination of sites using species data. We used one-way ANOVA with Tukey HSD (or Kruskal-Wallis test, hereafter referred to as H, when variances were not homogeneous) to compare cluster groups within each forest type (Sitka spruce and ash). Plot data were used.

5.3 RESULTS

There were a total of 18730 spiders collected in 139 species during this study. Of these species 15 were classified as having a preference for forest habitats and 19 were classified as having a preference for open areas (see Appendix 2). Of the spiders collected 4012 were juveniles and so were excluded from analysis.

We identified spider species that were new to each of the 14 counties included in this study (Table 35). These amounted to a total of 300 new county records, whose distribution is largely a reflection of previous sampling effort in each of these counties, as well as the number of sites from each county that were included in this study. The least new records were recorded for counties around Dublin or those situated close to national parks. The highest number of new county records (52) was recorded from Co. Limerick.

From the number of new county records it is clear that much of the distribution of Irish spiders is still unknown. There is no Invertebrate Red Data Book system in Ireland for the conservation status of spider species.

One new species to Ireland was recorded: *Baryphyma maritinum*. This species has only been found in a few localities in England along the East Coast from Suffolk to Humberside. It was typically recorded from marram grass on dunes in these areas (Roberts, 1993). During this study one male was found in the ash component of KILM, a five year old mix site. KILM is in Co. Cork, but not close to the coast, the pre-planting habitat was improved grassland.

Table 35. New county records identified by this study

County	Species
Carlow	*Theonoe minutissima, Meta mengei, Agyneta olivacea, Ceratinella brevis, Erigone arctica, Erigone longipalpis, Hilaira excisa, Lepthyphantes nebulosus, Lepthyphantes tenebricola, Maro minutus, Metopobactrus prominulus, Micrargus herbigradus, Porrhomma pallidum, Saaristoa abnormis, Walckenaeria dysderoides, Walckenaeria nodosa, Walckenaeria vigilax, Agyneta ramosa*
Clare	*Clubiona trivialis, Pirata latitans, Robertus neglectus, Zora spinimana, Agyneta decora, Asthenargus paganus, Bathyphantes parvulus, Dicybium tibiale, Lepthyphantes flavipes, Lepthyphantes tenebricola, Maro minutus, Meioneta saxatilis, Metopobactrus prominulus, Pelecopsis nemoralis, Pocadicnemis juncea, Porrhomma egeria, Saaristoa firma, Walckenaeria atrobtibialis, Agyneta ramosa*
Cork	*Agroeca proxima, Antistea elegans, Pirata uliginosus, Theonoe minutissima, Zora spinimana, Agyneta decora, Asthenargus paganus,* ***Baryphyma maritinum****, Bathyphantes parvulus, Ceratinella brevipes, Dicybium nigrum, Dicybium tibiale, Diplostylor concolor, Metopobactrus prominulus, Micrargus herbigradus, Micrargus subaequalis, Pocadicnemis juncea, Pocadicnemis pumila, Porrhomma pallidum, Saaristoa firma, Walckenaeria cuspidata, Walckenaeria nudipalpis, Walckenaeria vigilax,*
Galway	*Theridion instabile, Aphileta misera, Asthenargus paganus, Bathyphantes parvulus, Dicybium tibiale, Gongylidum rufipes, Hilaira excisa, Kaestneria pullata, Lepthyphantes obscurus, Lepthyphantes tenebricola, Meioneta saxatilis, Micrargus herbigradus, Micrargus subaequalis, Pocadicnemis juncea, Porrhomma cambelli, Porrhomma egeria, Porrhomma pallidum, Taranucnus setosus, Walckenaeria atrobtibialis, Walckenaeria dysderoides, Walckenaeria nudipalpis,*
Kerry	*Agroeca proxima, Theonoe minutissima, Allomengea scopigera, Aphileta misera, Agyneta olivacea, Asthenargus paganus, Bathyphantes parvulus, Centromerus dilutus, Dicybium tibiale, Gongylidum rufipes, Hilaira excisa, Lepthyphantes flavipes, Lepthyphantes tenebricola, Maro minutus, Metopobactrus prominulus, Micrargus herbigradus, Oedothorax gibbosus, Pocadicnemis pumila, Porrhomma egeria, Saaristoa firma, Walckenaeria nodosa, Walckenaeria vigilax,*
Kildare	*Agyneta decora, Asthenargus paganus, Centromerus dilutus, Ceratinella scabrosa, Dicybium tibiale, Diplocephalus picinus, Erigone hiemalis, Gongylidiellum vivum, Lepthyphantes alacris, Lepthyphantes flavipes, Lepthyphantes obscurus, Lepthyphantes tenebricola, Linyphia hortensis, Linyphia triangularis, Maro minutus, Micrargus herbigradus, Microneta viaria, Oedothorax retusus, Saaristoa abnormis, Saaristoa firma, Tapinocyba insecta,*
Laois	*Pardosa palustris, Pirata latitans, Trochosa terricola, Robertus lividus, Theonoe minutissima, Theridion instabile, Agyneta decora, Asthenargus paganus, Ceratinella scabrosa, Dicybium tibiale, Diplocephalus latifrons, Hilaira excisa, Lepthyphantes alacris, Lepthyphantes pallidus, Lepthyphantes tenebricola, Macrargus rufus, Maro minutus, Maso sundevalli, Micrargus herbigradus, Monocephalus fuscipes, Oedothorax fuscus, Porrhomma egeria, Porrhomma pallidum, Saaristoa abnormis, Saaristoa firma, Tapinocyba pallens, Walckenaeria nudipalpis, Walckenaeria vigilax,*
Limerick	*Pardosa nigriceps, Theridion instabile, Meta mengei, Meta merianae, Pachygnatha degeeri, Oxyptila trux, Agyneta conigera, Agyneta decora, Agyneta olivacea, Agyneta ramosa, Agyneta subtilis, Asthenargus paganus, Bathyphantes gracilis, Bathyphantes nigrinus, Bathyphantes parvulus, Centromerus dilutus, Dicybium nigrum, Dicybium tibiale, Diplocephalus latifrons, Dismodicus bifrons, Erigone hiemalis, Gongylidiellum vivum, Hilaira excisa, Lepthyphantes alacris, Lepthyphantes cristatus, Lepthyphantes flavipes, Lepthyphantes obscurus, Lepthyphantes pallidus, Lepthyphantes tenebricola, Lepthyphantes zimmermanni, Leptorhoptrum robustrum, Lophomma punctatum, Maro minutus, Micrargus herbigradus, Micrargus subaequalis, Microlinyphia pusilla, Monocephalus fuscipes, Neriene peltata, Oedothorax gibbosus, Oedothorax retusus, Pelecopsis nemoralis, Pelecopsis parallela, Pocadicnemis juncea, Pocadicnemis pumila, Porrhomma egeria, Porrhomma pallidum, Saaristoa abnormis, Saaristoa firma, Walckenaeria acuminata, Walckenaeria*
Offaly	*Theridion instabile, Bathyphantes nigrinus, Cnephalocotes obscurus, Dicybium tibiale, Kaestneria pullata, Lepthyphantes nebulosus, Leptorhoptrum robustrum, Meioneta saxatilis, Pocadicnemis juncea, Walckenaeria vigilax,*
Sligo	*Hahnia nava, Agyneta decora, Asthenargus paganus, Bathyphantes gracilis, Bathyphantes*

County	Species
	nigrinus, Centromerus dilutus, Dicybium tibiale, Diplocephalus latifrons, Dismodicus bifrons, Gongylidiellum vivum, Lepthyphantes alacris, Lepthyphantes cristatus, Lepthyphantes ericaeus, Lepthyphantes flavipes, Lepthyphantes pallidus, Lepthyphantes tenebricola, Leptorhoptrum robustrum, Maro minutus, Micrargus herbigradus, Monocephalus casteneipes, Pelecopsis nemoralis, Porrhomma pallidum, Saaristoa firma, Walckenaeria acuminata, Walckenaeria dysderoides, Walckenaeria nudipalpis,
Tipperary	*Clubiona diversa, Agyneta conigera, Agyneta decora, Agyneta olivacea, Asthenargus paganus, Bathyphantes parvulus, Cnephalocotes obscurus, Dicybium tibiale, Diplocephalus latifrons, Erigone longipalpis, Hilaira excisa, Kaestneria pullata, Lepthyphantes alacris, Lepthyphantes cristatus, Lepthyphantes nebulosus, Lepthyphantes obscurus, Lepthyphantes tenebricola, Maro minutus, Meioneta saxatilis, Metopobactrus prominulus, Micrargus herbigradus, Neriene montana, Oedothorax gibbosus, Pocadicnemis juncea, Porrhomma egeria, Porrhomma pallidum, Saaristoa abnormis, Saaristoa firma, Tapinocyba pallens, Walckenaeria atrobtibialis, Walckenaeria nudipalpis, Walckenaeria vigilax,*
Wexford	*Theonoe minutissima, Asthenargus paganus, Ceratinella scabrosa, Dicybium tibiale, Diplocephalus latifrons, Dismodicus bifrons, Lepthyphantes alacris, Lepthyphantes tenebricola, Metopobactrus prominulus, Micrargus herbigradus, Porrhomma egeria, Porrhomma pallidum, Saaristoa abnormis, Walckenaeria dysderoides, Agyneta ramosa*
Wicklow	*Asthenargus paganus, Ceratinella scabrosa, Diplocephalus latifrons, Diplocephalus picinus, Erigone hiemalis, Gongylidiellum vivum, Lepthyphantes alacris, Lepthyphantes pallidus, Lepthyphantes tenebricola, Maro minutus, Oedothorax fuscus, Pelecopsis parallela, Porrhomma egeria,*
Waterford	*Lepthyphantes tenebricola, Lepthyphantes tenuis, Monocephalus fuscipes, Oedothorax retusus,*

One female of *Baryphyma gowerense* was found in the age class 2 ash plantation at CorbP2 in Offaly. This species is listed in the British Red Data book as 'insufficiently known'. It has previously been found on the West Coast of Ireland and Wales in brackish marshes and in Norfolk in an inland fen (Roberts, 1993). It has been noted previously in 3 counties in Ireland: a salt marsh in Kerry (Mackie & Millidge, 1970); an inland, non-brackish floodplain (van Helsdingen, 1996); a non-brackish fen in Kildare (van Helsdingen, 1997). van Helsdingen (1996) notes that in one of the life stages of this species it is likely to be able to survive temporary inundation. However, the drainage at CORB was classified as good - moderate**.**

5.3.1 Spider assemblages

5.3.1.1 Ordinations of all sites

The NMS ordination of all sites (Figure 15) shows a separation of the pre-thicket Sitka spruce, pre-thicket ash, ash and pole ash sites from the more mature sites, along Axis 2. The ordination places approximately half of the closed maturing ash sites (COMM P6, COMM P7, and all COOL sites apart from P2) with the younger ash and spruce sites. Within this group the pure ash sites form a slightly tighter cluster than the pre-thicket Sitka spruce sites, which are mostly located around the edge of this cluster.

There is a separation of the mature ash sites along Axis 1. All semi-mature and mature ash sites form a loosely clustered group (the exception being DEME P1 which is more closely clustered with closed-maturing Sitka spruce. This plot was located beneath a layer of Sitka spruce underplanted below the ash canopy. Very little ground vegetation was present, which may explain its similarity to closed-maturing spruce stands). The remaining sites are tightly clustered, though some of the thicket Sitka spruce sites separate out slightly along Axis 2, according to age and cover of the lower field layer. Axis 2 is negatively correlated with factors associated with more open sites, such as lower and upper field layer (Table 36), and positively correlated with forest-related factors such as twig cover, deadwood, ground vegetation and litter depth. This may explain the separation of the younger, more open sites from the more mature sites in Figure 15. Axis 1 is negatively correlated with most of the forest-associated factors, but is positively correlated with needle litter cover and organic content. This may explain the position of the semi-mature and mature ash sites on Figure 15. Organic content is positively correlated with both axes.

The NMS ordination of the tightly clustered group (Figure 45) shows that sites are separated along Axis 3 according to cover of lower field layer. Sites with a scanty cover of the lower field layer include most of the closed-maturing Sitka spruce sites and a few thicket and reopening Sitka spruce sites. Axis 2 is correlated with mean litter depth and needle litter cover which may also explain the separation of sites along this axis. The majority of the mature Sitka spruce sites occurred together with thicket Sitka spruce, and a few mature ash sites, presumably indicating sites with a more complex vegetation structure. However, the mature spruce plot MSOP P4 was located in the group of sites with higher litter cover and depth.

Table 36. Pearson correlations of the environmental variables with the NMS ordination axes of Figure 15.

Environmental variable	Pearson correlation with Axis 1	Pearson correlation with Axis 2
Ground layer vegetation	-0.200	0.437
Lower field layer vegetation	-0.007	-0.622
Upper field layer vegetation	0.257	-0.146
Needle litter cover	0.206	0.612
Leaf litter cover	-0.577	0.019
Soil cover	-0.337	0.019
Twig cover	-0.268	0.450
Deadwood cover	-0.234	0.480
Organic content	0.219	0.306
Mean litter depth	0.088	0.465

5.3.1.2 Cluster analysis

Cluster analysis and the NMS ordination of the sites (Figure 15) suggest the best classification was a separation into 5 groups (Figure 52), this accounts for similarities identified by both methods. Cluster analysis separates the sites into similar groups as those identified in the ordination of all of the sites. However the pre-thicket mix and pure pre-thicket ash/pre-thicket spruce mix groups are not identified as distinct groups in the ordination, but are separated by the cluster analysis.

The first group consists mainly of the ash and Sitka spruce from pre-thicket mix sites, with two closed maturing ash and two pole ash sites, and will be referred to as the pre-thicket mix group. The second group primarily contains pre-thicket ash sites, but also includes some closed maturing ash plots, a pole ash plot and Sitka spruce plots from the pre-thicket mix sites, and will be referred to as the pure pre-thicket ash/pre-thicket spruce mix group. The third group consists entirely of semi-mature and mature ash sites, and will be referred to as the mature ash group. The fourth group includes most of the closed maturing, reopening and mature Sitka spruce sites, those thicket sites with the most closed canopies and two mature ash sites, and will be referred to as the mid/mature spruce group. Group five contains the thicket sites with a less well developed canopy, the mature mix Sitka spruce sites, three closed maturing ash plots and two mature ash plots, and will be referred to as the open thicket/open mature spruce group. These sites probably have sufficiently similar levels of openness or ground vegetation cover to separate them from the more closed sites in group four.

5.3.1.3 *Indicator species analysis*

The pre-thicket mix group has several good indicators which only have high maximum indicator values for that group (Table 37), notably *L. mengei* and *M. sundevalli.*

Table 37. Indicator species and indicator values for the groups identified from the cluster analysis. Only species with a maximum indicator value of 25 or more are included. The maximum indicator value is indicated in bold.

Species	Pre-thicket mix	Pure pre-thicket ash/ pre-thicket spruce mix	Mature ash	Mid/ Mature spruce	Open thicket/ open mature spruce	P value of max indicator
A. paganus	0	0	0	**50**	11	0.001
A. subtilis	1	0	1	11	**43**	0.001
B. gracilis	**36**	**36**	0	1	12	0.001
B. parvulus	**46**	29	0	0	4	0.001
D. tibiale	4	**36**	11	0	10	0.001
D. latifrons	0	1	20	**36**	19	0.001
D. concolor	0	1	**42**	0	0	0.001
G. vivum	7	**30**	0	15	18	0.001
L. alacris	0	0	0	29	**43**	0.001
L. mengei	**38**	0	0	0	0	0.001
L. tenebricola	0	0	**26**	19	16	0.004
L. tenuis	**33**	24	1	2	4	0.001
L. zimmermanni	11	3	20	**26**	**26**	0.001
M. sundevalli	**31**	1	0	1	4	0.002
M. herbigradus	0	5	0	3	**34**	0.001
M. fuscipes	0	11	11	**29**	25	0.001
O. fuscus	0	**28**	5	1	9	0.002
O. gibbosus	5	**45**	0	0	3	0.001
O. retusus	1	**31**	2	0	0	0.001
P. degeeri	2	**58**	0	0	0	0.001
P. amentata	0	**42**	0	0	1	0.001
P. pullata	22	**39**	0	0	1	0.001
P. juncea	23	**34**	0	0	0	0.001
R. lividus	3	4	1	**35**	32	0.001
S. abnormis	5	3	2	33	**34**	0.001
W. acuminata	4	5	3	16	**28**	0.002

Indicator species analysis identified a large number of good indicators for the pure pre-thicket ash/ pre-thicket spruce mix group. It contains *P. pullata*, the only 'open' species with a large indicator value. Six species associated with wet habitats had high indicator values for this group (see Appendix 2). Also present is the species which has the highest maximum indicator value, *P. degeeri*. This species is an orb web weaver when young and requires low vegetation. *O. gibbosus, O. fuscus, O. retusus, P. degeeri, P. amentata and P. pullata* are all good indicators of the pure pre-thicket ash/ pre-thicket spruce mix group. Several species have high indicator values in both the pre-thicket mix and pure pre-thicket ash/ pre-thicket spruce mix groups. These species are probably indicative of more open habitats in general.

In the mature ash group two species are identified as good indicators. *D. concolor* which only has a high indicator value for this group and *Lepthyphantes tenebricola*, which is associated with forest habitats (*L. tenebricola* also has relatively high indicator values in the other groups containing more mature forest). The mid/mature spruce group includes the highest indicator values for two of the forest associated species *A. paganus, M. fuscipes*). *A. paganus* seems to be a particularly good indicator of this group. In the open thicket/open mature spruce group the forest species *L. alacris* as well as *M. herbigradus* and *A. subtilis* are good indicators of this group.

Several species have high indicator values in the mature ash, mid/mature spruce and open thicket/open mature spruce groups. *L. tenebricola* is a known forest associated species and the high indicator values of *D. latifrons* and *L. zimmermanni* indicate that these species have a preference for forests. Several species have high indicator values in the mid/mature spruce and open thicket/open mature spruce groups only, this probably indicates species with a preference for Sitka spruce forests. *L. zimmermanni*, for example has maximum indicator values in both groups.

5.3.1.4 Comparison of the species assemblages in the ash and Sitka spruce components of the mix sites

The mean similarity per site of species assemblages in pairs of Sitka spruce plots and in pairs of ash and Sitka spruce plots are compared in Figure 46. In age class 2, the species assemblages of Sitka spruce plots were significantly more similar to each other than the assemblages of ash plots (age class2, $F_{1,3} = 46.3$, $p = 0.006$; age class 4, $F_{1,3} = 21.1$, $p = 0.04$). In age class 1 there was a significant interaction between the pair type and the site ($F_{3,68} = 6.09$, $p = 0.001$).

5.3.2 Trends in spider species richness between forest types and across the age cycle

5.3.2.1 Overall species richness

The overall mean species richness of ash and Sitka spruce sites was similar: 14.4 ± (0.75 se) in ash (n=60) and 16.4 ± (0.42 se) in spruce (n = 120); however, the difference between the species richness of the Sitka spruce sites and the ash sites was significant ($F_{1,170} = 13.17$, $p = < 0.001$). Trends in spider species richness across structural stage and canopy species are shown in Figure 47. There was a significant difference in species richness among the Sitka spruce structural groups ($H = 19.34$; $df = 4$; $p = <0.001$). Pre-thicket and thicket spruce plantations had the highest species richness of the spruce sites, and the closed maturing and reopening spruce forests had the lowest. Species richness in both semi mature and mature ash were significantly lower than in pre-thicket ash: $F_{4,59} = 9.93$, $p = 0.001$. Mean species richness in closed-maturing ash was significantly higher than in the mature ash sites.

There were no significant differences in total species richness between the following groups: Sitka spruce and ash components of mix stands; mix stands (ash and Sitka spruce together) and matching pure Sitka spruce stands; and Sitka spruce component of the mix and matching pure Sitka spruce. Figure 48 indicates that the spruce component of less mature mixes is generally more species rich than the ash component, whereas in more developed mixes, species richness is higher in the ash component.

5.3.2.2 Habitat specialists

The mean number of forest and open species found in each structural group is shown in Figure 49. Overall there were significantly more forest species found in the Sitka spruce sites ($F_{1,170} = 59.68$, $p = < 0.001$). The mean number of open species was higher in the ash sites, though this was not significant. The pre-thicket sites of both ash and Sitka spruce hold significantly higher numbers of open species than the more mature sites ($H = 36.16$; $df = 4$; $p = < 0.001$ and $H = 49.50$; $df = 4$; $p = < 0.001$ respectively). Open species richness declines over the forest cycle in both ash and spruce, but although reopening Sitka spruce sites did not support any open species, there is a slight increase in numbers of open species in more mature Sitka spruce sites.

In both the ash and Sitka spruce stands there was a higher number of forest species found in the more mature sites. There was a significant difference in the number of forest species among spruce structural groups (H = 55.61; df = 4; p = < 0.001), with the pre-thicket spruce sites holding a markedly lower number of forest species than the more mature sites. The number of forest species found in pre-thicket and pole ash sites was much lower than those found in more mature ash sites. The difference of forest species found among structural groups in ash sites was also significant (H = 25.71; df = 4; p = < 0.001).

As with total species richness, no significant differences in forest species richness or open species richness were found among the following groups: the Sitka spruce and ash components of mix stands; mix stands (ash and Sitka spruce together) and matching pure Sitka spruce stands; and Sitka spruce component of the mix and matching pure Sitka spruce.

Overall the Sitka spruce sites had a significantly higher number of ground layer species than the ash sites ($F_{1,170}$ = 32.81, p = < 0.001; homogeneity of variances were significantly different) (Figure 50). There was also a significant difference in the number of ground layer species found among the Sitka spruce structural groups (H = 21.77; df = 4; p = <0.001), ground layer species richness being lowest in sites with more ground vegetation (pre-thicket spruce sites). The pre-thicket ash sites held significantly higher numbers of ground layer species than more mature ash sites ($F_{4,59}$ = 5.35, p = 0.001). There was no significant difference in the number of low vegetation species found between ash and Sitka spruce sites. The overall trend in both tree species was for a decrease in the number of low vegetation species with structural maturity (Figure 50). This difference was significant in both ash and Sitka spruce sites (H = 13.08; df = 4; p = 0.01 and H = 26.4; df = 4; p = < 0.001 respectively). The pole ash structural group has a very high standard error, this may be due to the low number of sites surveyed in this group (n= 3), thus the results of this group must be viewed with caution.

Active predators were found in all sites apart from semi-mature and mature ash (Figure 51). Overall, ash sites hold significantly more active predators than the Sitka spruce sites ($F_{1,170}$ = 5.85, p = 0.02; homogeneity of variances were significantly different, data significantly deviated from normality. However there is a significant trend of decreasing numbers of active predators with structural maturity in both ash (H = 43.44; df = 4; p = < 0.001) and Sitka spruce sites (H = 53.55; df = 4; p = < 0.001). Sitka spruce sites had a significantly higher total species richness of web dwellers than the ash sites ($F_{1,170}$ = 21.93, p = < 0.001, homogeneity of variances were significantly different). There is a decrease in the number of web dwellers in ash sites with structural maturity (Figure 51). The number of web dwellers in semi-mature and mature ash being significantly lower than in pre-thicket sites ($F_{4,59}$ = 3.91, p = 0.007). There is a significant difference in the number of web dwellers among the Sitka spruce sites (H = 18.73; df = 4; p = < 0.001), with the thicket and mature sites holding the highest numbers of web dwellers.

5.3.3 Trends in spider species richness across cluster groups

There is a significant difference among the species richness of the cluster groups (H = 75.00; df = 4; p = <0.001). With the mature ash group having a much lower mean species richness than the other groups (Table 38). Mean open species richness is significantly different between cluster groups (H = 82.99; df = 4; p = < 0.001). It is negatively associated with canopy closure, being highest in the younger sites of the pre-thicket mix and pure pre-thicket ash/pre-thicket spruce mix groups, and in the more open sites in mid/mature spruce (Table 38). There is a significant difference in the number of forest species found in the different cluster groups (H = 119.5; df = 4; p = < 0.001). The number of forest species increases with structural development within ash and spruce cluster groups (Table 38), the highest number of forest species occurring in mid/mature spruce groups.

Table 38. Mean species richness (± standard error) of Spiders in cluster groups.

	Pre-thicket mix	Pure pre-thicket ash/ pre-thicket spruce mix	Mature ash	Mid/ Mature spruce	Open thicket/ open mature spruce
Total mean species richness	13.55 (± 1.23)	18.41 (± 0.72)	8.38 (± 0.69)	14.41 (± 0.31)	19.68 (± 0.72)
Mean open species richness	1.92 (± 0.24)	2.41 (± 0.32)	0.31 (± 0.12)	0.17 (± 0.05)	0.98 (± 0.17)
Mean Forest species richness	0.31 (± 0.11)	1.10 (± 0.17)	2.19 (± 0.32)	4.40 (± 0.16)	3.70 (± 0.20)

5.3.4 Relationships between spider species richness and habitat variables

5.3.4.1 Overall species richness

Correlations of total species richness with habitat variables were carried out on the five groups identified by the cluster analysis. Significant correlations are shown in Table 39. Total species richness is positively correlated with lower field layer vegetation in the more open sites. This relationship is significant in the pre-thicket mix and pure pre-thicket ash/pre-thicket spruce mix groups. There is also a positive correlation between the number of species found in open thicket/ open mature spruce and lower field layer vegetation. Species richness is negatively correlated with forest-associated variables such as deadwood and twig cover, in the pure pre-thicket ash/pre-thicket spruce mix group. The negative relationship between total species richness and soil cover in this group, and also in the mature ash groups, presumably reflects a lack a ground or lower field layer vegetation cover at these sites. There is a strong significant correlation between total species richness and organic content in the pre-thicket mix group.

Table 39. Correlations of species richness of groups identified by cluster analysis with environmental variables.

Cluster Group	Environmental Variable	Pearson Correlation	P (2-tailed)
Pre-thicket mix, n=20	Organic content	0.57	0.009
	Lower field layer vegetation	0.45	0.05
Pure pre-thicket ash/ pre-thicket spruce mix, n=34	Lower field layer vegetation	0.40	0.02
	Dead wood	-0.50	0.005
	Soil cover	-0.33	0.06
	Twig cover	-0.30	0.08
Mature ash, n=16	Soil cover	-0.47	0.06
Open thicket/ open mature spruce, n=44	Lower field layer vegetation	0.26	0.09

The results of partial correlations of species richness with the same environmental variables and cluster groups as used in Table 39, controlling for the effects of organic content, are presented in Table 40.

In the pre-thicket mix group, the correlation between species richness and lower field layer vegetation is no longer significant when organic content is controlled for. The relationships between species richness and environmental variables in the pure pre-thicket ash/ pre-thicket spruce mix and mature ash groups are only slightly less significant after controlling for organic content, while in the open thicket/open mature spruce group their significance is actually slightly increased.

Table 40. Partial correlations of species richness within cluster groups against environmental variables, controlling for soil organic content.

Cluster Group	Environmental Variable	Partial Correlation Coefficient	P (2 tailed)
Pure pre-thicket ash/ pre-thicket spruce mix	Lower field layer vegetation	0.39	0.03
	Deadwood	-0.50	0.003
	Soil cover	-0.35	0.05
	Twig cover	-0.29	0.09
Mature ash	Soil cover	-0.48	0.07
Open thicket/open mature spruce	Lower field layer vegetation	0.29	0.06

5.3.4.2 *Habitat specialists*

Significant correlations between the species richness of forest and open species and environmental variables, for each of the groups identified by cluster analysis, are shown in Table 41.

Table 41. Correlations of forest and open habitat specialist species richness in the groups identified by cluster analysis with environmental variables

Cluster Group	Habitat Specialist	Environmental Variable	Pearson Correlation	P (2 tailed)
Pre-thicket mix	Open	Ground vegetation	0.62	0.003
Pure pre-thicket ash/ pre-thicket spruce mix	Open	Soil cover	-0.47	0.004
	Open	Deadwood cover	-0.47	0.004
	Open	Twigs	-0.32	0.06
	Forest	Leaf litter cover	0.54	0.001
	Forest	Soil cover	0.45	0.007
	Forest	Ground vegetation	0.36	0.04
	Forest	Twig cover	0.34	0.05
	Forest	Upper field layer vegetation	-0.32	0.07
Mature ash	Forest	Lower field layer vegetation	-0.58	0.02
Mid/Mature spruce	Forest	Upper field layer vegetation	-0.27	0.03
	Open	Canopy cover	-0.31	0.04
Open thicket/open mature spruce	Open	Forest species richness	-0.32	0.04
	Open	Ground vegetation	-0.32	0.04
	Open	Organic content	-0.35	0.02
	Forest	Open species richness	-0.32	0.03
	Forest	Ground vegetation	0.45	0.002
	Forest	Twig cover	0.46	0.002
	Forest	Deadwood cover	0.27	0.08
	Forest	Upper field layer vegetation	-0.48	<0.001

In most of the clusters, open species richness is negatively correlated with forest-associated variables such as deadwood, twigs and soil cover. In the pre-thicket mix group, open species richness is positively correlated with ground vegetation, whereas in the open thicket/open mature spruce group these variables are negatively correlated. In the mid/mature spruce group open species richness is negatively correlated with canopy cover. Forest species richness is positively correlated with ground vegetation and factors associated with forests such as twig and deadwood cover. Forest species are negatively correlated with factors associated with open areas (i.e. herb and upper field layers. In the open thicket/open mature spruce group, forest and open species richness are negatively correlated with each other.

The results of partial correlations of forest species richness and open species richness with the same environmental variables and cluster groups as used in Table 41, controlling for the effects of organic content, are presented in Table 42. On the whole the significant results are unaffected, with small fluctuations in significance values between groups. The significance of most relationships decreases slightly, with the exception of the relationships between open species richness and ground vegetation in the pre-thicket mix group, and between forest species richness and twig cover in the pure pre-thicket ash/pre-thicket spruce mix group, which are slightly more significant.

Table 42. Partial correlations open and forest species richness with environmental variables, controlling for organic content.

Cluster Group	Habitat Specialist	Environmental Variable	Pearson Correlation	P (2 tailed)
Pre-thicket mix	Open	Ground vegetation	0.62	0.005
Pure pre-thicket ash/pre-thicket spruce mix	Open	Soil cover	-0.48	0.005
	Open	Deadwood cover	-0.47	0.005
	Open	Twigs	-0.32	0.07
	Forest	Leaf litter cover	0.53	0.001
	Forest	Soil cover	0.48	0.005
	Forest	Ground vegetation	0.36	0.04
	Forest	Twig cover	0.33	0.06
	Forest	Upper field layer vegetation	-0.34	0.06
Mature ash	Forest	Lower field layer vegetation	-0.59	0.02
Mid/Mature Spruce	Forest	Upper field layer vegetation	-0.22	0.09
	Open	Canopy cover	-0.27	0.08
Open thicket/open mature spruce	Open	Forest species richness	-0.34	0.02
	Open	Ground vegetation	-0.37	0.02
	Forest	Open species richness	-0.34	0.02
	Forest	Ground vegetation	0.45	0.002
	Forest	Twig cover	0.46	0.002
	Forest	Deadwood cover	0.27	0.08
	Forest	Upper field layer vegetation	-0.48	0.001

5.3.5 Trends in environmental variables

NMS ordination of environmental variables (Figure 53) separates plots into similar groups as identified in the cluster analysis (Figure 52) and NMS ordination of all the sites (Figure 52), although the distinction between cluster groups is less well defined than in Figure 15.

Ground vegetation is significantly different among the cluster groups (H = 52.8; df = 4; p = <0.001) with the groups comprising the more mature sites containing the highest ground vegetation cover (Table 43). There is a significant difference in the lower field layer vegetation cover between the cluster groups (H = 80.8; df = 4; p = <0.001). Lower field layer cover, is greatest in those groups which include the less well-developed sites, and lowest in the mid/mature spruce group. There is a significant difference in upper field layer cover among the groups (H = 18.66; df = 4; p = <0.001), with the mature ash group having less upper field layer than any other group.

Needle litter cover was significantly different among groups (H = 126.21; df = 4; p = <0.001), being very high in the mid/mature spruce group, and very low in the pre-thicket mix, pure pre-thicket ash/ pre-thicket spruce mix and mature ash groups. Leaf litter cover was highest in the mature ash groups, the difference among the cluster groups being significant (H = 59.28; df = 4; p = <0.001). Soil cover followed a similar pattern to leaf litter cover and again the differences among cluster groups were significant (H = 32.67; df = 4; p = <0.001). Organic content was significantly different among structural groups (H = 20.76; df = 4; p = <0.001), being highest in the groups containing the more mature spruce stands, and lowest in ash-dominated groups.

Deadwood cover and twig cover are both significantly different among cluster groups (H = 88.77; df = 4; p = <0.001 and H = 71.56; df = 4; p = <0.001 respectively). Cover of these variables was highest in the mature ash and mid/mature spruce groups. Only the more mature spruce sites had relatively high values of litter depth, with the mid/mature spruce group having the highest value. Again, the differences among cluster groups were significant (H = 117.8; df = 4; p = <0.001).

Table 43. Mean values of the environmental variables (± standard error) within the cluster groups. Means are calculated from the percent of cover of each variable.

Environmental Variable.	Pre-thicket mix	Pure pre-thicket ash/ pre-thicket spruce mix	Mature ash	Mid/ Mature spruce	Open thicket/ open mature spruce
Ground vegetation	0.08 (±0.03)	0.09 (±0.02)	0.43 (±0.05)	0.27 (±0.03)	0.40 (±0.04)
Lower field layer	0.50 (±0.04)	0.50 (±0.04)	0.30 (±0.04)	0.07 (±0.02)	0.33 (±0.04)
Upper field layer	0.44 (±0.05)	0.32 (±0.03)	0.13 (±0.04)	0.28 (±0.05)	0.49 (±0.06)
Canopy cover	0.46 (±0.08)	0.52 (±0.05)	0.74 (±0.01)	0.75 (±0.02)	0.59 (±0.04)
Needle litter cover	0 (±0.00)	0 (±0.00)	0.06 (±0.05)	0.62 (±0.04)	0.37 (±0.04)
Leaf litter cover	0.00 (±0.00)	0.04 (±0.02)	0.40 (±0.05)	0.03 (±0.01)	0.09 (±0.02)
Soil cover	0.02 (±0.02)	0.08 (±0.03)	0.17 (±0.04)	0.03 (±0.01)	0.05 (±0.01)
Deadwood cover	0.00 (±0.00)	0.01 (±0.00)	0.12 (±0.03)	0.13 (±0.02)	0.04 (±0.01)
Twig cover	0.00 (±0.00)	0.01 (±0.01)	0.13 (±0.02)	0.10 (±0.01)	0.05 (±0.01)
Litter depth	0.00 (±0.00)	0.00 (±0.00)	0.01 (±0.00)	0.23 (±0.03)	0.11 (±0.03)
Organic content	0.36 (±0.06)	0.22 (±0.02)	0.21 (±0.03)	0.50 (±0.04)	0.47 (±0.05)

5.4 DISCUSSION

5.4.1 Sampling biases

It is important to note the biases of using pitfall traps when considering the results of this survey. Pitfall traps are only an efficient method of collecting ground dwelling invertebrates, thus data involving species which are known to live on low vegetation or shrubs must be viewed with caution. During this survey relatively few of these species were caught (26 low vegetation species, 4 tree and bush species compared to 76 ground layer species). It is likely that most of the individuals of these species that come into contact with the traps have strayed from the microhabitat they usually occupy, due to a rare event such as dislodgement through to animal disturbance. However, it is to be expected that such rare events would occur more often in sites with a greater coverage of vegetation layers. The younger plantations have canopies which are much closer to ground level than those which are more mature. It is therefore more likely in these plantations that species which are associated with bushes and trees will come into contact with pitfall traps than those living in the canopy of trees in mature plantation.

The small size of the pitfall traps means that they are biased towards capturing the smaller ground dwelling spiders, most notably spiders from the family Linyphiidae, whose largest species is 5.5mm in body size in Ireland (Roberts, 1993). The larger active hunting spiders of the family Lycosidae (which have an upper body size range of 12–18 mm (Roberts, 1993) in Ireland) are less likely to be caught, as they can more easily scale the plastic walls of the cups and escape.

5.4.2 Changes over the forest cycle

Spider assemblages vary in relation to both structural development and forest type across the forest cycle. Tree species does not have such a strong effect in the younger sites, whereas tree species has a stronger effect on spider assemblage structure in the more mature stands. The pre-thicket sites of both ash and Sitka spruce forests are distinct from the more mature stands. These sites have yet to experience canopy closure and the species assemblages present are more typical of open habitats. The pre-thicket sites have high species richness and the highest number of species associated with open habitats. The pre-thicket sites had the greatest cover of lower field layer vegetation. Although it must be noted that greater vegetation structure in the pre-thicket sites leads to a higher proportion of species coming into contact with the pitfall traps, it also provides more web attachment points and hiding places for active predators, and also greater prey densities thus allowing more spider species to coexist

Pre-thicket sites of different pre-planting habitats did not appear to be distinct from each other in either spider communities or vegetation structure (using the parameters that were measured). Floristic differences between pre-planting habitat, which may persist up to and beyond canopy closure, are of little consequence to spider communities compared to vegetation structure. Prior to canopy closure the ground vegetation in these sites is generally allowed to grow unchecked, except for spot application of herbicides, whereas different pre-planting management regimes can impact on the ground vegetation of sites (for example grazing on improved grassland), resulting in a wider variety of vegetation structure in unplanted habitats.

The effect of canopy closure on species richness was much more apparent in the Sitka spruce sites than in the ash sites. After canopy closure, lower field layer vegetation cover was much lower in the spruce sites, whereas in the mature ash sites it did not decrease to such a great degree. The ground cover in the closed canopy spruce sites was very homogenous. There was a lack of vegetation cover at all understorey structural levels together with a high coverage of needle litter. This may account for the low species richness at mid/mature spruce sites compared to other spruce sites in the forest cycle. Canopy closure also results in a reduction in the numbers of species associated with open habitats (none were found in the reopening spruce structural group). At this stage, it is likely that many open species associated with pre-planting habitats are lost.

Lower field layer vegetation decreased after canopy closure, however ground vegetation increased during the forest cycle. The presence of a dense upper field layer in some of the more mature sites can lead to the shading out of lower field layer species to the benefit of the ground vegetation. The forest species identified are mostly ground dwellers, and would have a preference for ground vegetation, thus during the forest cycle the number of forest specialist species increases. Species typical of open habitats prefer lower field layer vegetation, thus they decline over the forest cycle.

In the spruce sites there are slightly more forest-associated species found in the reopening sites than in the mature sites. Towards the end of the forest cycle, the species assemblages of spruce sites are more similar to those of thicket spruce sites, which have not completely achieved canopy closure rather than to the species assemblages of mature ash or closed canopy spruce. These mature sites are more open (canopy cover is lower because of successive thinnings) and therefore have a more complex vegetation structure. There are more open species present towards the end of the forest cycle than at the closed-maturing or reopening stage. This group has the highest total species richness, presumably because the presence of the lower field layer allows open species to coexist with forest species which are still present in the more shaded areas.

The species assemblages of mature ash are distinct from those of more mature spruce sites. Mature ash sites hold relatively high numbers of low vegetation species compared to mature spruce, although total species richness and number of ground layer species in these sites was lower than in any other group of sites. Although the highest leaf litter cover recorded in mature ash, litter depth was very low. Many litter-dwelling invertebrate species are important as prey for spiders, especially for members of the family Linyphiidae, which constituted 90% of the spider species found in the ground layer. The lack of structure in the leaf litter may lead to low numbers of prey and consequently low spider species richness. This may also be a contributing factor to the lack of active predators recorded at these sites.

Levels of ground layer and lower field layer cover were high in mature ash sites, yet species richness was much lower than other groups which seem to benefit from high levels of these vegetation layers. In mature ash sites the ground and lower field vegetation layers were nearly all composed of ivy (*Hedera helix*), whereas most of these layers were composed of grasses in the less mature sites and grasses, ferns and brambles in the more mature spruce sites. It is possible that the presence of the ivy does not enhance species richness. In this study the ivy in the mature ash sites were usually classified as lower field layer, being greater than 10cm in height. However, the structure of the ivy maybe less suitable for spiders than lower field layer vegetation types recorded elsewhere. For example, the structure of ivy may not provide many microhabitats for web attachment points or promote high prey densities. This may explain why forest species are negatively correlated with lower field layer in mature ash sites. Total species richness is negatively correlated with soil cover, this is probably due to the effect of ivy which shades out ground species such as mosses.

There was no difference in the number of open species found between the ash and spruce components at the pre-thicket, thicket and mature stages (age classes 1, 2 and 4). These were the stages where the spruce stands were relatively open. Had it been possible to sample age class 3 spruce-ash mixes then a difference might have been seen The ash stands tend to experience canopy closure later in the forest cycle than Sitka spruce (Section 3.3.4) and so have a greater degree of openness at this stage allowing them to support more open species.

Although the presence of an ash stand did not add to the species richness of the Sitka spruce component of the mix there were differences in the species composition between the ash and spruce components. Some species found in the mix sites only occurred in either the ash or the spruce component. Comparison of the similarity of species assemblages in the ash and Sitka spruce components of the mix sites shows that in age classes 2 and 4, the ash component of the mix sites supports a different species assemblage to the Sitka spruce component. This suggests that, adding ash to a Sitka spruce plantation will increase biodiversity at these stages. Because the two forest types support different assemblages of species, having more than one tree species is likely to enhance species richness at the plantation scale.

Given the general lack of published research on spider communities (and indeed on other invertebrates) in Ireland, it was not possible to compare the spider fauna of Irish plantation forests with semi-natural woodlands. Cameron *et al.*, (2004) conducted a large-scale study of spider communities in various environmentally sensitive areas across Northern Ireland which included several semi-natural ash woodlands. The latter sites supported a distinct spider assemblage, of which several of the most abundant species were also found in high numbers in the present study. However there does not appear to be any other published literature on the many other woodland types within Ireland. This highlights the need for the further study of spiders in forested environments, without which it will be difficult to assess the impact of plantation forests on the Irish spider fauna. This is especially important as they have potential for supporting forest specialist spiders; however, further data are required on the spider assemblages in semi-natural and ancient woodlands to determine if plantations can fulfil this role.

5.4.3 Indicators of structural/cluster groups

5.4.3.1 Structural indicators

Examination of the NMS ordinations of all sites using species data (Figure 15) and habitat variables (Figure 53) indicate that sites are separated into very similar groups. This suggests that spider assemblages and the habitat variables that were measured are subject to the same variations, thus the variables recorded are appropriate for indicating changes in spider assemblages.

Species richness in spiders is strongly influenced by vegetation structure. This provides a heterogeneous environment which supports habitats and prey resources. Although this is true for all vegetation levels within a forest, this study focused on the collection of ground dwelling invertebrates. Thus any effects of upper field layer vegetation and canopy cover on the recorded species richness are likely to be indirect. High levels of canopy cover and upper field layer decrease light levels within a forest. This causes lower field layer plant species to decline and in turn more typical forest ground layer plant species to increase. Forest spider species are positively correlated with ground vegetation, thus high levels of canopy cover and the upper field layer indirectly have positive effects on species richness. The most important determinant of total spider species richness is lower field layer cover, sites with higher percentage of cover supporting more species. The principle mechanism by which lower field layer influences spider species richness is likely to be through the diversification of habitat structure, which facilitates the coexistence of a greater number of spider species, rather than by an increase in plant species diversity. The positive effect of lower field layer can be seen within the cluster groups containing pre-thicket sites, and also in the open thicket/ open mature spruce group. In this latter group the growth of lower field layer is facilitated by thinnings or wind throw events, indicating that the degree of openness of a forest affects the species richness. Lower field layer can also be used to distinguish between cluster groups; for example the mid/mature spruce group is the only one with a very low lower field layer cover (due to a closed canopy) and this is likely to be the main cause of the low spider species richness in this group.

Within the mature ash structural group lower field layer is not an indicator of high species richness. Although canopy cover is high in these sites, they have relatively high levels of lower field layer cover. This is doubtless because mature ash stands allow more light through to the vegetation below and are also more open than the Sitka spruce (Section 3.3.4). Because ash is deciduous, evergreen and vernal plant species can make use of increased light during the winter and early spring. Environmental variables such as ground cover of needle litter, leaf litter, twigs, deadwood and soil which are typical of more mature forest environments have an overall negative effect on species richness. After canopy closure most vegetation is shaded out and structural diversity of the habitat is low. These variables are indicators of low overall species richness within cluster groups. However it must be noted that forest specialists are positively affected by these variables.

5.4.3.2 Species indicators

Although several species were identified as indicators in each of the cluster groups it is unlikely that these will be more useful than structural indicators in terms of forest management. It will nearly always be more efficient method to use the presence of certain habitat features to indicate spider community composition and species richness rather than identifying indicator species of spiders. When ecological surveys are necessary studying a sub-section of the spider community (i.e. ground dwellers or canopy dwellers) will yield more meaningful results than attempting to identify several indicator species.

The mature ash forests were distinct from the other groups; *Diplostylor concolor* was identified as a good indicator of this group. *D. concolor* is a ground dwelling species which builds a sheet web across the vegetation. Ground vegetation was dominated by ivy in the mature ash sites and it is possible that *D. concolor* has a preference for building webs on or near ivy, either because of its specific growth form, or because of the prey for which it provides a refuge. However, without more detailed knowledge of this species' ecology the reason for its strong association with this group cannot be determined.

5.4.3.3 Rare species

During the forest cycle the number of species associated with open habitats declines. Two of these species are ecologically interesting. *Baryphyma gowerense,* which was found in CORB, a pre-thicket ash plantation and *B. maritinum*, which was found in the ash component of a pre-thicket mix site (KILM). Little is known about the ecology and distribution of these species in Ireland or Great Britain. Only one specimen of each species was found and so it is not possible to determine whether these species were vagrants or whether they have established populations at these sites.

Several of the forest species are known from only a few counties. *Walckenaeria dysderoides*, which is typically found in needles and moss, has rarely been recorded before this study. It occurred in the mature spruce sites of KILA and SINB, and one specimen was also found in GLYN. Other forest species such as *Monocephalus casteneipes* and *Tapinocyba pallens* had only previously been recorded in a few counties (van Helsdingen, 1996; Cawley, 2001). They have relatively widespread distributions in the UK, and this is probably true for Ireland as well. However as there has been a lack of study in Irish forests in general it is reasonable to assume that they have not been widely recorded before because they are not found away from forest habitats. As a consequence of the lack of forest habitats in Ireland, the status of forest species such as these is rare.

5.5 CONCLUSIONS

There is no substitute for gaining real data on ground dwelling spider communities. However, the results of this survey suggest that measurement of the structural characteristics of the ground flora will give insight into the species richness of spiders in a forest. In general, sites with a more open canopy will contain a more complex vegetation structure, which supports a greater number of spider species. This can be seen in the younger ash and spruce sites as well as in the mature spruce forests.

Forest species richness increases over the forest cycle, and although it is not indicative of total species richness, it is nevertheless an important component of spider biodiversity in Ireland. The paucity of natural woodlands in Ireland means that populations of some forest species could be sustained by plantations. An assessment of the relative importance of total and forest spider species richness is needed. Since they show opposite trends with canopy closure, the question as to which is more important and which should be managed for needs to be addressed.

At the plantation scale, spider species richness is enhanced if both Sitka spruce and ash components are present.

It is important to note that the findings of this study relate to ground dwelling spiders and do not necessary reflect the patterns in spider species at other levels of the forest strata.

5.5.1 Management recommendations

Sites that retain areas of open habitat throughout the forest cycle will support a greater species richness and a greater richness of assemblage. Multiple thinnings are likely to have a substantial positive affect on ground species diversity. Forest managers should encourage the growth of lower field layer vegetation species at all stages of the forest cycle, whilst retaining features typical of a mature forest. This will enhance the biodiversity of open and forest species at a site level.

On a landscape scale, a mosaic of different aged plantations adjacent to each other will provide the heterogeneity of habitat types necessary to sustain both open and forest specialists.

5.5.2 Modifications to the *Forest Biodiversity Guidelines*

The management recommendations identified by this study are similar to those of the *Forest Biodiversity Guidelines* (Forest Service, 2000b). However, there is no explicit mention of invertebrates in the current biodiversity guidelines. It is recommended that the guidelines specifically mention the management of forests in order to promote the biodiversity of invertebrates.

Although more detailed knowledge of forest dwelling invertebrates is needed, it would be difficult for forest managers to carry out a study of invertebrates within plantations, and the guidelines should focus on identifying structural indicators within sites. Vegetation structural diversity should be promoted at all stages of the forest cycle, especially in mid-rotation forests, where the effects of canopy closure are strongest.

6 HOVERFLIES

6.1 INTRODUCTION

The Syrphidae (popularly known as hoverflies in Europe and flower flies in America) are one of the largest families of Diptera (true flies). Around 6000 species have been described (Sommagio, 1999) with approximately 700 in Europe (Speight *et al.*, 2000b) and 173 in Ireland (Speight, 2000a). Adult hoverflies feed on pollen or nectar, but hoverfly larvae show a wide range of feeding habitats, including phytophagy (feeding on live plant material), saprophagy (feeding on decaying plant material), mycophagy (feeding on fungal fruiting bodies) and zoophagy (feeding on other insects).

Hoverflies have been recommended as a suitable group for use in site evaluation due to the relative lack of identification problems, the availability of reliable species lists, good knowledge of species habitat associations and larval microhabitats, occurrence in nearly all terrestrial and freshwater habitats, the range of generation times providing information about short and longer term changes in site conditions, and the availability of standardised sampling techniques (Speight, 1986; Speight *et al.*, 2000b). Hoverflies have been used as indicators of agricultural pollution, habitat disturbance and habitat quality (Sommagio, 1999). Some examples include their use as indicators of ancient woodland in Britain (Stubbs, 1982) and assessment of ecosystem function in alluvial habitats in France and Ireland (Castella *et al.*, 1994; Castella & Speight, 1996).

In recent years, information about European hoverflies has become widely accessible through the development of the *Syrph The Net* database (Speight *et al.*, 2003b). This includes coded information on species macrohabitats, microsites, traits and range and status; it is updated annually. The database can be used to analyse recorded species assemblages in relation to their habitat associations. The database also includes a detailed review of the Irish hoverfly fauna. The availability of this database has made hoverflies a powerful tool for biodiversity assessment.

There have been few studies of hoverfly assemblages of European forests. Humphrey *et al.* (1999) studied hoverfly assemblages of a range of British plantation forests. They reported that hoverfly species diversity was greater in plots with higher field layer cover and lower in plots with high canopy cover. Watt *et al.* (1997) studied hoverfly assemblages of Scottish Sitka spruce plantations with varying degrees of birch invasion. They reported that hoverfly species diversity did not appear to be influenced by the presence of birch, was particularly low in natural birch woods and was higher in older (15-20 years) compared to younger (5-10 years) spruce plantations. However, the results of both these studies are difficult to interpret due to the potential of the “clearing area effect” (see Section 6.4.1) to have biased their data. Kula (1997) studied the hoverfly fauna of spruce stands subject to varying degrees of pollution damage in the Czech Republic. He reported higher species richness of hoverflies in stands damaged by air pollution and attributed this to the more open canopy in these stands allowing the development of herb and grass layers in these stands.

Hoverfly nomenclature in this report follows Speight at al. (2001a). Full species names are given in Appendix 3.

6.2 METHODS

6.2.1 Sampling sites

For logistical reasons we were not able to sample the full range of sites that were included in the survey design (see Section 2.2). We did not sample the following sites:

- The pure Sitka spruce sites in the age class 1 pure and mixed Sitka spruce pairs.
- The age class 1 pure ash sites.

In addition, cattle trampled the malaise traps that we installed in one of the age class 2 pure ash sites (CORB) during the first sampling period. Therefore, we did not collect any hoverfly samples from this site.

6.2.2 Hoverfly sampling

We used malaise traps (Southwood, 2000) to sample hoverflies. In most sites, we used two traps. The exceptions were the ash component of the mixed sites and one ash age class 5 site, where we used one trap.

We located malaise traps at least 100 m apart to attempt to make each trap an independent sample. Where possible, we located traps 100 m from the edge of the forest type being surveyed. This was not, however, possible for some sites, such as the ash component of the mixed sites. There are no good data on the effective sampling range of a malaise trap for hoverflies, and it is likely to vary between species and in relation to the habitat and topographical features of the site. Therefore, 100 m is an arbitrary criterion, but we consider it sufficient:

- to make the malaise traps largely independent with respect to localised microhabitat features (e.g. wet flushes); and
- to greatly reduce the incidence of hoverflies from outside the habitat being sampled.

In sites with closed, or partially-closed canopies, we located malaise traps in the largest canopy gaps or clearings that we could find. We generally positioned the traps so that the long axis was orientated approximately north-south, with the collection bottle at the southern end, unless site conditions dictated otherwise. Hoverflies that enter malaise traps tend to fly towards the point of highest light intensity, so placing traps under a closed canopy would greatly reduce their effectiveness, while orientating the traps north-south will maximise their effectiveness. Where partially shaded rides were present, we included these as potential locations for malaise traps. However, we did not locate traps on forest roads or wide, continuously unshaded rides, as these are likely to be used as flight paths by non-local hoverflies.

We installed the malaise traps in most sites in mid-late June and operated them continuously for a nine-week period, until mid-late August (see Table 44). The exceptions were the pure Sitka spruce sites in the age class 4 mix pairs. Due to time constraints we were not able to install malaise traps in these sites until early July. The start dates of these traps coincided with the first change of the malaise traps in the mixed sites with which they were paired, and we operated these traps for a six-week period. This sampling period is greater than the minimum recommendation by Speight et al. (2000b) for adequate sampling of the syrphid fauna of a target site; however, the age class 5 pure ash and the pure Sitka spruce sites in the age class 4 mix pairs were not sampled for the recommended ten day period in June.

During the sampling period, we collected the contents of the traps at approximately three week intervals. On each collection date, we recorded details of any damage to the traps, and repaired the damage where necessary. Also, where necessary, we cut back any herbaceous vegetation that was blocking the central panel of the trap.

Table 44. Malaise trap sampling durations. See Section 2.2.1 for explanation of the site types.

Site type	Start date	Finish date
Geographic clusters	18-20/6/01	20-22/8/01
Age class 1 mix pairs	13-18/6/02	16-22/8/02
Age class 4 mix pairs - mix sites	15-17/6/01	15-16/8/01
Age class 4 mix pairs - pure Sitka spruce	1-4/7/01	14-16/8/01
Age class 1 pure ash	13-17/6/02	16-19/8/02
Age class 5 pure ash	27/6 - 1/7/01	29-30/8/01

6.2.3 Hoverfly identification

We extracted all the hoverflies from the malaise samples. We used Stubbs and Falk (2002) to identify to genus level. We used the same authority for identifying to species level, but supplemented this with keys for particular genera as listed in Table 45. Voucher specimens were checked by Dr. Martin Speight of the National Parks and Wildlife Service.

Table 45. Literature used for hoverfly identification.

Genus	Literature used
Platycheirus	(Speight & Vockeroth, 1988; Speight & Goeldlin de Tiefenau, 1990; Rotheray, 1998; Van Steenis & Goeldlin de Tiefenau, 1998)
Eupeodes	(Dusek & Laska, 1976)
Melangyna	(Speight, 1988b)
Parasyrphus	(Speight, 1991)
Syrphus	(Goeldlin de Tiefenau, 1996; Speight, 1999b)
Chrysogaster	(Speight, 1980)
Melanogaster	(Speight, 1980)
Neroascia	(Speight, 1988a)
Sphegina	(Thompson & Torp, 1986)
Eristalis	(Hippa *et al.*, 2001)
Helophilus	(Speight, 1988b)
Chalcosyrphus	(Speight, 1999a)
Xylota	(Speight, 1999a)

6.2.4 Habitat recording

6.2.4.1 Trap location

We recorded the area of the clearing or canopy gap in which each trap was located. We did this by visual estimation of the length and breadth of the clearing, each distance being the distance between the edges of the canopy. We then calculated the clearing area as the rectangular area, with approximate adjustments for any irregularities in the clearing shape.

We used tree heights recorded for the nearest vegetation survey sample plot to provide an indication of the height of the trees adjoining the clearing.

6.2.4.2 Macrohabitats

We used the macrohabitat classification defined by Speight *et al.* (2001a). This classification is based upon the CORINE classification (Commission of the European Communities, 1991), but with modifications to reflect habitat characteristics of importance to hoverflies that are not covered by CORINE. A special feature of this macrohabitat classification is the concept of supplementary habitats. A supplementary habitat is a habitat feature that can occur in association with a macrohabitat (e.g., a wet flush in a forest). Supplementary habitats are used to refine the coding of the association of hoverfly species with macrohabitats: in many cases, a hoverfly species is only likely to occur in a particular macrohabitat if the supplementary habitat is present. We made three modifications to the *Syrph The Net classification*: we included *Molinia* grassland on mineral soils (CORINE 37.31) in the humid oligotrophic (gen.) grassland category (STN code 23122), we distinguished between hedges and treelines (see Table 54) and we extended the definition of the temporary pool supplementary habitat (see Table 55).

We recorded the spatial extent of each macrohabitat type in a 100 m radius around each malaise trap. In pre-thicket forests we recorded both the forest macrohabitat type and a secondary macrohabitat type defined by the ground vegetation. We further sub-divided forest macrohabitats into separate parcels where there was significant variation in dominant canopy species, canopy structure, or secondary macrohabitat type.

6.2.4.3 *Habitat parameters*

We recorded habitat parameters separately for each forest habitat parcel. The principal method used was to walk 100 m transects from the trap along four perpendicular compass bearings.

6.2.4.3.1 *Canopy cover*

Each forest parcel was assigned a single canopy cover category, as defined in Table 46.

Table 46. Canopy cover definitions.

Category	Definition
Open	Adjacent trees do not form continuous canopy
Large gaps	Gaps greater than canopy spread of average canopy forming tree
Medium gaps	Gaps 0.25-1 x the canopy spread of average canopy forming tree
Small gaps	Gaps less than 0.25 the canopy spread of average canopy forming tree
Closed	No gaps

6.2.4.3.2 *Clearings*

We defined a clearing as a canopy gap greater than three times the canopy spread of average canopy forming tree. The frequency of clearings in each forest parcel was recorded using the scale defined in Table 47.

Table 47. Frequency scale for recording clearings.

Category	Definition
Abundant	Open canopy
Frequent	A few large clearings or many (> 10 in 3 ha) small clearings
Occasional/Rare	One large clearing or a few (< 10 in 3 ha) small clearings

6.2.4.3.3 *Tree/shrub species*

We recorded the dominant canopy species and any additional tree/shrub species present. In age class 3-5 sites we also recorded the dominant understorey tree (see Table 48) species, if present. Where discrete patches of trees/shrubs were present (e.g. a hedgerow/treeline or a blackthorn (*Prunus spinosa*) thicket), these were recorded as separate macrohabitats, and the tree/shrub species were not recorded under the main forest macrohabitat.

6.2.4.3.4 *Vegetation structure*

We used the *Syrph The Net* classification of vegetation types (Speight *et al.*, 2000a) because this work relates the association of hoverfly species to these vegetation types. We estimated the cover of the vegetation types defined in Table 48 using the Dominant-Abundant-Frequent-Occasional-Rare (DAFOR) scale. For habitat parcels containing the malaise traps we recorded low shrub, tussock, tall herb and short herb cover for both the entire parcel and for the immediate proximity (within c. 10 m) of the trap. Where forest habitat parcels included grassy or tall herb clearings (i.e., supplementary habitats 211f, 234f and 7331f as defined by Speight et al., 2001), we recorded two separate sets of vegetation structure data: for the main area of habitat under the canopy, and for the clearings.

6.2.4.3.5 *Dead wood*

We recorded the frequency of dead wood features along approximately 10 m wide bands around each transect. The dead wood categories used were small branches, large branches, stumps, standing and fallen; small branches were defined as those with a diameter of less than 7 cm, The frequency scale used is defined in Table 49.

Table 48. Vegetation types used for hoverfly habitat recording.

Type	Definition[1]
Overmature/senescent trees	Trees with microhabitats for saproxylic[2] organisms (i.e. sap runs, rot-holes, trunk cavities, observable areas of dead wood or loose bark).
Mature trees	Canopy trees that have reached the age of fructification without yet developing the features described under "overmature/senescent".
Understorey trees	Trees of more than 2 m in height that at maturity do not reach the forest canopy, e.g. *Crataegus monogyna*, *Sorbus aucuparia*, or are immature specimens of canopy-forming species.
Tall shrubs	Woody plants between the heights of 0.5 and 2 m, e.g. *Ulex europaeus*, *Viburnum opulus*, *Rubus fruticosus* and young trees (saplings).
Low shrubs	Woody plants up to the height of 0.5 m, e.g. *Vaccinium myrtillus*, *Calluna vulgaris*, *Rubus fruticosus*, *Salix repens*.
Tussocks	Tussocks formed by grasses, sedges and rushes (Graminae, Cyperaceae, Juncaceae).
Tall herbs	Tall, strong forbs over 0.5 m in height, e.g. *Digitalis purpurea, Cirsium palustre, Senecio jacobea, Urtica dioica*.
Short herbs	Ground-living, non-woody flowering plants up to 0.5 m in height.

[1] modified from Speight et al. (2000a).

[2] dependent upon the dead or dying wood of moribund or dead trees, or upon the presence of other saproxylics).

Table 49. Frequency scale for recording dead wood features.

	Small branches	Large branches/Stumps/Standing/Fallen
Abundant	Dense accumulations of twigs along thinned lines, or a uniform thick cover of twigs	Several/large volume in each 10 m section
Frequent	Occasional piles of twigs, or a uniform light cover of twigs	Present in most 10 m sections
Occasional	Occasional light cover of twigs	Present in less than half of the 10 m sections
Rare	Scattered isolated twigs	A few scattered examples

6.2.5 Data Analysis

6.2.5.1 Data processing

6.2.5.1.1 Species

Interpretation of abundance data from malaise traps is difficult. For example, very large catches of some migratory species occurred in late summer of 2001. Also, particular characteristics of individual trap sites are likely to affect the numbers caught (e.g. a flowering hawthorn next to the trap will attract some species, but not others). Therefore, we have used presence-absence data for all our analyses.

Some species (“stray species”) caught at particular sites require habitats for breeding that do not occur within the forest, e.g. *P. amplus*, an acid fen species, at DOOG. Therefore, they distort the measurement of biodiversity that the particular forest type supports. In some sites, several such species were caught. Furthermore, they are more likely to occur in the more open sites. Therefore, to address this problem, we compared the species list for each traps against the macrohabitats that we recorded. We used the classifications of habitat associations in the *Syrph The Net* database (Speight *et al.*, 2001a). These classifications are based upon a thorough synthesis of published and unpublished work on European hoverflies. We classified each species as either:

- “Main” if it associated with the macrohabitats recorded from the site, according to the information in Speight et al. (2001a).

- "Outside" if it is not associated with the macrohabitats recorded from the site, according to the information in Speight et al. (2001a).

We reviewed the initial listing of "Outside" species and identified species where there was something to indicate that the recorded habitat associations are incomplete (e.g. if one species turns up at several sites that do not contain any suitable habitat, or is very abundant at a site). We then reviewed this list of queries with Dr. Martin Speight. In some cases there were valid reasons for maintaining the categorisation of the species as "Outside": adult hoverflies are known to move quite widely between feeding and breeding sites, so it is not unlikely that hoverfly species that are abundant in farmland habitats will occur quite frequently in adjacent plantations, even if they do not breed in the latter. However, if a particular occurrence could be explained in terms of known, or likely, features of the breeding ecology of the species then the coding was amended to reflect the habitat association that we had recorded (the revised codings have been included in the revised edition of *Syrph The Net* (Speight *et al.*, 2003a)). We then re-classified occurrences of species in that habitat as "Main". In a few cases, species have been classified as "Main" because of special circumstances, although their coding has not been amended. These special circumstances are where habitat features occur that are typical of the macrohabitats with which they are associated (Table 50).

Table 50. Species classified as main due to special circumstances.

Species	Site	Reason
C. nemorum	BARN	Presence of overmature oak trees
M. florea	COOAM3	"Wet wood" character of boundary hedgerow/treeline
P. clypeatus and *P. occultus*	CUMMM1	Presence of frequent small clearings with oligotrophic wet grassland habitat
P. granditarsus	MARYM1 and MARYM2	Association with brook floodplain habitat counted due to presence of small remnants of this habitat

All analyses, unless otherwise stated, have been done using the "Main" species only.

6.2.5.1.2 Habitat data

For analyses involving structural and vegetation microhabitat parameters, we have only used data from the habitat parcel containing the malaise trap. In a few cases, the trap was located at the boundary of two habitat parcels. In these cases, we have used the mean of the values of the parameters for the two parcels. For analyses involving wet supplementary habitats and tree/scrub macrohabitats we have used data from all the habitat parcels.

6.2.5.1.3 Sites

Depending on the objectives of the analyses, we have used either data for individual traps or data for sites, combining data from two traps. For the site level data for the mix sites, we have used either the combined data for the two Sitka spruce traps, or the data for the ash trap and the Sitka spruce trap closest to the ash, depending on the objectives of the analyses.

The data for the three pure Sitka spruce sites in the age class 4 mix pairs represents a shorter sampling period than the data for all the other sites. Therefore, we have not included these sites in most of these analyses. Where we have included them, we have adjusted the data for the other sites so that they represent the same sampling period.

Damage or interference occurred to many of the traps. In most cases, the damage was minor (e.g., one guy rope coming loose, small holes in the net). We have generally ignored this level of damage. In a few cases (DEMEM1, KILAM1, UNIOM1 and UNIOM2), more major interference occurred resulting in the complete loss of a sample from one collecting period.

We have excluded these traps from the analyses of the effect of clearing area and tree height on species richness. However, coincidentally, all these traps caught high numbers of species relative to other traps in the same structural group. Therefore, we have retained these traps in our other analyses.

Our data analysis has indicated that, in the more structurally developed sites, the trapping efficiency of traps located in very small clearings/gaps was very poor (see Section 6.3.2). In preliminary analyses, we found that including these traps in the ordinations resulted in very distorted ordinations because of the very low number of species recorded for these traps. Therefore, we have excluded the following traps from most analyses of trap data: BALYM2, DERRM1, COMMM1, COMMM2, RATHM1. These traps have been included in the analyses of the effect of clearing area and tree height on species richness.

6.2.5.2 *Species classification*

In order to compare different facets of hoverfly biodiversity, we have used a number of species groupings. We used the recorded macrohabitat and microsite associations in the *Syrph The Net* database (Speight *et al.*, 2001b; Speight *et al.*, 2003a) to derive these classifications. The classifications and the criteria that determined them are summarised in Table 51, and details of the species classifications are given in Appendix 3.

6.2.5.3 *Analyses of assemblage structure*

We carried out analyses on all the sites, and on sub-groups of particular structural classes. For most of the ordinations, we used a single sample for each site representing the total species assemblage from two malaise traps; samples from a single trap can be heavily biased by particular features of the immediate trap location, and by the clearing area effect (see Section 6.4.1). For the mix sites, this sample could either be a trap from the ash component and a trap from the Sitka spruce component, or two traps from the Sitka spruce component. Therefore, we carried out two ordinations on all the sites, one using the ash-Sitka spruce combination and one using the Sitka spruce-Sitka spruce combination. For the ordination of the pre-thicket sites, we used the individual trap data as the samples. In these sites, the clearing area effect does not apply and the relatively homogeneous microhabitats mean that the particular features of the immediate trap location are less likely to bias the samples.

We used global non-metric multidimensional scaling analysis (NMS; see Section 2.5.3), flexible-beta cluster analysis (with beta set at –0.25) and indicator species analysis for examining assemblage structure. All analyses were carried out using PC-Ord (McCune & Mefford, 1997). For the NMS and cluster analyses we used Sørensen (also known as Bray & Curtis) distance measures. The parameter set-up that we used for the NMS analyses is shown in Table 52. Where the NMS analysis produced a solution with more than two axes, the axes that explain the highest percent of variance in the distance matrix were used for graphical representation of the results. We examined the correlations of potentially relevant environmental variables with the ordination axes.

6.2.5.4 *Trends in species richness between forest types and across the age cycle*

We used a two-level nested design ANOVA (with structural group as the nested factor within the main factor, canopy species) to identify differences in species richness between the pure Sitka spruce and pure ash stands. We used this design, rather than a full factorial design, because structural groups in Sitka spruce and ash are not directly comparable. We excluded the pole ash structural group from this analysis as we only had one replicate from this group.

Table 51. Definitions of hoverfly species groupings used for data analysis.

Species groupings	Categories	Definitions/Criteria[1]
Forest use	Forest specialist	Restricted to one or more of the following macrohabitats: Deciduous forests (gen.); Deciduous plantations; Wet woods (gen.); Alluvial forest (gen.); Coniferous forests (gen.); Coniferous plantations (gen.)
	Tree/shrub specialist[2]	Restricted to one or more of following macrohabitats: Deciduous forests (gen.); Scrub (gen.); Deciduous plantations; Wet woods (gen.); Alluvial forest (gen.); Coniferous forests (gen.); Coniferous plantations (gen.); Scattered trees in open ground (gen.); hedges; orchards; urban parks; gardens, ornamental
	Canopy tolerant	Coded as 2 or 3[3] for the relevant macrohabitat: i.e. Fraxinus-overmature, Fraxinus-mature, Deciduous plantations - Ash, Conifer plantations-Abies/Larix/Picea-mature
Anthropophilic/ Anthropophobic[4]	Anthropophilic	Occurs in one or more of the following macrohabitats: Improved grassland - heavily grazed; Intensive grassland; Culture Macrohabitats (gen.)
	Anthropophobic	Does not occur in any of the macrohabitats listed under the Anthropophilic category[5]
Functional groups (larvae)[6]	Foliage	Occurs in one or more of the following microsites: Mature trees, Understorey trees, Shrubs/bushes/saplings
	Herb layer	Occurs in the following microsite: Herb layer (gen)
	Ground debris	Occurs in the following microsite: Among/under surface debris (gen.)
	Root zone	Occurs in the following microsite: Root zone (gen.)
	Wet substrates	Occurs in one or more of the following microsites: On/in water plants (gen.), Submerged sediment/debris (gen.), Water-saturated ground (gen.)
	Dead wood	Occurs in one or more of the following microsites: Overmature/senescent trees (gen.), Timber (gen.)

[1] Macrohabitat names and definitions follow Speight *et al.* (2003a) and microsite names and definitions follow Speight *et al.* (2001b).

[2] This category includes all the species included in the Forest specialist category.

[3] Speight *et al.* (2003a) uses the following codings to describe the degree of association of a species with a particular macrohabitat: 1 – can occur in this macrohabitat under certain circumstances (e.g. if an appropriate supplementary habitat is present) but would generally be predicted for this macrohabitat (e.g. in the absence of any appropriate supplementary habitat); 2 – preferred macrohabitat; 3 – maximally preferred macrohabitat.

[4] See Speight and Castella (2001) for definitions of these terms.

[5] Species associated with conifer plantations are included in this category if they are not associated with any other habitat in the Anthropophilic category, because an objective of our analyses was to determine whether plantation forests can support species that otherwise cannot persist in intensively farmed landscapes.

[6] Note that a species can be classified in more than one of these groups.

Table 52. Standard parameter set-up used for NMS.

Parameter	Value used
Number of axes	6
Number of runs with real data	20
Stability criterion	0.001
Iterations to evaluate stability	10
Maximum number of iterations	500
Step down in dimensionality	Yes
Initial step length	0.20
Starting coordinates	Random
Number of runs of Monte Carlo test	50

We used paired t-tests to analyse differences in species richness between: the Sitka spruce and ash compartments of the mixed stands; the mixed sites and the matching pure Sitka spruce sites; and the Sitka spruce component of the mixed sites and the matching pure Sitka spruce sites. We also examined differences in the number of "unique" species (i.e. species only caught in one trap in a site) caught in the ash and Sitka spruce components of the mix sites. These analyses were all carried out separately for the various age classes sampled (age classes 1, 2 and 4). We did not use the structural groups for these analyses because the paired samples did not always fall within the same structural groups.

We used one-way ANOVA with Tukey HSD (or Welch's Robust Test of Equality of Means with Tamhane multiple comparisons, when variances were not homogeneous) to compare species richness between structural groups within each forest type (Sitka spruce and ash). For these analyses we used site data for Sitka spruce and trap data (due to the low number of sites) for ash. We excluded the reopening stage from the Sitka spruce analysis and the pole stage from the ash analysis, due to the low number of replicates.

We carried out the above analyses on main species richness, and, where we considered relevant, on the species richness of the various species groups.

These analyses were carried out using SPSS (2001).

6.2.5.5 Relationships between hoverfly species richness and habitat variables

We investigated relationships between species richness and habitat variables within the following groups: pre-thicket ash and Sitka spruce; pole and closed-maturing ash and thicket Sitka spruce; and closed-maturing, reopening and mature Sitka spruce (including the ash component of SUNS). Pre-thicket sites had very distinct hoverfly assemblages compared to the other groups. The other two groups were separated for these analyses because of the potentially confounding effect of clearing area (Section 6.4.1). This affects the closed-maturing, reopening and mature Sitka spruce group, but not the pole and closed-maturing ash and thicket Sitka spruce group. For all correlation analyses involving the closed-maturing, reopening and mature Sitka spruce group we carried out partial analyses with log-transformed clearing area as the covariable. Although tree height may also be involved in the clearing area effect, addition of tree height as a covariable did not affect these analyses. For some analyses, we further subdivided the closed-maturing, reopening and mature Sitka spruce into dry (KILA, RATH, SINB and SUNS) and wet sites to reflect the differences in assemblage structure between these sites. This division does not correspond exactly to the classification of site drainage in Table 8, as it is based upon the observed availability of discrete wet habitats (such as flushes) rather than overall soil drainage. For analyses of wet substrate species at the pre-thicket stage we excluded one site (KILM) that lacked any wet habitats. For analyses of dead wood species we used a group of Sitka spruce sites defined by age class (age classes 3 and 4) because the closed-maturing structural class group includes some age class 2 sites without any significant presence of dead wood.

We used correlation analyses to investigate relationships with the semi-quantitative structural and vegetation microhabitat parameters, and only carried out analyses where there could be a potentially meaningful relationship (Table 53). We coded canopy cover from 0 (open) to 4 (closed), clearing frequency from 0 (absent) to 3 (abundant), dead wood features from 0 (absent) to 4 (abundant) and other habitat variables measured on the DAFOR scale from 0 (absent) to 5 (dominant).

We analysed relationships with wet supplementary habitats and tree/scrub macrohabitats in two ways: independent sample t-tests of the relationship with presence/absence of these habitats; and correlation analysis of the relationship with distance from the trap of the nearest habitat patch (with a value of 100 m assigned to traps where no habitat patch was recorded). In this way we investigated the relationship of the numbers of tree/shrub specialists and foliage species with the following macrohabitats: hedge, treeline, hedge/treeline, and scrub (see Table 54 for definitions). Similarly, we examined the relationship of numbers of wet substrate species with the following supplementary habitats (see Table 55 for definitions): flushes and small open areas with flushes (all groups); seasonal brooks, drainage ditches and river/brook edges (pre-thicket group and pole and closed-maturing ash and thicket Sitka spruce group); and temporary pools and seasonal brook/river edge/brook edge (closed-maturing, reopening and mature Sitka spruce group). We also carried out correlations of the relationship of numbers of wet substrate species with wet habitat diversity (the number of wet supplementary habitats recorded).

Table 53. Correlations investigated between species richness of various species groups and structural and vegetation microhabitat parameters

Habitat variable	Main	Tree/shrub specialist	Anthropophobic	Foliage	Herb layer	Ground debris	Root zone	Dead wood
Canopy cover[1]	√	√	√	√	√			
Clearings[1]	√	√	√	√	√			
Mature trees[2]	√	√	√	√				
Understorey trees	√	√	√	√				
Tall shrubs	√	√	√	√				
Tussocks	√		√		√	√	√	
Tall herbs	√		√		√	√	√	
Short herbs	√		√		√	√	√	
Low shrubs	√		√		√	√	√	
Tussocks/ trap	√		√		√	√	√	
Tall herbs/ trap	√		√		√	√	√	
Short herbs/ trap	√		√		√	√	√	
Low shrubs/ trap	√		√		√	√	√	
Small branches[3]								√
Large branches[3]								√
Stumps[3]								√
Standing dead wood[3]								√
Fallen trees[3]								√

[1] not investigated for the pre-thicket group.

[2] only investigated for the pole and closed-maturing ash and thicket Sitka spruce group.

[3] only investigated for Sitka spruce age class 3 and 4.

Table 54. Definitions of tree and scrub habitats used in the data analysis.

Habitat	Definition[1]
Hedge	Linear strips of deciduous shrubs, forming a dense and continuous band of woody vegetation a few metres high, with an associated herb layer and, frequently, isolated, emergent trees at irregular intervals (CORINE 84.2[2])
Treeline	Linear strips of deciduous trees, forming a dense and continuous band of woody vegetation greater than 5 metres high, with an associated herb layer
Scrub	Thickets encompassing scrub formations of the phytosociological units Prunetalia on rich and poor soils (CORINE 31.81, 31.83; and 31.85[2]).

[1] Modified from Speight et al. (2001a).

[2] Commission of the European Communities (1991).

Table 55. Definitions of wet supplementary habitats used in the data analysis.

Habitat	Definition[1]
Flush	Helocrene water sources emerging on the forest floor
Seasonal brook	Shallow, ground-water fed brooks flowing autumn/spring, when the ground-water levels are high, but not usually throughout the year
Temporary pool	Small, temporary water bodies flooded by fluctuation in ground-water level, and/or rain, considered both when containing water and when not. Deep, semi-permanent, water-filled ruts along forest tracks were included in this category.
Small open areas with flushes	Glades and small clearings within forest, containing helocrene groundwater outflows with a ground cover of tall-herb communities, or predominantly grassy with *Juncus* and or *Carex* spp.
Drainage ditch	Intermittently-flooded, man-made drainage channels
Brook edge	The banks of small, freshwater, running water bodies, i.e. That part of a brook channel not permanently submerged in water and its immediate environs.
River edge	The rising land bordering a river channel, subject to periodic inundation by water.

[1] Modified from Speight et al. (2001a).

Where we found significant relationships we investigated the form of the relationship in more detail, examining the ecological characteristics of the species involved, and the identity of the sites involved.

These analyses were carried out using SPSS (2001).

6.3 RESULTS

6.3.1 Species recorded

We recorded a total of 72 species (see Appendix 3). These included 54 new county records of 34 species (see Table 56). Two of the species we recorded are categorised as threatened by Speight and Castella (2003): *P. amplus* and *X. florum*. We caught two *P. amplus* in the ash component of an age class 2 Sitka spruce-ash mix (DOOG, Co. Clare). In Europe, this species is associated with acid fen, and there are only two previous Irish records. DOOG has oligotrophic wet grassland adjoining the ash. We caught one *X. florum* in the ash component of an age class 4 Sitka spruce-ash mix (KILA, Carlow/Wicklow border). In Europe, this species is usually associated with alluvial forest, and the two previous Irish records are both from riparian deciduous forest. The larvae are saproxylic. There is no apparently suitable habitat within, or immediately adjoining, the plantation at KILA, suggesting that the specimen caught was a stray individual.

Table 56. New county records of hoverflies[1].

County	New records of:
Carlow	*B. elongata, E. balteatus, E. bucculatus, M. auricollis, M. cinctella, P. rosarum, S. clunipes, S. vitripennis, X. florum, X. jakutorum, X. sylvarum*
Clare	*M. arctica, M. auricollis, P. amplus, P. nielseni, P. occultus, Sericomyia lappona, S. clunipes*
Cork	*C. fasciatum, P. nielseni*
Kildare	*C. berberina*
Laois	*P. clypeatus, P. nielseni, P. occultus, R. splendens, X. jakutorum*
Limerick	*B. elongata, C. bicinctum, M. auricollis, M. cinctella, M. florea, P. angustatus, P. nielseni, R. splendens, S.lappona, S. clunipes, V.pellucens, X. sylvarum*
Sligo	*M. cincta*
Tipperary	*A. superbiens, C. bergenstammi, C. berberina, E. corollae, E. latifasciatus, L. metallina, L. lucorum, M. mellinum, M. cinctella, N. podagrica, P. clypeatus, P. occultus*
Waterford	*M. florea*
Wexford	*C. nemorum, M. cincta*

[1] Species are listed as new county records if they are not recorded for that county in Speight (2000a).

6.3.2 Exclusion of species

The number of species excluded from the subsequent analyses (see Section 6.2.5.1.1), because they were not ecologically associated with the habitats present, varied from 0-5 in most trap samples. Two exceptional samples were the ash components of KILM and KILA with 10 and 7 species respectively, excluded. Both these sites contained open canopy ash with dry grassland on hillsides above wet valleys. Most of the excluded species were associated with wet habitats.

Across all sites the total and main species richness were significantly correlated (Figure 44). The percentage of excluded species was negatively correlated with the main species richness (r = -0.280, p = 0.011, n = 81). The percentage of excluded species was higher in the later structural stages (Figure 55) with semi-mature and mature ash having the highest percentage of excluded species. This was due mainly to the exclusion of species associated with wet habitats from these dry sites. Similarly, the drier Sitka spruce sites tended to have higher percentages of excluded species.

6.3.3 Hoverfly fauna of ash and Sitka spruce plantations

Following the exclusion of species not associated with the habitats present, we recorded 64 species utilising forest plantation habitats. Eight species were recorded from more than 50% of the sites. These were generally ubiquitous, anthropophilic species, but included *S. clunipes* and *S. silentis*. *S. clunipes* is a saproxylic forest specialist, not previously thought to be associated with conifer plantations (Speight, 2000a). *S. silentis* is known to be associated with wet forests, unimproved humid grasslands and wetlands. We recorded six forest specialists, mainly saproxylic species, and ten tree/shrub specialists, with the additional species being foliage species (Table 57). We recorded 19 anthropophobic species. The most frequent larval microhabitat for the anthropophobic species was wet substrates.

Table 57. Numbers of recorded hoverfly species associated with various larval microhabitats.

Species group	Total	Foliage	Herb layer	Ground debris	Root zone	Wet substrates	Dead wood
Main	64	17	26	14	18	21	8
Forest specialist	6	0	1	0	1	2	5
Tree/shrub specialist	10	4	2	0	1	2	5
Anthropophobic	19	4	5	1	2	10	5

6.3.4 Effect of clearing area and tree height

Initial inspection of our data indicated that traps in small clearings in mature forests caught very low numbers of hoverflies. Therefore we investigated the relationship between species number, clearing area and tree height. Plots of data from all the traps (see Figure 56) show that the structural groups can be combined into two broad groups that differ in their responses. In the more structurally developed sites there is a strong positive relationship between species richness and clearing area, but this relationship does not hold for the less structurally developed sites. Across all sites there is a strong negative relationship between tree height and species richness. However, this relationship is merely a function of the lower species richness in the more structurally developed sites, and within the two broad structural groupings there is not an obvious relationship between tree height and species richness.

Based upon the above results, we investigated the relationship between species richness, clearing area and tree height in the more structurally developed sites in more detail. A multiple regression of species richness against log-transformed clearing area and tree height shows that tree height explains an almost significant amount of the residual variation in the species richness-clearing area relationship (Table 58). Species richness of the canopy-tolerant species shows the same relationship with clearing area, but tree height does not explain a significant amount of the residual variation in this relationship (Table 58). The species richness of all the functional groups is positively correlated with clearing area, but this relationship is not quite significant for the wet substrates and dead wood functional groups (Table 59). However, when the analysis is restricted to Sitka spruce of age class 3 and 4, dead wood species richness is significantly related to clearing area and almost significantly related to tree height (Table 58).

Table 58. Multiple regression of species richness against clearing area and tree height

	Main species	Canopy-tolerant species	Dead wood species
Adjusted r^2	0.48	0.44	0.29
$F_{2,32}$	16.97, $p < 0.001$	14.84, $p < 0.001$	4.787, $p = 0.022$
Beta (log clearing area)	0.77, $p < 0.001$	0.68, $p < 0.001$	0.53, $p = 0.015$
Beta (tree height)	-0.27, $p = 0.063$	-0.12, $p = 0.343$	-0.38, $p = 0.069$

Table 59. Correlations of species richness of larval microsite functional groups against log clearing area.

Functional group	Pearson Correlation	P (1-tailed)
Foliage	0.59	< 0.001
Herb layer	0.68	< 0.001
Root zone	0.71	< 0.001
Ground debris	0.49	0.001
Wet substrates	0.23	0.088
Dead wood	0.24	0.083

6.3.5 Hoverfly assemblages

6.3.5.1 All sites

The NMS ordinations of all the sites (Figure 57 and Figure 58) separate out clusters of pre-thicket Sitka spruce and ash sites and semi-mature and mature ash sites at either end of the ordination. The semi-mature/mature ash cluster in Figure 57 includes one of the age class 4 mix sites (RATH) in which the ash component was classified in the mature ash structural class. The remaining sites are quite tightly clustered in the centre of the ordination. The thicket Sitka spruce sites show a weak separation from the closed-maturing, reopening and mature Sitka spruce sites. The closed-maturing/reopening and mature Sitka spruce sites show a separation between the driest (KILA, SINB and SUNS) and the remaining sites.

The cluster analysis shows broadly similar groupings (Figure 57 and Figure 58). However, these analyses fail to separate the thicket from the closed-maturing, reopening and mature Sitka spruce sites. In the analysis using pairs of ash-Sitka spruce traps from the mix sites (Figure 57), three of the pre-thicket sites are grouped together with the drier mature Sitka spruce sites, and most of the thicket Sitka spruce sites. This cluster is separated from another containing the closed-maturing, reopening and the wetter mature Sitka spruce sites.

Indicator species analysis (Table 60 and Table 61) illustrates the distinctiveness of the pre-thicket sites. These sites have a large number of good indicator species, mainly associated with open, wet habitats, and lack tree/shrub species (*B. elongata* and *S. clunipes*) that are present in the other clusters. The semi-mature and mature ash cluster is distinguished by the presence of three saproxylic species (*C. berberina*, *F. cuprea* and *M. florea*) associated with deciduous woods. The drier mature Sitka spruce sites are distinguished by the absence of species associated with wet forest habitat features (*E. pertinax*, *H. pendulus* and *S. silentis*) and the presence of a group of three species with diverse ecological traits (*M. cincta*, *M. cinctella* and *V. pellucens*). *M. cincta* is associated with mature beech and oak and was recorded as single individuals from two of the four sites, both of which contained pockets of mature beech. *M. cinctella* occurs in a wide range of woodland and scrub habitats. *V. pellucens* has larvae that are scavengers/predators in wasp (*Vespula* sp.) nests and is associated with well drained soils.

Correlations between the ordination axes and the environmental variables (Table 62 and Table 63) show that the main gradient of separation, between the pre-thicket and mature ash sites, is associated with increasing cover of mature trees and decreasing frequency of clearings. The separation in Figure 57 of the group of drier mature Sitka spruce sites and most of the thicket Sitka spruce sites from the group of closed-maturing, reopening and the wetter mature Sitka spruce sites is associated with a more open canopy, and increased cover of tall shrubs and tussocks in the former group.

6.3.5.2 *Pre-thicket*

The NMS ordination of the pre-thicket ash and Sitka spruce traps (Figure 59) separates out traps according to the pre-planting habitat type (i.e., the secondary macrohabitat type; see Section 6.2.4.2). The three traps on improved grassland are clearly separated from the rest of the traps (but note that these traps are all from the same site), except for one trap on oligotrophic *Molinia*. The remaining traps show a tendency for a separation between the more oligotrophic and the more eutrophic grasslands.

6.3.6 Trends in hoverfly species richness between forest types and across the age cycle

The overall mean species richness across all traps was similar between ash and Sitka spruce: 12.5 ± 1.20 se in ash (n = 22) and 11.5 ± 0.74 se in Sitka spruce (n = 42); $F_{1,55} = 0.05$, $p = 0.82$. The mean species richness across all traps of dead wood species was significantly higher in ash compared to Sitka spruce: 2.14 ± 0.32 se in ash (n = 22) and 1.64 ± 0.25 se in Sitka spruce (n = 42); $F_{1,55} = 11.0$, $p = 0.002$. There were no significant differences in any of the other species groups.

Table 60. Indicator species for the groups identified from the cluster analysis using pairs of ash-Sitka spruce traps from the mix sites. Only species with a maximum IndVal of 25 or more are included. The max IndVal is indicated in bold.

	A: Pre-thicket	B: Semi-mature and mature ash	C: Wet closed-maturing, reopening and mature Sitka spruce	D: Dry mature mixes, pre-thicket, and thicket	P value of max IndVal
B. elongata	0	**38**	20	32	0.009
C. bicinctum	**54**	0	2	24	0.014
E. intricarius	**100**	0	0	0	0.001
E. latifasciatus	**100**	0	0	0	0.001
E. pertinax	7	0	**52**	7	0.001
F. cuprea	0	**43**	0	1	0.042
H. hybridus	**67**	0	0	0	0.008
H. pendulus	**36**	0	36	20	0.016
M. auricollis	**54**	0	0	31	0.008
M. mellinum	**54**	0	7	13	0.016
P. albimanus	**33**	2	22	33	0.036
P. angustatus	**100**	0	0	0	0.001
P. clypeatus	**71**	0	0	12	0.003
P. granditarsus	**66**	0	1	12	0.006
P. occultus	**48**	0	0	7	0.013
S. clunipes	0	**36**	30	25	0.006
S. silentis	**36**	0	36	20	0.016
T. flavitarsis	**67**	0	0	0	0.008
V. pellucens	0	0	0	**58**	0.013
X. jakutorum	0	0	**47**	1	0.038

Table 61. Indicator species for the groups identified from the cluster analysis using pairs of Sitka spruce traps from the mix sites. Only species with a maximum IndVal of 25 or more are included. The max IndVal is indicated in bold.

	A: Pre-thicket	B: Semi-mature and mature ash	C: Thicket-mature Sitka spruce (excluding dry mature)	D: Dry mature Sitka spruce	P value of max IndVal
C. berberina	0	**67**	0	0	0.006
C. bicinctum	**64**	0	6	0	0.011
E. intricarius	**50**	0	0	0	0.025
E. pertinax	9	0	**63**	0	0.002
H. pendulus	38	0	**55**	0	0.001
M. auricollis	**70**	0	2	4	0.003
M. cincta	0	0	0	**50**	0.022
M. cinctella	11	0	25	**44**	0.008
M. florea	0	**61**	1	0	0.009
M. mellinum	**62**	0	9	4	0.001
N. podagrica	**48**	0	7	0	0.035
P. angustatus	**67**	0	0	0	0.004
P. clypeatus	**89**	0	1	0	0.001
P. granditarsus	**78**	0	0	0	0.002
P. occultus	**61**	0	1	0	0.009
P. rosarum	**33**	0	0	0	0.049
S. clunipes	0	**37**	33	21	0.044
S. silentis	33	0	**48**	3	0.001
V. pellucens	0	0	0	**69**	0.006

Table 62. Significant correlations between axes from NMS ordination of all sites (with one ash and one Sitka spruce trap included for the mix sites) and environmental variables.

Axis	1	2
Canopy cover	.244^{ns}	-.579**
Clearings	-.677**	.408*
Mature trees	.650**	-.588**
Tall shrubs	.142^{ns}	.560**
Tussocks	-.339^{ns}	.594**

n = 30, ^{ns} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$.

Table 63. Significant correlations between axes from NMS ordination of all sites (with two Sitka spruce traps included for the mix sites) and environmental variables.

Axis	1	2	3
Canopy cover	-.384*	.561**	.018^{ns}
Clearings	.729**	.060^{ns}	-.189^{ns}
Mature trees	-.685**	.026^{ns}	-.099^{ns}
Tall shrubs	.119^{ns}	-.563**	-.282^{ns}
Tussocks	.519**	-.387*	-.302^{ns}
Tall herbs	.199^{ns}	-.302^{ns}	-.453**
Short herbs	.034^{ns}	-.279^{ns}	-.509**

n = 29, ^{ns} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$.

Trends in hoverfly species richness across the forest cycle in Sitka spruce forests are shown in Figure 60. Overall hoverfly species richness was highest in pre-thicket and thicket sites. Species richness of forest and tree/shrub specialists and dead wood species increased between the pre-thicket and thicket stages, but did not significantly change with further structural development of the forest. Numbers of canopy tolerant, anthropophobic and foliage species did not vary significantly between structural groups. Numbers of herb layer, ground debris and root zone species all showed a general trend of decrease with increasing structural development, but the differences were generally only significant between the pre-thicket and the closed-maturing and mature stages. Numbers of wet substrate species were much lower in the mature sites compared to the thicket and closed-maturing groups.

Trends in hoverfly species richness across the forest cycle in ash forests are shown in Figure 61. Overall hoverfly species richness was highest in pre-thicket and closed-maturing sites. Species richness of forest and tree/shrub specialists and dead wood species increased between the pre-thicket and closed-maturing stages (but this difference was not significant for the forest and tree/shrub specialists), but did not change with further structural development of the forest. Numbers of canopy tolerant, anthropophobic, and foliage species and wet substrate species did not vary significantly between structural groups. Numbers of herb layer, ground debris and root zone species all showed a general trend of decrease with increasing structural development, with the pre-thicket stage generally having significantly higher species numbers compared to the semi-mature and mature stages. Numbers of wet substrate species were significantly lower in the mature stage compared to the pre-thicket and closed-maturing stages.

Trends in the mean species numbers in the ash and Sitka spruce components of the mix sites are shown in Table 64. In age classes 1 and 4 there were no significant differences between hoverfly species richness in the ash and Sitka spruce components (age class 1, $F_{1,7} = 3.4$, $p = 0.47$; age class 4, $F_{1,6} = 1.6$, $p = 0.25$). In age class 2, hoverfly species richness was significantly higher in the ash component ($F_{1,5} = 6.0$, $p = 0.058$). Trends in the number of "unique" species (i.e. species caught in only one trap in a site) in the components of the mix sites are shown in Table 65. In age classes 1 and 4 there were no significant differences between the numbers of unique species in the ash and Sitka spruce components (age class 1, $F_{1,7} = 0.07$, $p = 0.81$; age class 4, $F_{1,6} = 0.9$, $p = 0.37$). In age class 2, numbers of unique species were significantly higher in the ash component ($F_{1,5} = 6.9$, $p = 0.047$). These differences in species richness and numbers of unique species in the age class 2 sites were due to the higher species richness of the ash components of DOOG and GFIN. Species richness of the mixed and paired pure Sitka spruce sites are compared in Table 66. In age class 2 the numbers of species in the mix and non-mix sites were not significantly different (paired t-test $t = 1.5$, $p = 0.23$, $n = 4$).

Table 64. Mean (± se) species richness in the ash and Sitka spruce components of the mix sites.

	Age class 1	Age class 2	Age class 4
ash	13.5 ± 1.2	20.0 ± 2.9	9.0 ± 1.4
Sitka spruce	14.3 ± 2.3	13.0 ± 3.1	7.9 ± 1.2

Table 65. Mean (± se) number of "unique" species (i.e. species caught in only one trap in a site) in the ash and Sitka spruce components of the mix sites.

	Age class 1	Age class 2	Age class 4
ash	4.3 ± 1.1	8.7 ± 3.2	3.3 ± 0.6
Sitka spruce	3.1 ± 0.9	1.8 ± 0.7	1.9 ± 0.4

Table 66. Species richness of the mixed and paired pure Sitka spruce sites. The mix sites are the combined data of the trap from the ash component and one trap from the Sitka spruce component.

	Age class 2				Age class 4	
	COMM/ KDUF	CUMM/ CLYD	DOOG/ GLYN	GFIN/ MARY	KILA/ MUNG	RATH/ UNIO
Mix	18	23	27	16	16	4
Non-mix	19	20	20	14	8	10

6.3.7 Relationships between hoverfly species richness and habitat variables

There were a number of significant correlations between species richness of various species groups and structural and vegetation microhabitat parameters (Table 67). However, more detailed examination of these relationships does not indicate any functional relationships. The correlations between main species richness and short herbs are due to the low species richness and low short herb cover at one site (KILM) where the pre-planting habitat was improved grassland; this site did not have particularly low numbers of herb layer hoverfly species. The negative correlation between tree/shrub specialists and canopy cover does not make any functional sense. The correlations involving anthropophobic species are due to the presence or absence of two species: *S. lappona* and *X. jakutorum*. *S. lappona* is a species with larvae that develop in wet substrates while *X. jakutorum* is a saproxylic species. The correlations of herb layer, ground debris and root zone species with various measures of herb cover result from the presence-absence of species that do not use any microhabitat components that could be related to the herb cover variable involved. For example, the ground debris species include several that only use the dung component of this microhabitat.

There were a number of differences in species richness and structural and vegetation microhabitat parameters between the wet and dry (see Section 6.2.5.5) closed-maturing, reopening and mature Sitka spruce sites (Table 68). The higher number of anthropophobic species in the wet sites is due to the presence of anthropophobic wet substrate and saproxylic species in these sites (see below). The higher number of ground debris species is due to the occurrence of species that only use the dung component of this microhabitat and are more likely to have been associated with the wet microhabitats. The difference in numbers of foliage species between these groups is not obviously attributable to the presence of any particular species.

Table 67. Significant correlations between species richness of various species groups and structural and vegetation microhabitat parameters.

Species group	Habitat variable	r	p
Pre-thicket (n = 17)			
Main	Short herbs	0.522	0.032
Main	Short herbs (trap vicinity)	0.720	0.001
Herb layer	Tall herbs (trap vicinity)	-0.517	0.034
Ground debris	Short herbs	0.685	0.002
Ground debris	Short herbs (trap vicinity)	0.742	0.001
Root zone	Short herbs (trap vicinity)	0.593	0.012
Thicket Sitka spruce and closed- maturing ash (n = 16)			
Tree/shrub specialists	Canopy cover	-0.558	0.025
Ground debris	Short herbs (trap vicinity)	0.529	0.035
Wet closed-maturing, reopening and mature Sitka spruce (n = 18)			
Main	Tussocks (trap vicinity)	0.478	
Anthropophobic	Understorey trees	-0.481	
Anthropophobic	Tall shrubs	-0.596	
Anthropophobic	Short herbs	-0.502	
Anthropophobic	Low shrubs	-0.524	

Table 68. Comparison of mean (± se) richness of various species groups and structural and vegetation microhabitat parameters in wet and dry closed-maturing, reopening and mature Sitka spruce sites.

	Dry	Wet	t	df	p
Anthropophobic species richness	0.88 (± 0.23)	1.88 (± 0.22)	3.15	19.4	0.005
Foliage species richness	4.25 (± 0.45)	2.41 (± 0.47)	-2.43	23.0	0.023
Ground debris species richness	1.88 (± 0.23)	3.47 (± 0.27)	4.50	21.9	0.000
Canopy cover	2.38 (± 0.18)	3.88 (± 0.19)	4.78	9.1	0.001
Clearings	0.75 (± 0.31)	2.35 (± 0.12)	-2.22	16.0	0.041
Short herbs	3.13 (± 0.44)	2.12 (± 0.17)	-2.61	23.0	0.016
Low shrubs	2.75 (± 0.59)	0.53 (± 0.21)	-4.41	23.0	0.000
Tussocks/ trap	1.00 (± 0.53)	2.71 (± 0.41)	2.43	23.0	0.023
Low shrubs/ trap	3.00 (± 0.71)	1.29 (± 0.39)	-2.29	23.0	0.032

The species richness of wet substrate species in the pre-thicket stage was positively correlated with the distance of the trap from the nearest drainage ditch (r = 0.589, p = 0.027, n = 14). This relationship is due to the absence of drainage ditches from the two sites (DOOG ash and MVAN) with the highest number of wet substrate species. The species richness of wet substrate species and the diversity of wet habitats were significantly higher in the wet closed-maturing, reopening and mature Sitka spruce sites, compared to the dry sites in this group (Table 69).

Table 69. Comparison of mean (± se) wet substrate species richness and wet habitat diversity in wet and dry closed-maturing, reopening and mature Sitka spruce sites.

	Wet substrate species richness	Wet habitat diversity	Sample size
Wet	4.24 (± 0.16)	2.82 (± 0.24)	17
Dry	0.75 (± 0.17)	0.50 (± 0.33)	8
t	13.3	5.48	
p	< 0.001	< 0.001	

The species richness of tree/shrub specialists in the pre-thicket stage was significantly higher where scrub was present (0.9 ± 0.38 vs. 0, t = 2.38, n = 17, p = 0.02, 1-tailed) and was negatively correlated with the distance of the trap from the nearest scrub habitat (r = -0.57, n = 17 p = 0.009, 1-tailed). These relationships were due to the presence-absence of *B. elongata*. The numbers of foliage species in closed-maturing, reopening and mature Sitka spruce sites was significantly correlated with the distance of the trap from the nearest treeline (r = -0.47, n = 25, p = 0.019). This reflected a difference between the higher numbers of foliage species in the dry sites (see Table 68) and the greater frequency and proximity to traps of treelines in these sites compared to the wet sites (mean distance to nearest treeline: 45 m ± 14 dry vs. 83 m ± 7.4 wet, $t_{23} = 2.63$, p = 0.015)

The species richness of dead wood species in age class 3 and 4 Sitka spruce was positively correlated with the frequencies of standing dead wood (r = 0.62, p = 0.002, 1-tailed, partial) and fallen trees (r = 0.57, p = 0.004, 1-tailed, partial). However, dead wood species richness and frequencies of standing dead wood and fallen trees were all significantly higher in the wet sites compared to the dry sites (Table 70). Within the groups of wet and dry sites, the relationships between dead wood species richness and the frequencies of standing dead wood and fallen trees were no longer significant.

Table 70. Comparison of mean (± se) dead wood species richness and dead wood frequency in wet and dry age class 3 and 4 Sitka spruce.

	Dead wood species richness	Standing dead wood frequency	Fallen trees frequency	Sample size
Wet	2.54 (± 0.14)	1.39 (± 0.27)	2.00 (± 0.32)	13
Dry	1.14 (± 0.40)	0.43 (± 0.20)	0.71 (± 0.57)	7
t	3.98	2.42	2.14	
p	0.0009	0.0264	0.0459	

6.4 DISCUSSION

6.4.1 Clearing area effect

In the more structurally developed sites, we found a very strong positive logarithmic relationship between species richness and the area of the clearing in which the malaise trap was located. This relationship was present when all species were included, as well as for the various larval functional groups. There are a number of possible causes of this relationship.

Many hoverfly species require the presence of clearings, or habitats associated with clearings, to provide suitable microhabitats for larval development. Therefore, the clearing area effect could be a direct consequence of larger clearings providing more suitable microhabitat conditions for larval development. However, the clearing area effect was still present when the analyses were restricted to species groups (such as canopy-tolerant species and dead wood species) where larval microhabitats will not be related to the presence or size of clearings.

The adults of most hoverfly species feed on pollen and/or nectar, and tend to prefer large plants with open-structured flowers, such as bramble, hogweed (*Heracleum sphondylium*), etc. Therefore, the clearing area effect could be a direct consequence of larger clearings providing more suitable floral resources for adult hoverflies. However, the dead wood species in the Sitka spruce forests (*S. clunipes*, *X. jakutorum*, and X. *segnis*) generally do not visit flowers (Stubbs & Falk, 2002), but still showed a significant relationship with clearing area. Also, the availability of floral resources is not necessarily directly correlated with clearing area: some of the mature Sitka spruce sites (KILA, RATH and SUNS) had open canopies allowing the development of a good ground flora cover, but traps located under small canopy gaps in these sites still only caught low numbers of species.

Malaise traps catch hoverflies as a result of the fact that they tend to fly towards the point of highest light intensity (i.e. the sun) on contact with the trap. Therefore, in shaded conditions without a strong source of light, malaise traps are likely to operate less efficiently: i.e., a lower proportion of the hoverflies encountering the trap will be caught. This suggests that the clearing area effect reflects the fact that small clearings receive less sunlight, and, therefore, malaise traps located in small clearings are less efficient at catching hoverflies. This would also explain the negative relationship with tree height: as the height of the trees surrounding the clearing increases, the amount of sunlight reaching the clearing will decrease. Given the absence of any convincing alternative explanation, we believe that this is the most likely explanation for the clearing area effect. This means that analyses of hoverfly biodiversity involving Sitka spruce sites from the closed-maturing, reopening and mature structural groups and ash sites from the semi-mature and mature structural groups will be biased by the clearing area effect.

The clearing area effect does not appear to have been previously reported, although it would seem to be a logical result of using malaise traps in forests. Previous work in which malaise traps have been used to sample forests (Watt *et al.*, 1997; Humphrey *et al.*, 1999) do not consider the potential for this effect to have biased their data. In both cases, the information in the published work indicates that malaise traps were located in fixed positions (the centre of a sampling plot) without consideration of the effect of the adjoining tree canopy on the efficiency of the traps. This makes evaluation of the results of these works difficult, because the extent to which the clearing area effect biased comparisons between sites cannot be gauged.

6.4.2 Hoverfly assemblages of Sitka spruce and ash plantation forests

Generalist, anthropophilic species dominated the hoverfly assemblages that we studied. Only around 30% of the species were anthropophobic. These are species not able to survive in intensively farmed landscapes: i.e., landscapes dominated by improved grassland and/or cultivated and built land according to Fossitt's (2000) classification. This compares with a range of 35-50% reported by Speight (2000c) for species associated with most native forest macrohabitats. However, unlike Speight (2000c), we have included species associated with conifer plantations in our anthropophobic category (because an objective of our analyses was to determine whether plantation forests can support species that otherwise cannot persist in intensively farmed landscapes). Also, our anthropophobic species include species that occur in plantation forests due to their association with non-forest habitat at the pre-thicket stage; when these are excluded the proportion of anthropophobic species falls to 25%. Therefore, our results indicate that plantation forests support a lower proportion of conservation-dependent species compared to that potentially supported by native forest macrohabitats.

Our analyses illustrate the distinctiveness of the pre-thicket stage. This is not surprising as the fauna is dominated by species associated with the pre-planting habitat. After the pre-thicket stage, as the Sitka spruce forest matures, relatively little change in the assemblage structure is evident from our data. The most obvious difference is between the assemblages of age classes 3 and 4 Sitka spruce of wet and dry sites. Mature ash, on dry sites, appears to have a distinctive hoverfly assemblage.

The main change in hoverfly biodiversity over the forest cycle that is evident from our data are decreases between the pre-thicket/thicket and the closed-maturing/reopening/mature stages in Sitka spruce and between the pre-thicket/closed-maturing and the semi-mature/mature stages in ash. This decrease occurs in both the main species richness and that of the herb layer, ground debris and root zone functional groups. The species richness of groups that might be expected to increase with structural development of the forest habitat (forest and tree/shrub specialists and dead wood species) generally only show significant increases between the pre-thicket and thicket stages in Sitka spruce and between the pre-thicket and closed-maturing stages in ash. In interpreting these trends, the potential bias due to the clearing area effect needs to be considered, and it is notable that, in both

Sitka spruce and ash, the stage at which the decrease in main species richness occurs coincides with the stage where the clearing area effect becomes significant.

Comparisons of species richness between the ash and Sitka spruce components of the mix sites, and between the mix sites and matching pure Sitka spruce sites do not provide very convincing evidence that adding ash to a Sitka spruce plantation increases hoverfly biodiversity. Where there is some evidence of an effect (in age class 2), it is due to two sites: DOOG and GFIN. At DOOG, the ash component had a varied mix of associated habitats, including oligotrophic wet grassland and flushes, with well-developed scrub and grassland in close proximity to the trap; both the Sitka spruce traps were located in dense bracken surrounded by Sitka spruce. At GFIN, the ash component included a remnant section of mature brook floodplain forest with eutrophic wet grassland adjacent, while the Sitka spruce traps were located in small clearings surrounded by well-developed (closed-maturing) Sitka spruce. In both cases, the additional species present in the ash component reflect both the additional habitats present and the better trapping conditions. While the second factor is a sampling artefact, the first of these factors is probably a reflection of a real difference between ash and Sitka spruce at this stage: the Sitka spruce has developed a closed canopy largely eliminating the pre-planting habitats while the ash remains more open allowing a greater habitat diversity to persist. This may, however, depend upon site conditions: at the age class 1 site COOA, the ash component had reached the pole stage and had developed a closed canopy after five years while the Sitka spruce component remained at the pre-thicket stage. But in general, the slower development of ash is likely to cause increased hoverfly biodiversity in mixed sites at the thicket Sitka spruce stage by allowing species associated with the pre-planting habitat to persist.

Another factor likely to cause increased hoverfly biodiversity in mixed sites is not evident from simple analyses of species numbers. This is the occurrence of certain species that are mainly dependent upon broadleaved woodland. In our study we found four such saproxylic species (*C. berberina*, *F. cuprea*, *M. florea* and *X. sylvarum*), although one of these (*M. florea*) can also occur in anthropogenic habitats such as cow dung and silage. While these species were most frequent in the semi-mature and mature ash, they all occurred in earlier stages, including in the mixed sites. There are also another eight species (*C. albitarsis*, *Cheilosia antiqua*, *C. illustrata*, *C. pagana*, *Cheilosia vernalis*, *C. bicinctum*, *Leucozona glaucia*, and *Leucozona laternaria*) that are widespread in Ireland, are associated with ash plantations with grassy/tall herb clearings and do not occur in Sitka spruce plantations according to Speight *et al.* (2003a). Most of these species are also associated with hedgerow and/or scrub habitats. We recorded four of these species in this study (*C. albitarsis*, *C. illustrata*, *C. pagana*, and *C. bicinctum*) but none were particularly associated with ash, because they also occurred in Sitka spruce plantations that had scrub and hedges in or adjoining them. Three of the remaining species (*C. antiqua*, *C. vernalis* and *L. glaucia*) rarely occur in association with hedges in Ireland (Speight, 2000a). Therefore, our results suggest that adding ash to a Sitka spruce plantation could add up to four species of saproxylic hoverflies, three of which are unlikely to occur in the standard farmed landscape. Consideration of the information on recorded habitat associations suggests that if the ash contains adequate amounts of open space, up to another eight species could be added, three of which are unlikely to occur in the standard farmed landscape.

6.4.3 Relationships between hoverfly species richness and habitat variables

Coniferous forests in general support a poorer hoverfly fauna, compared to deciduous forests (Speight & Castella, 2001). While some conifer-specialist aphid-feeding hoverflies have colonised Ireland, other elements (aquatic/subaquatic, herb layer, and saproxylic species) of the conifer-specialist hoverfly fauna have not, to any significant extent (Speight, 2000b). Semi-natural ash woodland appears to be a relatively poor habitat for hoverflies (from analysis of data in Speight et al. (2003; 2003a). Therefore, the forest types that we have studied are likely to be relatively poor for hoverflies compared to many types of semi-natural Irish woodlands, and plantations of native broadleaves (excluding ash). There are no published data comparing the syrphid assemblages of semi-natural and plantation woodlands in Ireland, although, in Scotland, Watt et al. (1997) found low hoverfly diversity in native birch woodlands, compared to spruce plantation.

While we found several significant relationships between hoverfly species richness and habitat variables, it is likely that this is mainly an artefact of the large number of possible relationships that we analysed. When we examined these relationships in more detail, very few appeared to reflect real functional relationships.

The positive relationship between the numbers of wet substrate species and the distance from the nearest drainage ditch could reflect the greater availability of more "natural" wet habitats (such as flushes and seasonal brooks) in sites that have not been drained. However, this relationship is based upon the absence of drainage ditches from the two sites (DOOG ash and MVAN) with the highest number of wet substrate species, so further data would be required to verify this.

The positive relationships between species richness of tree/shrub specialists in the pre-thicket stage and the presence and proximity of scrub were due to the presence-absence of *B. elongata*. The larvae of this species are described by Ball and Morris (2000) as feeding on "ground-layer" aphids in shaded situations, including the bramble aphid *Sitobion fragariae*. Therefore, the above relationship could be due to the fact that, at the pre-thicket stage, the crop trees do not provide sufficient shade, and the species requires some additional scrub habitat.

Within the group of closed-maturing, reopening and mature Sitka spruce sites, there were several significant correlations between species richness of various groups and habitat variables (not reported here). However, these correlations appear to be mainly due to significant differences in the species richness of these groups between the wet and dry sites. When these relationships were examined within the groups of wet and dry sites, many were no longer significant. Not surprisingly, the species richness of wet substrate species was significantly higher in the wet sites as was the diversity of wet habitats. Probably also related to this was the greater number of ground debris species in the wet sites. Many of these species only use the dung component of the ground debris microhabitat, and were more likely to be associated with the wet substrate microhabitat that they also use. For both these groups, the significant correlations with habitat variables appear to be due to the differences in species assemblages between the wet and dry sites.

The numbers of dead wood species were significantly higher in the wet sites as was the frequency of standing dead wood and fallen trees. In this case it is less clear whether this relationship is due to a difference in the species assemblages between the wet and dry sites, or to a direct relationship with these habitat variables. There were only three species involved (*S. clunipes*, *X. jakutorum* and *X. segnis*), and all three were recorded from both the wet and dry sites. The range of variation of dead wood species number in the wet sites and dead wood frequency in the dry sites was very small, limiting the potential to detect significant relationships within these groups. The one trap with a high frequency of fallen trees in the dry group had a high number of dead wood species. However, all three species can also use additional microhabitats (water-saturated ground and rotting tree roots) that are more likely to have been present in the wet sites. The larvae of one of the dead wood species, *X. jakutorum*, are known to develop in the borings of pine weevils (*Hylobius abietus*) in conifer stumps (Rotheray & Stuke, 1998), and are described as being "particularly abundant in areas felled 2-3 years previously, after which the stumps become suitable for the weevil larvae" (Ball & Morris, 2000). However, we recorded this species (in good numbers) from one site (DERR) where there had been no thinning or felling.

6.5 CONCLUSIONS

6.5.1 General conclusions

The hoverfly assemblages of Irish plantation forests that we studied were dominated by generalist species that are associated with intensively farmed landscapes. However, some species that cannot survive in such landscapes and/or are exclusively associated with forest or scrub habitats do occur in plantation forests, and these include a few species that are widespread in these forests. Therefore plantation forests do have the potential to cause some increase in hoverfly biodiversity at the landscape scale when they are located in intensively farmed landscapes. The most important habitat features for these species are features associated with wet substrates and dead wood.

We found little overall difference in the hoverfly biodiversity of ash and Sitka spruce plantation forests, but ash forests do appear to support a greater number of saproxylic species. Adding ash to a Sitka spruce plantation is likely to increase the hoverfly biodiversity at the plantation scale, especially if the ash component includes grassy clearings.

6.5.2 Biodiversity indicators

The presence of wet habitat features (temporary pools, flushes and watercourses) increases hoverfly biodiversity due to the occurrence of species associated with these features. Drainage in pre-thicket sites may cause reduced hoverfly biodiversity by removing wet habitat features other than drains. In Sitka spruce stands, saproxylic species appear to be associated with the occurrence of standing dead wood and fallen trees.

6.5.3 Management recommendations and modifications to the *Forest Biodiversity Guidelines*

We have identified the importance of wet habitat features for hoverfly biodiversity in plantation forests. In the sites we studied these were mainly very small, localised features such as wet flushes and narrow seasonal brooks. These features can easily be lost through drainage at the site development stage, and our results indicate that drainage ditches can have a negative impact on the hoverfly fauna of pre-thicket sites. While drainage will often be required for silvicultural reasons, there are opportunities for retention of wet habitat features as part of the *Area for Biodiversity Enhancement* (ABE), or through planting of species such as alder and birch that are tolerant of wet conditions. Therefore, the *Forest Biodiversity Guidelines* (Forest Service, 2000b) should emphasise the importance of these features, explain that even small examples can be valuable, recommend that they be included in the ABE, discourage site drainage where not required for silvicultural reasons and encourage the use of appropriate crop species to avoid or reduce the requirement for drainage.

The *Guidelines* recognise the importance of retaining overmature trees and dead wood, and specify that 2 m^3/ha of deadwood should be present after thinning and 5 m^3/ha after final harvesting. However, the *Guidelines* do not specify the type(s) of deadwood that should be retained, and could be interpreted as implying that the composition of the deadwood is not important. Our results indicate that large diameter deadwood (standing and fallen trees) support a richer saproxylic fauna in Sitka spruce stands compared to smaller diameter deadwood. More generally, larger diameter deadwood tends to be a scarcer resource and tends to be more important for the rarer saproxylic invertebrates (Fry & Lonsdale, 1991). Therefore, the *Guidelines* should emphasise the importance of large diameter deadwood and require that large diameter deadwood (i.e. standing and fallen trees) is included in the deadwood retained after thinning and felling.

Applications for afforestation grants on improved/enclosed land must contain a minimum of 10% broadleaves, site permitting (Forest Service, 2000d). The *Guidelines* also require that applications include 5-10% open space in sites larger than 10 ha. Consideration of the recorded hoverfly fauna associated with ash plantations in Ireland suggests that where ash is the 10% broadleaved component of a conifer plantation, the inclusion of an area of open space large enough to allow the development of grassy clearings can potentially increase the biodiversity of the plantation by providing habitat for species that do not normally occur in conifer plantations. Therefore, the *Guidelines* should recommend that the open space and broadleaved components be placed together, where possible.

7 BIRDS

7.1 INTRODUCTION

Birds are suitable as indicators of forest biodiversity since they are a diverse, ubiquitous and well-studied group, easy to identify and quantify and sensitive to differences in habitat (Ferris & Humphrey, 1999). Bird species richness of Irish forests is low in comparison with similar habitats in Britain and the rest of Europe. Part of the reason for this may be that Ireland is 2.8 times smaller than Britain, with a lower diversity of habitats (Hutchinson, 1989). Many forest specialist species (including all Woodpecker species, Nuthatch, Tawny Owl, Marsh Tit and Willow Tit) are absent from Ireland, and some summer migrant forest breeders (e.g. Wood Warbler, Pied Flycatcher and Redstart) are very rare indeed (Hutchinson, 1989). However, a wide variety of bird species use forest habitats of different types.

Some forest bird species are of conservation interest. It has been hypothesised that plantation forestry has a positive effect on Irish red and amber listed species of conservation concern (Newton *et al.*, 1999; Walsh *et al.*, 2000). Red-listed species that might benefit from plantation habitat are Hen Harrier and Nightjar (Walsh *et al.*, 2000), both species that are known to use young plantation habitat for nesting (Morris *et al.*, 1994; Sim *et al.*, 2001). A number of forest specialists (i.e. species that cannot breed outside extensive forest habitat) are amber-listed in Ireland, namely: Woodcock, Redstart, Wood Warbler, Pied Flycatcher and Redpoll.

In addition to the matter of those few species of conservation concern that are of relevance to forest habitats, birds can provide more general information about relative biodiversity and habitat quality of different types of forest habitat. Because their ecology is well-studied, they can conveniently be classed into groups according to whether they are habitat specialists or generalists, and into functional groups based on feeding or nesting habits.

Preliminary studies of the bird communities of Irish plantations have already been undertaken (Batten, 1976; O'Halloran *et al.*, 1998). Although the most extensive of these, a survey of 380 ha of coniferous plantations of seven tree species in both summer and winter seasons, found 38 species of bird (O'Halloran *et al.*, 1998), only three common species (Goldcrest, Robin and Chaffinch) made up 75% of the breeding population in these sites. Hence, although many species are at times associated with conifer plantation, most occur rarely within the habitat. The study indicated factors that were positively associated with bird species richness and/or density, such as presence of broadleaf species, proximity to the edge and presence of undergrowth. It was not possible, however, to compare the bird communities of different plantation tree species, and because sampling was concentrated in mature pole stage plantations, no attempt was made to examine the influence of tree age on birds. No such survey of broadleaf plantations has yet been undertaken.

In view of the low bird diversity of much Irish plantation forest, it is important that the factors that can enhance it in certain areas be determined. The requirement for broadleaf planting at a rate of 10% per afforestation project (Forest Service, 2000d) is beginning to change the composition of Irish plantations, and is expected to have beneficial effects. Bird diversity is generally higher in more structurally complex broadleaf woodland than in coniferous monocultures (Fuller, 1995). Mixed forests with both coniferous and broadleaf elements also tend to be more species rich and to support more individuals (Hobson & Bayne, 2000; Hausner *et al.*, 2002). A study in boreal forests in eastern Canada showed that increased avian diversity in mixed forest compared to pure conifer or pure broadleaf forest may not be due entirely to the mixing of bird species associated with each forest type, but also to the increased capacity of mixed forest to support certain conifer or broadleaf specialists (Hobson & Bayne, 2000). Future Irish plantations are likely to consist of a mixture of broadleaf and coniferous compartments, rather than intimately mixed stands, and may support more diverse bird communities than would be found in extensive monocultures.

Even in monocultures there may be sources of structural heterogeneity that could be exploited in order to enhance bird diversity. One major possible source of structural diversity is variation in age of the stand. A recent study not only compared broadleaf forest with conifer plantations, but also areas of even-aged conifer plantation with a more structurally diverse mosaic of old and young patches (Steverding & Leuschner, 2002). The structurally diverse spruce stands held a substantially higher number of bird species per plot area and supported a higher density of bird territories than either even-aged spruce plantation or semi-natural, old-growth beech forest.

Changes in breeding bird communities over the forest cycle are well documented in many contexts, but not yet in Ireland. Generally, three main stages are recognised: an early stage when trees are still very small and open space specialists (e.g. Stonechat, Yellowhammer) can persist with gradual arrival of low vegetation specialists (e.g. Bullfinch, Warbler species); a second phase with low diversity and abundance of birds, when the canopy closes and generalists (e.g. Robin, Song Thrush) or conifer specialists (e.g. Goldcrest) take over; and thirdly (and rarely), a later increase in diversity when a stand is allowed to age and under-storey vegetation can recover (Marion & Frochot, 2001). A two-year survey of upland spruce plantations in England and Scotland found that, in both years, breeding bird numbers and species richness were highest in stands aged 9-25 years, while in winter older stands were preferred (Patterson *et al.*, 1995).

Our wide-scale study compared the breeding bird communities of ash and Sitka spruce plantations at different stages of the forest cycle and in different biogeographic regions of Ireland. Bird species richness and abundance were compared along with other measures of bird diversity in order to develop compositional, structural and functional indicators of biodiversity in such forests.

7.2 METHODS

7.2.1 Sampling sites

Three rounds of visits were made to sites in order to sample birds. These are referred to hereafter as Visit 1 (late April-early June), Visit 2 (early June-early July) and Visit 3 (early July-early August). In 2001, due to a late start to fieldwork caused by the Foot and Mouth Disease outbreak, the early season visits (Visit 1) were missed and a round of very late visits (Visit 3) was made instead. In 2002, a round of early visits (Visit 1) and a round of late visits to sites missed in 2001 (Visit 2) were made. Due to weather constraints, and the fact that no Visit 3 surveys were made in 2002, which was the first year in which age class 1 sites were visited, some sites received more visits than others (Table 71).

7.2.2 Bird sampling

Point counts were used to sample bird communities at each site (Bibby *et al.*, 1992). The number of point counts carried out in each site ranged from 4-9, depending on the size of the plantation and the variability of the site (Table 71). Points were located in the field using a GPS, accurate to within approximately 5 m. The location of each point was decided using digitised maps of the forestry parcels. Points were situated at a minimum of 100 m from one another, and at as great a range of distances from the forest edge as possible, given the size and shape of the plantation. Where the actual boundaries of the plantation differed from the digitised boundaries used to position the points, new locations were chosen in the field, and the new positions noted from the GPS.

Table 71. Number of bird survey points located in, and bird surveying visits made to, the study sites.

Site code	No. points	Visit 1	Visit 2	Visit 3
BALE	7	yes	yes	
BALY	5		yes	yes
BARN	4	yes	yes	yes
BEND	6	yes	yes	
BOKY	6	yes	yes	yes
BRAC	6		yes	
CLYD	6	yes	yes	yes
COMM	9	yes	yes	yes
CONA	5		yes	yes
COOA	7	yes	yes	
COOL	6		yes	yes
COON	6	yes	yes	yes
COOS	5	yes	yes	
CORB	6	yes	yes	yes
CORR	6	yes	yes	yes
CUMM	8	yes	yes	yes
DEME	6	yes	yes	yes
DERR	6	yes	yes	yes
DOOG	6	yes	yes	yes
FURY	6	yes	yes	yes
GFIN	6	yes	yes	yes
GLYN	6	yes	yes	yes
HIGG	6		yes	
INCH	5	yes	yes	
KDUF	6	yes	yes	yes
KESH	4		yes	
KILA	5		yes	yes
KILM	7	yes	yes	
KILW	6		yes	
LACK	6		yes	
LURG	6		yes	
MARY	5	yes	yes	yes
MOAN	6	yes	yes	yes
MONT	6	yes	yes	yes
MSOP	6	yes	yes	yes
MUNG	6		yes	yes
MVAN	4	yes	yes	yes
RATH	6		yes	yes
REEN	5	yes	yes	yes
RINC	4	yes	yes	yes
SAGG	6	yes	yes	yes
SINB	7	yes	yes	yes
SUNS	7	yes	yes	yes
UNIO	6		yes	yes

On arrival at a point, information about the forest stand structure and surrounding vegetation was noted (see below). The point count was then conducted, for 10 minutes, during which all birds observed by sight or by sound were recorded on a stylised map of the point. The exact positions of all birds judged to be within 50 m of the observer were estimated. All observations judged to be beyond 50 m were placed immediately outside the 50 m band, regardless of their actual distance. For each observation, the method of detection was noted (i.e. either seen or heard or both) as well as the behaviour (calling/singing/flying /nesting/pair/food in bill/hunting, etc.) and, where possible, sex and age.

Fieldwork was restricted to relatively fine days, i.e. surveys were not carried out in heavy or persistent rain, or in strong (greater than Beaufort Scale 4) winds. Timing of visits was varied such that all points that received more than one visit were visited at least once in the early morning and once in the late afternoon.

7.2.3 Habitat recording

7.2.3.1 Structural recording at point locations

Within a circle of radius 30 m from the observer, or as far as the observer could see from the position of the point count, whichever was shorter, the following structural variables were recorded: canopy height (m); canopy cover (%); shrub layer cover (%); herb and moss cover (%). Shrub layer was defined as all woody vegetation between 0.5 and 2m in height, not including the commercial crop.

For each site, mean values of structural variables were calculated from the habitat data collected at all the points in the site.

7.2.3.2 Remote environmental survey

The environmental variables listed in Table 72 were measured remotely, using geographical information databases. For each site, the mean values of each environmental variable from all of the survey points at the site were calculated.

Table 72. Methods used for calculating environmental variables from GIS databases.

Environmental variable	Calculation method and source data
Distance from edge	Mean of the nearest distances of the bird survey points to the edge of the forest. Forest included all adjacent compartments of similar age and tree species composition (as shown by the Coillte database).
Distance from old woodland	Shortest distance from a bird survey point to an area of woodland shown on digitised OS 6" map series (3rd ed.), to the nearest 100 m. If no old woodland was recorded within 1km of any point, the distance was recorded as 1000 m.
Area of old woodland	Combined area of old woodland shown on digitised OS 6" map series (3rd ed.) within 1 km of the centre of the study site.
Altitude	Mid-point of altitudinal range of bird survey points shown on digitised Irish OS Discovery map series, to the nearest 10 m.
Point range	Maximum distance between bird survey points, to the nearest m.

7.2.4 Data preparation

7.2.4.1 Calculation of bird species densities using Distance

Bird species differ in the rate at which they are detected. Therefore, in order to compare and contrast counts of the bird species found in our study sites, it was necessary to first take account of the discrepancy between the numbers of birds observed and the numbers of birds actually present. We used distance sampling techniques, following the methodology of Buckland *et al.* (2001), to estimate the actual densities of different species present in each of our study sites.

7.2.4.1.1 Estimation of detection function

The likelihood of an observer detecting a bird is affected by individual species' behaviour, by structure of the habitat, and by the distance between bird and observer. Distance sampling theory states that the probability of the observer detecting the bird is equal or close to 1 when the distance between bird and observer is close to zero, and that as this distance increases, the probability of detection declines according to a detection function. We used the computer programme Distance (Buckland *et al.*, 2001) to fit detection functions to our data. These were based on the distribution of observations over distance bands, whose number and intervals were adjusted to maximize the fit of the data to one of a number of likely algorithms. Because birds judged to have been further than 50m from the observer when they were recorded were assigned to an 'open-ended' distance band, they could not be included in the distance analysis.

Ideally, each species would have been allocated a different detection function for each habitat in which it had been recorded. However, for most species-habitat combinations, we had fewer than fifty observations, the minimum number recommended to ensure that estimated detection functions are robust. Species and habitat combinations were therefore put into groups based on knowledge of species' ecology and behaviour, on the effects of different habitats on the ability of observers to see and hear birds, and on the distribution of observations within each species-habitat combination over crude (10 m) distance bands. Distance then fitted several model detection functions to the data, one of which was selected, principally according to the Akaike information criterion (AIC), an index which combines a measure of goodness of fit with an assessment of the model's parsimony. However, the form of the detection function at near-zero detection distances has a disproportionate effect on density values, and the AIC does not take into account the increased importance of model fit in this critical region. Thus, only models that provided a close fit to observations from 0-15m from the observer were considered for selection according to AIC. Details of the species-habitat groups and the detection functions selected for each group are given in Appendix A4.2. These detection functions were used to produce estimates of species densities of each species observed at every survey point.

7.2.4.1.2 Correction of survey effort for location, number and timing of visits

Species densities calculated from the detection functions were adjusted in Distance to take account of survey effort. Basic survey effort for a visit to a point, E, was calculated as the proportion of a 50m radius circle around the point that fell within the forest site being surveyed. Thus, if a point was situated on the edge of a forest, and the forest edge continued in a single straight line that extended 50m or more in both directions from the point, E=0.5.

Basic effort was adjusted to account for the different numbers of visits made to study sites, and for the timings of these visits, as follows. For species a in visit x, number : effort ratio R_{ax} was calculated as:

$$R_{ax} = \frac{\sum_{i=1}^{i=p} N_i}{\sum_{i=1}^{i=p} Ei} \qquad (1)$$

where N_i is the number of species a seen during visit x at point i, E_i is the basic effort for point i, and p is the number of points visited during visit x. For each species, all values were converted to survey effort modifiers, M, by dividing them by the maximum R value for that species:

$$M_{ax} = \frac{R_{ax}}{R_a \max} \qquad (2)$$

where notation is the same as for equation 1. For each species, this has the effect of assigning an M value of 1 to the visit with the highest R value. For each species-point combination, total survey effort was calculated as the sum of the basic survey effort multiplied by the appropriate effort modifier, for each visit made to that point.

7.2.4.2 Bird species groupings

In order to compare different facets of bird diversity, a number of species groupings were utilised. The classifications and the criteria that determined them are summarised in Table 73. Species nesting in cavities of tree trunks are classed as Hole nesters. Total species richness as well as species richness of each of these groups was calculated for each site.

Table 73. Bird species groupings used in analyses

Species groupings	Categories	Definitions/Criteria	Reference(s)
Conservation Status	Red/Amber	According to Irish list of birds of conservation concern	(Newton *et al.*, 1999)
Functional groups: forest use	1 - 3	1 = Forest species (i.e. do not breed outside forest/woodland habitat or mostly associated with woodland habitats); 2 = Generalists (i.e. associated with both woodland and many open habitats); 3 = Open species (i.e. dependent on both trees and open habitat or not associated with trees)	(Sharrock, 1976; Hutchinson, 1989; Fuller, 1995)
Functional groups: feeding	1 - 4	1 = Seedeater passerines; 2 = Resident insectivores; 3 = Migrant insectivores	(Snow & Perrins, 1998)
Functional groups: nest site	1 - 4	1 = Hole nester; 2 = Ground nester (nests on or near ground); 3 = Canopy nester	(Snow & Perrins, 1998)

7.2.4.3 Correction of species richness for number of visits and points

The number of species detected in a sample is dependent on survey effort. Survey effort per site varied due to two factors:

1. Numbers of point counts conducted within a site varied between four and nine.
2. Different numbers of visits were made to sites.

To control for the number of points counted in a site, residuals were taken from the regression of number of species detected against number of point counts. Standardised values of species richness were obtained by adding these residuals to the regression-derived number of species for six point counts.

Number of visits was controlled for using values that had been standardised for number of points, as follows. For all sites that had been visited three times, the total numbers of species detected in the following combinations of visits was calculated:

Visit 1 only

Visit 1 + Visit 2

Visit 1 + Visit 3

Regressions of the total number of species detected on all visits against number of species detected on the above selections of visits were then derived (e.g. Figure 44). The equations from these regressions were used to extrapolate the data collected from sites that were visited only once or twice. For instance, from the equation given in Figure 44,

$$y = 0.9545x + 2.5$$

where y = number species found on all visits, and x= number species found on visits 1 and 2. If ten species were recorded from a site that was surveyed only on Visit 1 and Visit 2, the extrapolated number of species for all visits = $(0.9545\times10) + 2.5 = 12.045$. Total species richness values and the species values of all the groupings described in Section 7.2.4.2 were standardised in this way. The regression equations and associated r^2 for each grouping are shown in Appendix A4.3.

7.2.5 Data analysis

7.2.5.1 Analyses of bird assemblage structure

Analyses were carried out on bird species data across all sites, and also on three sub-groups derived from ordination and cluster analysis of the bird habitat data (see Section 7.2.5.2, below). Densities for each of the species observed at a site were estimated as the mean of the point estimates of density at that site. Densities in the ash and spruce components of mixed sites were combined, because the sample sizes on which bird densities in the ash were based were nearly all too small (the average number of point counts situated in the ash components of the twelve mixes was 1.33) for these densities to be analysed separately.

NMS, flexible-beta cluster analysis and indicator species analysis were used for examining bird assemblage structure. Again, for the NMS and cluster analyses Sørensen distance measures were used. The parameter set-up used for the NMS analyses is shown in Table 74. All species occurring in less than 5% of the sites in a particular ordination were excluded from that ordination. The relationships between ordination axes and measured environmental variables were investigated using correlation analysis both across all sites and within sub-groups. Indicator species analysis according to the method described in Dufrêne and Legendre (1997) was used to identify the species which typified bird assemblages in sub-groups of sites defined by the bird habitat ordination. By this method, an indicator value was calculated for a given species in a given group of sites as the product of the relative density of the species in that group (expressed as a proportion of the sum of densities found in all groups) and the proportional frequency of the species in that group. A species was considered typical of a group when the indicator value was larger than 0.25 and the Monte Carlo test (1000 runs) result was significant.

7.2.5.2 Ordination of habitat variables recorded at bird points

The structural types defined in Section 3.3.4 were not suitable for general classification of the bird data, because the Sitka spruce/ash mixed were classified according to their Sitka components (see Section 7.2.5.1), so the number of sites in each of the ash structural types apart from Pre-thicket ash was either two or one. In order to identify alternative structural classes, an ordination of habitat variables recorded at the bird sampling points was carried out. Global non-metric multidimensional scaling (NMS; see Section 2.5.3) and flexible-beta cluster analysis (with $\beta=-0.25$) were performed using PC-Ord (McCune & Mefford, 1997) . Sørensen (or Bray & Curtis) distance measures were used. The parameter set-up used for the NMS analyses is shown in Table 74. The following variables were used in the analysis:

Canopy height; canopy cover; herb and moss cover; tree density (stems per m^2)

All of the variables were transformed by dividing by the maximum value so that they shared a scale of 0 to 1. Because ash and Sitka spruce sites did not appear to separate into distinct groups in the ordination of all sites (Figure 63), and also because of the small number of pure ash sites corresponding to more mature structural classes, pure ash, pure Sitka spruce, and mixed sites were classified together.

Table 74. **Parameter set-up used for NMS ordination of bird data**

Parameter	Value used
Number of axes	6
Number of runs with real data	50
Stability criterion	0.0005
Iterations to evaluate stability	20
Maximum number of iterations	500
Step down in dimensionality	Yes
Initial step length	0.20
Starting coordinates	Random
Number of runs of Monte Carlo test	50

7.2.5.3 *Trends in species richness between forest types and across the forest cycle*

ANOVAs were used to examine the influence of stand structure and tree species on a number of measures of bird species richness. Total bird species richness per site as well as the species richness of functional groups were used in the following analyses. The differences in species richness between spruce structural classes were investigated. For such analyses, all mixed sites were also classified according to the spruce component, which dominated the mixes at the scales perceived by birds. No comparison of ash structural classes was possible due to lack of replication in all but the pre-thicket stands (see Section 7.2.5.2). Paired t-tests were used to compare species richness of pure Sitka spruce sites with that of their matching spruce/ash mix sites, within each age class. Finally, one-way ANOVAs were used to test for an effect of tree species composition on species richness within each of the sub-groups obtained from the Cluster analysis of bird habitat data described in Section 7.2.5.2.

7.2.5.4 *Relationships between bird species richness, habitat and environmental variables*

Correlations of environmental variables and various measures of total or functional group species richness were carried out using parametric and non-parametric tests as appropriate. Before carrying out parametric correlations some of the variables were transformed, in order to normalise their distributions. Left-skewed variables (including axes 1 and 2 of the ordination on all sites) were logarithm transformed, while right-skewed variables (including axes 1 and 2 of the ordination on Older sites, and axis 3 of the ordination on Young sites) were transformed by squaring. In the case of variables with some negative values, this transformation was preceded by the addition of a constant equal to the largest negative value in the range of the untransformed variable, so that the minimum value in the range of the variable before transformation was set to 0. Percentage variables (including canopy cover and herb and moss cover) were converted to proportions and arcsin transformed.

The distributions of variables that could not be normalised were analysed using Spearman's rank correlations. The data were analysed separately, and according to the sub-groups obtained from the NMS ordination of bird habitat data. All significant correlations were inspected to check that they were not the result of outlying data-points. Correlations and ANOVAs were conducted using SPSS (2001).

7.3 RESULTS

7.3.1 Species recorded

A total of 62 species were recorded, of which 15 were not used in subsequent analyses because they were classed as non-breeding over-flyers, or because they were not recorded within 50 m of the observer. Individuals of the following species that were recorded only in flight were excluded from subsequent analyses: Hooded Crow, Herring Gull, Magpie, Rook, Raven, Starling, Pied Wagtail, Swallow, Sand Martin, Common Gull, and Jackdaw. A list of the species recorded and their membership of the different functional groups described in Table 73 is provided in Appendix A4.1. Fourteen species of conservation importance (i.e. either red or amber listed) were recorded, including two over-flying hirundines (Swallow and Sand Martin), and two birds of prey (Hen Harrier and Peregrine). The other species were all typical of open or scrubland habitats, with the exception of Crossbill, Redpoll and Spotted Flycatcher.

7.3.2 Bird habitat sub-groups and bird assemblages

As explained in Section 7.2.5.2, NMS ordination and subsequent cluster analysis of the bird habitat variables revealed three clear clusters of sites. The cluster membership of each site is listed in Table 75. We refer to these three groups collectively as bird habitat sub-groups, and separately by the names Younger sites, Intermediate sites and Older sites, in order to avoid confusion with other structural classes. These groups effectively differentiate between different parts of the forest cycle but not between tree species. Younger sites were all classified as pre-thicket in terms of structural class, with the exception of INCH, a pole ash stand. The division between Young and Intermediate sites corresponds with the separation between CUMM and DOOG in the spruce structural type ordination (Figure 11). Intermediate sites consist of three closed-maturing spruce sites, all thicket spruce sites and pure closed-maturing ash sites, and one pre-thicket spruce site (CUMM). The Older sites consist of all the mature ash, mature spruce, semi-mature ash and reopening spruce sites, and five closed-maturing spruce sites.

Table 75. Cluster membership of sites according to results of flexible beta cluster analysis on habitat variables measured at bird survey points.

Younger	Intermediate	Older
REEN	SAGG	RINC
MVAN	GFIN	BARN
INCH	MARY	SUNS
CORB	CLYD	SINB
LACK	COMM	MONT
COOS	KDUF	MUNG
COOA	COOL	DEME
BEND	GLYN	RATH
BRAC	DOOG	MSOP
BALE	CUMM	KILA
LURG		MOAN
KESH		UNIO
KILW		BALY
KILM		COON
HIGG		BOKY
		CORR
		CONA
		DERR
		FURY

The NMS ordination of bird data from all sites together separated sites principally according to different stages of the forest cycle (Figure 63). The arrangement of sites within the ordination reflects, for the most part, the structural classes described in Section 3.3.4, with a gradient of decreasing maturity from bottom-left to top-right of the ordination space. However, there is substantial overlap between several of the structural classes, and there appears to be little if any separation of sites according to tree species.

Axes 1 and 2 were strongly correlated with a suite of growth-stage related variables (Table 76), both being negatively correlated with age, canopy height and canopy cover, and positively correlated with herb and moss cover and tree density. Both axes were also correlated with distance from edge, and Axis 2 was also negatively correlated with point range, indicating that either proximity and abundance of edge habitat or size of site has an effect on the bird assemblage of these sites. Weaker correlations between the ordination axes and both distance to old woodland and area of old woodland may be partly explained by the relationship of these variables to growth-stage related variables such as canopy height (for this variable, correlations with distance to old woodland and area of old woodland are: Spearman's P=-0.274, n=44, p=0.07; and Spearman's P=0.355, n=44, p=0.02, respectively). However, they may indicate that proximity and abundance of old woodland also has an affect on the avian communities of forestry plantations.

Table 76. Significant Pearson's r and Spearman's rank P correlations between main ordination axes and habitat and environmental variables.

Habitat/environmental variable	Ordination axis	Pearson's r/ Spearman's P	p
Tree age	1	r=-0.589	<0.001
	2	r=-0.800	<0.001
Canopy height	1	r=-0.648	<0.001
	2	r=-0.788	<0.001
Canopy cover	1	r=-0.538	<0.001
	2	r=-0.811	<0.001
Tree density	1	P=0.621	<0.001
	2	P=0.689	<0.001
Herb and moss cover	1	r=0.470	0.0013
	2	r=0.700	<0.001
Distance from edge	1	r=-0.318	0.035
	2	r=-0.417	0.005
Distance from old woodland	1	P=0.322	0.033
Area of old woodland	1	P=-0.437	0.003
Point range	2	r=-0.403	0.007

When the bird species ordination was labelled according to bird habitat sub-group, this revealed clear species composition groupings (Figure 64).

Species that typified each of the bird habitat sub-groups were identified by indicator analysis (Table 77).

Table 77. Indicator species and their indicator values for bird habitat sub-groups. Only species with a maximum IndVal of 25 or more are included. The max IndVal is indicated in bold.

Species	Younger	Intermediate	Older	P value of max IndVal
Linnet	**43**	1	0	0.002
Redpoll	**49**	31	2	0.007
Meadow Pipit	**48**	2	0	0.002
Reed Bunting	**54**	4	0	0.001
Stonechat	**40**	0	0	0.001
Whitethroat	**37**	0	0	0.006
Blackbird	6	**52**	34	0.009
Chiffchaff	0	**39**	15	0.049
Dunnock	16	**52**	3	0.003
Robin	8	**53**	35	0.002
Wren	15	**45**	34	0.021
Chaffinch	10	32	**55**	0.001
Coal Tit	4	20	**66**	0.001
Goldcrest	3	25	**65**	0.001
Sparrowhawk	0	0	**32**	0.016
Treecreeper	1	0	**33**	0.021

7.3.3 Correlations of environmental variables with sub-group ordination axes

Ordinations were performed on the bird community data of each bird habitat sub-group, the results of which are summarised in Table 78. The relationships between the axes from these ordinations and the environmental variables described above were explored in order to determine which of these environmental variables might have an influence on the bird communities of each habitat sub-group. All statistically significant correlations between these axes and the environmental variables are listed in Table 79.

Table 78. Results of ordinations sites by bird species densities in bird habitat sub-groups.

Bird habitat sub-group	No. axes	Final stress	Final instability	Axis1 r^2	Axis2 r^2	Axis3 r^2
Younger	3	7.533	0.00030	0.500	0.236	0.166
Intermediate	2	7.223	0.00007	0.435	0.431	N/A
Older	3	8.534	0.00003	0.410	0.356	0.159

Variation in the bird assemblages of Younger forests is correlated with age and other growth-related variables such as canopy height and herb and moss cover. Other variables which are related to the avian communities of Younger forests are shrub layer and distance from old woodland. All of these variables are related to Axis 3 of the ordination, which accounts for just 16.6% of the variation, as opposed to Axes 1 and 2, which together describe 73.6% of variation in the ordination. Axis 3 is also correlated with area of old woodland, but this correlation is driven entirely by two data points representing sites with young, poorly developed trees and little shrub cover around the points, and probably has little if anything to do with old woodland.

Age and distance from the edge of the forest (as well as tree density and point range, which are related to these variables) are correlates of the ordination axes for the group of Intermediate forest sites, as well as for ordination Axis 3 of the Older sites, as discussed above. Also correlated with the variation in the bird communities of Intermediate sites is altitude.

In Older sites the environmental factor most highly correlated with any ordination axis is average Distance from the edge of the forest, which is correlated with Axis 1. Altitude and shrub layer are also (but less strongly) correlated with Axis 1, which accounts for only 15.9% of the variation in the ordination. Axes 2 and 3, which between them describe 77.6% of the variation in the ordination, are not correlated with any of the environmental variables tested by us.

7.3.4 Trends in bird species richness between structural classes, bird habitat sub-groups, and tree species composition

Total species richness did not vary significantly between different spruce structural classes. However, the following functional groups were significantly influenced by structural class: Open species, Seedeaters, Red/Amber listed species and Ground-nesters. These are mostly species associated with open or scrubby habitats. Species richness of these groups was significantly higher in pre-thicket and thicket classes than in later stages of the forest cycle. (Figure 65).

The effect of growth stage on species richness is more obvious when species richness values of the three bird habitat sub-groups are compared. Neither total species richness nor the species richness of Generalist birds (c.f. Appendix A4.1) differs significantly between habitat sub-groups. However, habitat sub-group does have a significant effect on the species richness of Forest birds, which is lowest in Younger sites, and significantly higher in Intermediate and Older sites, and also on species richness of Open birds, which decreases from its highest value in Younger sites, to lower values in Intermediate sites and Older sites (Figure 66).

Species richness of birds of Irish conservation concern was highest in young sites and lowest in old sites (F=15.17, df=2, 41, p<0.001). Species richness of ground nesting birds declined from its highest value, in young sites, to a significantly lower value in old sites, but species richness of hole nesters and canopy nesters did not vary significantly between bird habitat sub-groups (Figure 67). Species richness of both seed-eating birds and migrant insectivores was significantly lower in young to sites than in old sites, but there was no relationship between species richness of resident insectivores and bird habitat sub-group (Figure 68).

Table 79. Statistically significant correlations of environmental variables with the axes of the ordinations of sites in each bird habitat sub-group by the variation in their bird communities. Correlations in italics appear to be spurious (see text).

Habitat sub-group	Axis no.	Environmental variable	Pearson's r/ Spearman's P	N	P (2-tailed)
Young sites	Axis 3	Age	r=0.69	15	0.004
Young sites	Axis 3	Canopy height	r=0.54	15	0.038
Young sites	Axis 3	Herb & moss cover	r=0.78	15	0.001
Young sites	Axis 3	Shrub layer	P=0.82	15	<0.001
Young sites	*Axis 3*	*Dist from old woodland*	*P=0.57*	*15*	*0.028*
Young sites	Axis 3	Area of old woodland	P=0.70	15	0.004
Intermediate	Axis 2	Age	r=0.75	10	0.013
Intermediate	Axis 2	Distance from edge	r=0.65	10	0.041
Intermediate	Axis 2	Altitude	r=0.74	10	0.015
Intermediate	Axis 1	Point range	r=-0.67	10	0.033
Intermediate	Axis 2	Tree density	P=-0.81	10	0.005
Old sites	Axis 1	Distance from edge	r=0.77	19	<0.001
Old sites	Axis 1	Altitude	r=0.51	19	0.026
Old sites	Axis 1	Shrub layer	P=-0.54	19	0.018

Table 80. Results of ANOVAs and t-tests for differences in total bird species richness and species richness of bird forest use groups between pure spruce sites, pure ash sites, and spruce/ash mixed sites, within each of the three bird habitat sub-groups. In the Intermediate sub-group, the comparison is restricted to pure spruce and spruce/ash mixed sites, due to lack of replication of pure ash sites (n=1) .

Bird habitat sub-group	Measure of species richness	df	F	p
Older	Total	2,16	1.134387	0.346
Older	Forest	2,16	1.086205	0.361
Older	General	2,16	2.112284	0.153
Older	Open	2,16	2.279275	0.135
Younger	Total species richness	2,12	0.11933	0.889
Younger	Forest	2,12	2.193025	0.154
Younger	General	2,12	1.041657	0.383
Younger	Open	2,12	0.06235	0.940
		df*	t	p
Intermediate	Total	6.871796	1.441152	0.194
Intermediate	Forest	6.623814	0.772191	0.467
Intermediate	General	4.810806	1.15436	0.302
Intermediate	Open	6.801607	0.964832	0.368

*df for t-tests adjusted for assumption of non-equal variance

There were no significant differences in any measure of species richness between pure spruce, pure ash, and spruce/ash mixed sites within any of the bird habitat sub-groups (Table 80).

7.3.5 Correlations of environmental variables with species richness

7.3.5.1 Total species richness, and species richness of forest use categories

Within habitat subgroups, total species richness was negatively correlated with tree density in young sites, with age in Intermediate sites, and with both distance from the edge and altitude in Older sites (Table 81).

Table 81. Statistically significant correlations of environmental variables with total species richness of the sites in each bird habitat sub-group.

Habitat sub-group	Environmental variable	Pearson's r	N	P (2-tailed)
Young sites	Tree density	r=-0.53	15	0.042
Intermediate	Age	r=-0.69	10	0.027
Old sites	Distance from the edge	r=-0.72	19	0.001
Old sites	Altitude	r=-0.50	19	0.031

None of the environmental variables we examined were correlated with species richness of forest-preferring birds (Table 82). In old forests, higher numbers of generalist bird species are associated with a well-developed shrub layer and edge habitat. Intermediate forests also hold more generalist species where proportion of edge habitat is high.

In Older sites, richness of Open bird species is higher when proportion of edge habitat is higher. In Intermediate forests, Open bird species richness is negatively correlated with age and canopy height, indicating that Open birds prefer forests at a less advanced growth stage.

Table 82. Statistically significant correlations of environmental variables with species richness of the birds in each forest-use category, in the sites belonging to each bird habitat sub-group.

Forest-use category	Habitat sub-group	Environmental variable	Pearson's r Spearman's P	N	Sig. (2-tailed)
Forest	-	-	-	-	-
Generalist	Old sites	Distance from the edge	r=-0.66	19	0.002
Generalist	Old sites	Shrub layer	r=0.61	19	0.006
Generalist	Intermediate	Distance from the edge	r=-0.65	10	0.043
Open	Old sites	Distance from the edge	r=-0.65	19	0.002
Open	Intermediate	Age	r=-0.78	10	0.009
Open	Intermediate	Canopy height	r=-0.74	10	0.015

7.3.5.2 Species richness of Red/Amber grouping

Within bird habitat sub-groups, none of the environmental variables we assessed were significantly correlated with species richness of birds identified as being of conservation concern.

7.3.5.3 Species richness of nesting categories

In Older forests, species richness of Hole nesters is negatively related to altitude, and positively (though less strongly) related to shrub layer (Table 83), which is also negatively correlated with altitude. The relationship between species richness of Hole nesters and tree density in Intermediate sites is quite weak, its statistical significance being entirely due to one extreme point. This point represented a site (CLYD) with high tree density in which no Hole nesters were recorded, probably due more to the upland nature of site (as in the relationship with altitude in Older sites) than to the tree density *per se*.

In Older forests, there are more species of ground nesting birds in lower altitude forests and in forests with a large proportion of edge habitat or small area (edge and area are, of course, correlated at the site scale). Within Intermediate forests, species richness of ground nesting birds is greater in younger plantations, with a higher density of tree stems. Both age and tree density are closely correlated with canopy closure.

Table 83. Statistically significant correlations of environmental variables with species richness of the birds in each nesting category, in the sites belonging to each bird habitat sub-group.

Nesting category	Habitat sub-group	Environmental variable	Pearson's r Spearman's P	N	Sig. (2-tailed)
Hole	Old sites	Altitude	r=-0.61	19	0.006
Hole	Old sites	Shrub layer	P=-0.46	19	0.046
Hole	Intermediate	Tree density	P=0.63	10	0.049
Ground	Old sites	Altitude	r=0.61	19	0.006
Ground	Old sites	Distance from the edge	r=-0.54	19	0.016
Ground	Old sites	Point range	r=-0.49	19	0.035
Ground	Intermediate	Age	r=-0.69	10	0.027
Ground	Intermediate	Tree density	r=0.66	10	0.038
Canopy	-	-	-	-	-

7.3.5.4 Species richness of diet/migration categories

In Older sites, the Resident insectivore assemblage is more species-rich when a high percentage of the site is close to the forest edge (Table 84). Resident insectivore species in Intermediate forests are also found in greater numbers in forests at an early growth stage, and with a well-developed shrub layer, and so appear to be negatively affected by canopy closure.

As for Resident insectivores, the Migrant insectivore assemblage of Old sites is more species rich in forests with a higher proportion of edge habitat. The relationship between species richness of Migrant insectivores and distance from old woodland is driven by two data points from upland plantations with very little scrub nearby. Other plantations equally far from areas defined as old woodlands from the 6″ maps, but with more scrub in the landscape around them, had as many species of migrant insectivores as forests situated closer to old woodland. In Younger forests, more species of Migrant insectivores occur in forests in which the commercial crop is older or better grown, and in areas with high levels of shrub cover.

7.3.6 Correlations of individual species densities with species richness.

Species richness across all sites was most strongly correlated with species densities of Dunnock, Wren and Blackbird (Table 85). All of the other species showing positive correlations with species richness are associated with scrubby, broadleaved, or quite well wooded habitats. The only species to show a negative correlation with total species richness is the Goldcrest.

Among the five most strongly correlated species with species richness in Older sites are four of the five indicators of Intermediate forest. Of the remaining six species, four (Pheasant, Greenfinch, Great Tit and Blue Tit) are all associated with landscapes that have a lowland character, with a scrubby or broadleaf component, while Song Thrush is characteristic of forests that have a well developed understorey (Fuller, 1995).

The two most strongly correlated species with species richness in Intermediate sites are two migrant insectivores, the Willow Warbler (known to inhabit young, open forests) and the Blackcap (which inhabits scrubby forests with lots of undergrowth) (Fuller, 1995). Three species are indicators of Intermediate sites, one species is associated with Older sites (Chaffinch), and another is more typical of Younger sites (Redpoll). The remaining three species (Long-tailed Tit, Song Thrush and Bullfinch) are all birds of scrub or forest undergrowth (Fuller, 1995).

Table 84. Statistically significant correlations of environmental variables with species richness of the birds in each diet/migration category, in the sites belonging to each bird habitat sub-group. Correlations in italics appear to be spurious (see text).

Nesting category	Habitat sub-group	Environmental variable	Pearson's r Spearman's P	N	P (2-tailed)
Seedeaters	-	-	-	-.	-
Res. insectivores	Old	Distance from edge	r=-0.56	19	0.012
Res. insectivores	Intermediate	Age	r=-0.71	10	0.021
Res. insectivores	Intermediate	Canopy height	r=-0.67	10	0.033
Res. insectivores	Intermediate	Canopy cover	r=-0.64	10	0.048
Res. insectivores	Intermediate	Shrub layer	P=0.72	10	0.020
Mig. insectivores	Old	Distance from edge	r=0.72	19	0.001
Mig. insectivores	*Intermediate*	*Distance from old woodland*	*P=-0.66*	*10*	*0.039*
Mig. insectivores	Young	Age	r=-0.73	15	0.002
Mig. insectivores	Young	Canopy height	r=-0.56	15	0.030
Mig. insectivores	Young	Herb and moss cover	r=-0.65	15	0.009
Mig. insectivores	Young	Shrub cover	P=0.68	15	0.006

Table 85. Statistically significant Pearson's correlations of total species richness with species densities, across all sites, and in each of the three bird habitat sub-groups (Younger, Intermediate and Older).

	All sites		Younger		Intermediate		Older	
Species	r	p	r	p	r	p	r	p
Dunnock	0.55	0.0001	0.59	0.0202	0.74	0.0137	0.63	0.0039
Wren	0.49	0.0007			0.64	0.0454	0.78	0.0001
Blackbird	0.47	0.0013	0.63	0.0115	0.74	0.0136	0.58	0.0087
Willow Warbler	0.43	0.0036			0.76	0.0115		
Pheasant	0.42	0.0047					0.57	0.0111
Song Thrush	0.42	0.0047			0.66	0.0378		
Blackcap	0.37	0.0126			0.81	0.0044		
Bullfinch	0.36	0.0156			0.64	0.0463		
Blue Tit	0.36	0.0168					0.47	0.0409
Redpoll	0.31	0.0414			0.68	0.0317		
Goldcrest	-0.30	0.0479						
Treecreeper			0.55	0.0344			0.52	0.0225
Chiffchaff			0.55	0.0344				
Long-tailed Tit					0.73	0.0169		
Chaffinch					0.72	0.0193		
Robin							0.53	0.0204
Stonechat							0.52	0.0232
Greenfinch							0.51	0.0272
Great Tit							0.50	0.0282

Of the four species correlated with species richness in Younger sites, three are among the five species identified as being typical of the Intermediate bird habitat sub-group, all of which prefer to nest in low-lying, scrubby vegetation, while the fourth species is Treecreeper, which is generally restricted to areas where there are quite mature trees (Fuller, 1995).

The species richness of Open birds and Red/Amber birds is higher in pre-thicket plantations than in older forests (Section 7.3.4), due to the loss of species from these groups after canopy closure. Species whose densities are correlated with the number of Open or Red/Amber species in Younger sites could therefore be used before afforestation to indicate areas which, due to the vulnerability of their bird assemblages, should not be planted. The densities of three species were correlated with Open species richness of Younger sites, these being Stonechat and Goldfinch (positively correlated), and Song Thrush (negatively correlated). The densities of five species were correlated with Red/ Amber species richness of Younger sites. Four of these correlations were positive, these being with densities of Whitethroats, Grasshopper Warblers and Redpolls. The last correlation, with density of Long-tailed Tits, was negative.

Table 86. Statistically significant correlations of Open species richness and Red/Amber species richness with species densities in the Young bird habitat sub-group.

Species	Open r	Open p	Red/Amber r	Red/Amber p
Stonechat	0.70	0.0039	0.53	0.0409
Goldfinch	0.52	0.0475		
Song thrush	-0.67	0.0068		
Whitethroat			0.61	0.0149
Grasshopper Warbler			0.59	0.0213
Redpoll			0.55	0.0324
Long-tailed Tit			-0.53	0.0401

7.4 DISCUSSION

Point count methodology, although an efficient way of surveying forest birds, and comparable with other studies, has some disadvantages. In particular, point counts do not favour detection of certain groups of birds, such as birds of prey, and shy or nocturnal species. For example, species such as Woodcock, Long-eared Owl and Hen Harrier may well have been under-recorded in this study and would require different and more time-consuming sampling methodologies in order to detect them (Bibby *et al.*, 2000). Also, by increasing the number of visits to each point, the probability of detecting new species at the revisited points would have increased, but at the expense of the number of areas we were able to survey.

Bird assemblages respond clearly to the structure of the plantation, though at a coarser scale than the structural classes defined in Section 3.3.4. Birds of open habitats are most strongly influenced by forest structural stage. These tend to be ground-nesters and seedeaters and they occur only in very young forest stages, regardless of tree species; they are eliminated from communities of older forest stages. The presence of these species in young plantations is probably more dependent on the original habitat and vegetation of a site, prior to afforestation, rather than to features attributable to forestry. It is noteworthy that the richness of Red/Amber species was not correlated with any of the measured environmental variables.

A large proportion of the Red/Amber listed species recorded during this survey are declining species of open farmland and scrub, such as Grasshopper Warbler, Skylark, Stonechat and Whinchat. While forestry might initially favour some of these birds (especially in areas of intensive agriculture), through increases in shrub and herb cover associated with the relaxation of grazing pressure on recently planted land, they will be lost from forest plantations by the time of canopy closure. Areas of open habitat which support a high diversity of Open birds, and particularly of Red/Amber listed species, should be safeguarded from afforestation. These will usually be areas of marginal land, not dominated by improved grassland. The species in Table 86, whose densities are correlated with species richness of Open birds and Red/Amber birds, could be used to help identify such areas. Notable among the species in Table 86 are Stonechat, which is positively correlated with both Open species richness and species richness of Red/Amber birds, and Whitethroat, which is positively correlated with Red/Amber species richness though it is not a member of this group. Other positive correlations, between Goldfinch density and Open species richness, and between the densities of Grasshopper Warbler and Redpoll and Red/Amber species richness, mean that these species also have a potential use as indicators. The last two, Song Thrush and Long-tailed Tit, are negatively correlated with species richness of these groups, and should be used only in conjunction with the positive indicators. Presence and abundance of an indicator species can be used to infer when and to what extent the ecological requirements of a species are met. Absence or rarity of a species, however, can be due to a wide variety of ecological circumstances.

Species classified as Forest species for the purposes of the analysis appear to prefer more mature plantations. However, the only one of these that is a true forest specialist, requiring large areas of interior forest, is the Crossbill, which was recorded in only three sites (all of which were Older pure Sitka spruce sites). Of the nine Forest species recorded, four were species known to actively prefer coniferous forest habitat (i.e. Goldcrest, Coal Tit, Crossbill and Siskin) (Avery & Leslie, 1990; Gibbons *et al.*, 1993). Within the bird habitat sub-group of Old sites, the number of Forest species we recorded did not respond to any of the measured environmental variables. This suggests that the forest species in question, beyond showing a preference for the more mature forest stands, are quite generalist in their forest habitat requirements within the stand or at the landscape scale. With the exception of Crossbill, the only true forest interior species occurring in Ireland (Redstart, Pied Flycatcher and Wood Warbler) are restricted to semi-natural oak woodlands and were absent from every site surveyed. The paucity of bird species of conservation importance at latter stages of the forest cycle can partly be attributed to the extreme rarity of true forest specialists in Ireland. As mentioned above, however, the survey methods did not allow a thorough investigation of the importance of spruce and ash plantations for some nocturnal or poorly detectable forest species.

The differences between communities in spruce or ash plantations seem to be minimal; forest structure is of more importance in determining bird species composition. The lack of major differences in species richness between spruce and ash plantations is surprising, in view of the fact that semi-natural Irish broadleaved forests were found to support more species of birds than Irish conifer forests by Batten (1976). However, the broadleaved forests investigated were of semi-natural oak and therefore not directly comparable with ash plantations. In northern Europe, higher numbers of invertebrate species are associated with oak than with ash (Key, 1995), which could have consequences for the range of ecological niches available for occupation by insectivorous birds. Also, natural and semi-natural forests can differ substantially from planted forests, even when tree species composition is similar, in a number of different aspects (e.g. structural heterogenity, availability dead wood) that could affect bird assemblages (Fuller, 1995). Finally, we examined only two mature and two semi-mature ash plantations, between which there was substantial variation in understorey, edge habitat, and the surrounding landscape. All of these forests were inter-mixed with other tree species, and three of the four had substantial non-native conifer elements. With a greater replication of Intermediate and Older ash sites, it is more likely that differences between Sitka spruce and ash would emerge.

Two separate studies (Wilson, 1977; Nairn & Farrelly, 1991)of the bird assemblages in a total of five semi-natural woodlands (all predominantly sessile oak woodland) in Killarney and the Wicklow mountains found more bird species than we found in the 22 study sites in the Older bird habitat sub-group (woodland mean = 19.60±0.40; Older sites mean = 13.63±0.82), but lower total bird densities (woodland mean = 12.50±0.90 pairs/ha; Older sites mean = 16.07±0.98 pairs/ha). In the Older sites, the five most common species (Goldcrest, Chaffinch and Coal Tit, Robin and Wren) accounted for 78% of the total bird density across all sites. The five commonest species in the semi-natural woodlands were the same as for the Older sites, with the exception of Blue Tit, which was commoner than Wren; these accounted for 68% of total bird density. Goldcrest was either the most common species or the second most common species in 19 out of 22 Older sites, but was only one of the two most common species in 1 out of 5 semi-natural woodlands.

Coal Tit was always the most common tit in the Older sites, and in all but two sites was present at higher densities than those of Blue Tits and Great Tits combined. Blue Tit was the most common tit in three out of 5 semi-natural woodlands surveyed by Wilson (1977) and Nairn and Farrelly (1991); in the remaining two woodlands the combined densities of Blue Tits and Great Tits either equalled or surpassed that of Coal Tits. Interestingly, in three of the four Older pure ash sites, either Great Tit or Blue Tit were among the five commonest birds, whereas neither of these species was among the five commonest birds in any of the 18 Older pure spruce and mixed sites. Both of the semi-natural woodlands where Coal Tits outnumbered Blue Tits were situated adjacent to large areas of conifer plantation (Wilson, 1977). Mean density of Treecreepers (which, like the three tit species mentioned above, are cavity nesters) was approximately 10 times higher in semi-natural woodland than in Older sites. A study of birds in logged and unlogged forest in Canada and Fennoscandia (Imbeau *et al.*, 2001) concluded that cavity nesting species are among the most sensitive to intensification of forest management. Coniferous forest plantations typically have less standing dead wood and a more homogenous, younger age structure than semi-natural woodland, which might partly explain why cavity nesters such as Blue Tits, Great Tits and Treecreepers are all much more abundant in semi-natural woodlands than in our study sites. However, Coal Tits are also cavity nesters, but were commoner in coniferous plantations (this study) than in semi-natural woodland (Wilson, 1977; Nairn & Farrelly, 1991). An alternative explanation for the greater abundance of some cavity nesting species in semi-natural woodland is that the tree species of native broadleaved trees hold greater densities of insect prey, and so are preferred by these species for foraging purposes. A study of foraging habits of tits in Japan (Hino *et al.*, 2002) found Coal Tits to be more ready to forage on tree species that supported low densities of prey items than other tits.

Negative correlations between species richness and Distance from the forest edge may be due to enhanced detection of species typical of open habitats at forest edges, or to the use of forest edge as a preferred habitat by species associated with forests and scrub. It has recently been suggested that, as well as representing a unique habitat for some species, exposed edges of mature forest fragments are also used by early-successional species because true shrubby habitats are lacking (Imbeau *et al.*, 2003).

The correlations between species richness and shrub layer confirm that the presence of shrubs has a positive effect on bird diversity at different stages of the forest cycle. The relationship between measures of species richness and altitude is probably due to the broad differences between upland and lowland forestry, rather than to an effect of altitude *per se*. Many upland sites are planted in areas with a near or total absence of semi-natural scrub or woodland, whereas lower altitude sites are more likely to have small areas of broadleaved woodland, scrub, or gardens nearby. In addition, many upland forests are planted on peat, where the vegetation immediately surrounding the forest is often much less scrubby than on other soil types.

The variables Area of old woodland and Distance to old woodland were not found to have a pronounced effect on bird species richness. These variables were calculated using data from a series of maps that ranges in age from 70-100 years old, and does not show many small areas of woodland or any recently abandoned land that has reverted to scrub. Such areas are often the most scrub-rich, broadleaf-dominated elements of habitat to be found in afforested areas, and may play an important role in determining the bird communities of plantation forests. A better way to assess these areas would be using aerial photographs, which would enable a more effective study of the relationships between forest bird communities and the surrounding landscape.

All of the species associated with Younger sites are described as Open birds in our forest functional group classification, with the exception of Redpoll, which, although classified as a Forest bird, traditionally breeds in young, open forests (Sharrock, 1976; Fuller, 1995). Typical species of Intermediate sites are all Generalists apart from Chiffchaff, a Forest bird that inhabits forests with a well-developed understorey (Fuller, 1995). The five birds identified as being typical of Older sites are all Forest birds except Chaffinch, which is classified as a Generalist due to its very occurrence in a wide range of habitats, but is commonest in post-canopy closure forest (Fuller, 1995). Despite this strong correspondence between sub-group and forest functional group, the species typifying Intermediate sites were correlated with species richness over all sites, as well as in the separate habitat sub-groups, whereas typical species of Young and Forest sites were not. Intermediate species (Dunnock, Robin, Blackbird, Wren and Chiffchaff) are all typical of scrubby forests or hedgerows, and are probably correlated with some of the environmental variables discussed above, such as edge habitat and shrub layer. Also, because they are associated particularly with Intermediate sites, high densities of these species in Young or Old sites may indicate forests that tend towards Intermediate, and therefore support elements of the bird community from a wider range of growth-stages, as shown by Steverding & Leuschner (2002). Although this group is successful at indicating species richness in the sites studied, they are all very generalist species, and were found in nearly all of our study sites. It is the abundance rather than simply the presence of these species that we suggest should be used as an indicator of forests with high values of species richness.

The other species whose densities are correlated with bird species richness values vary between the different habitat sub-groups, but are generally species that are either associated with other habitat sub-groups (for instance, in Intermediate sites, both Redpolls and Chaffinches, which are associated with Young and Old sites, respectively, are correlated with total species richness), or are associated with well developed, scrubby understoreys.

The only species negatively correlated with species richness is Goldcrest, the bird most typical of mature conifer forestry. This correlation is not very strong, and is only significant over all sites (not in any of the three habitat sub-groups). The reason for the negative relationship between Goldcrest numbers and bird diversity is that Goldcrest density is correlated with growth stage and lack of understorey.

7.5 CONCLUSIONS

7.5.1 General conclusions

The structure of the forest was the main determinant of bird community composition and bird species richness.

Younger stages of the forest cycle were characterised by the presence of a number of ground-nesting seedeaters, some of which were Red/Amber species of conservation concern. The presence of such species was probably more influenced by the original habitat of the site than by features of the young plantation. In order to preserve such assemblages, afforestation of unimproved open habitats with good open bird assemblages should be avoided where possible.

The birds of intermediate forest stages tended to be generalists such as Robin, Wren and Dunnock. Stands of any age with high densities of these species tended to support species-rich assemblages.

Older stages of the forest cycle supported more Forest species as defined for the purposes of this study, however, the lack of any true forest specialist species, requiring large expanses of interior forest habitat, was marked. Such species are scarce in Ireland. Indeed, the Forest species we recorded showed a preference for the forest edge and for well-developed shrub and herb and moss layers. Older stands were typified by Goldcrests, high densities of which were associated with species-poor forest stands.

The influence of species of tree on bird assemblage appeared to be negligible, however, pure mature ash stands could not be found for study. Other species of broadleaves and conifers would also be worthy of further investigation.

7.5.2 Biodiversity indicators

Although, across all sites, growth stage had no effect on overall species richness, age-related variables did correlate with several measures of species richness in Young and especially Intermediate sites. This is because many species of open habitats that breed in the early stages of plantation forestry are excluded from sites as canopy closure is achieved.

The abundance of some species is correlated with species richness of open or Red/Amber listed species. High abundance of Stonechat, for example, is a good indicator for high species richness of both Red/Amber listed and open species. Such compositional indicators could be used for identifying open habitats which should not be afforested.

As the forest develops, the amount and type of edge habitat becomes an important indicator of bird species diversity. Average distance from the edge of the forest is strongly correlated with many measures of species richness in Old sites, and with one measure of species richness in Intermediate sites. Bird groups that are more species-rich in forests with high proportions of edge habitat are those associated with scrub-rich or open forest habitats. This is because the interface between forest and open habitats is often scrubbier than either of the habitats that surround it. Even within the forest, that part of the forest floor closest to the edge often supports a more vigorous understorey due to increased light penetration.

Shrub layer has a positive affect on the species richness of several bird groups in all growth stages of forest. The species involved all use the shrub layer for foraging and especially for nesting, and this correlation indicates that lack of shrub layer can limit the avifauna of plantation forests at all stages.

The bird species whose densities are correlated with species richness across all sites, as well as within the three bird habitat sub-groups, are mostly associated with scrub-rich or open forest habitats. High abundances of these generalist species have the advantage of indicating high species richness at any forest cycle stage.

7.5.3 Management recommendations and modifications to *Forest Biodiversity Guidelines*

The bird species of greatest conservation importance that were found during this study were birds of open habitats, rather than of forest. Such birds were most abundant and diverse in Younger sites, many species disappearing from forests as they developed and the canopy closed. Several of the species we found in recently planted sites have been identified as being of conservation concern, the most common threat to these species being habitat loss. Apart from trying to provide more open habitat in and around plantation forests, the most obvious conservation recommendation to make for such species is to avoid planting in areas where species-rich assemblages of these birds exist.

In general, the findings of this study support the recommendations in the *Forest Biodiversity Guidelines* (Forest Service, 2000b). We agree with the recommendation that a mix of tree ages should be maintained within a plantation, and confirm that *Areas for Biodiversity*

Enhancement (ABEs) could be used to increase the availability of scrub and open habitats within the forest, and the diversity of bird species within it.

Edge management is clearly important for birds in Irish plantation forests. As discussed by O'Halloran *et al.* (2002), although increases in edge habitat (resulting from forestry activities and fragmentation of large forested areas) can reduce available habitat for species that depend on forest 'interior', this problem rarely applies in Ireland, because the Irish avifauna lacks such forest specialists (see below). Their anticipation that increasing the amount of edge habitat would increase bird diversity is supported by the findings of the present study. The availability and quality of edge habitat could be increased by making forest boundaries more irregular, by encouraging heterogeneity of both structure and species composition along forest edges, and through management of internal edge habitat (e.g. along roads and fire breaks). Because it is the vegetation associated with edges, rather than the edge itself, that is important for birds, leaving a wide, unplanted margin at the edge of forests, in which a mixture of native trees, scrub and open habitats are allowed to develop, would increase the range of species that an area of forest was able to support. All of the above recommendations are mentioned in the *Forestry and Bird Management and Planning Guide* (O'Halloran *et al.*, 2002), and are also in broad agreement with existing recommendations of the *Forestry and the Landscape Guidelines* (Forest Service, 2000c).

True specialists of forest habitats were not encountered during this study, largely as a consequence of their rarity in Ireland. In areas where forest specialists are known to occur, appropriate conservation management will vary from species to species, but could include the provision of nest boxes (e.g. for Pied Flycatchers), the establishment of areas of broadleaved, especially oak and birch woodland (e.g. for Redstart, Pied Flycatcher, Wood Warbler), the creation within and around forests of large open areas, with patches of scrub, for foraging by Nightjars. These and other species-specific conservation measures are summarised in the *Forestry and Bird Management and Planning Guide* (O'Halloran *et al.*, 2002).

8 SYNTHESIS

8.1 INTRODUCTION

In this section we attempt to identify the major similarities and differences between the taxonomic groups in the ways in which their biodiversities change over the forest cycle and vary between forest types, and in the factors that correlate with their biodiversity. We do this in two ways. Firstly we review the main findings of the preceding sections to identify the common patterns that emerge, and contrast the differences between groups. Secondly we carry out formal analyses of the similarities between the taxonomic groups in their assemblage structure and in their variation in species richness between sites.

8.2 COMPARISON OF TRENDS BETWEEN GROUPS

8.2.1 Assemblages of ash and Sitka spruce plantation forests

In all the taxonomic groups, the pre-thicket sites were clearly separated from the more structurally developed sites, reflecting the distinctiveness of the species assemblages that occur at this stage. In spiders, hoverflies and birds, the pre-thicket assemblages show much greater variation between sites compared to the assemblages of most of the other structural groups. This pattern is not evident in the vegetation assemblages where variation between sites is broadly similar in all the structural groups (taking into account the difference in the number of sites included in the structural groups). In vegetation, spiders and hoverflies the semi-mature and mature ash sites are clearly separated from the other structural groups, reflecting the strong preferences for, or are restricted, to deciduous woodland amongst these groups. This is not the case for birds, as such specialist species are generally absent or very rare in the Irish avifauna. It is also true that the semi-mature and mature ash sites were associated with old woodland (see Section 3.3.3.1), thus some of the distinctiveness of the species assemblages associated with these sites may be due to this factor, rather than to intrinsic differences between ash and Sitka spruce. However, the spider assemblages did not include high numbers of forest species (as might be expected under this scenario), and the distinctiveness of the hoverfly assemblages was due mainly to the presence of species that require broadleaved woodland

8.2.2 Trends in biodiversity across the structural cycle

The trends in total species richness across the age-cycle are summarised in Table 87 and Table 88. Most groups that show differences, except bryophytes, have high species richness in the pre-thicket stage and low species richness in the intermediate stages. In Sitka spruce, the mature stage generally has high species richness, except for hoverflies. Total species richness of birds varied (though was not significantly different) between the Sitka spruce structural groups, with the highest species richness in pre-thicket spruce and the lowest in closed-maturing spruce (there were not enough sites to analyse for ash).

Table 87. Trends in total species richness across the age-cycle in Sitka spruce.

	Vegetation (overall)	Vascular plants	Bryophytes	Spiders	Hoverflies	Birds
Pre-thicket	High	High	Low	High	High	No statistically significant differences
Thicket				High	High	
Closed-maturing	Low	Low	↓	Low	Low	
Reopening				Low	(Not analysed)	
Mature	High	High	High	High	Low	

Table 88. Trends in total species richness across the age-cycle in ash.

	Vegetation (overall)	Vascular plants	Bryophytes	Spiders	Hoverflies
Pre-thicket	No statistically significant differences	High	Low	High	High
Pole					(Not analysed)
Closed-maturing		↑	↓		High
Semi-mature				Low	Low
Mature		Low	High	Low	Low

The numbers of forest-associated species tend to increase with increasing structural development in all the taxonomic groups. However, in hoverflies, this increase was only significant between the pre-thicket and thicket stage in Sitka spruce and between the pre-thicket and closed-maturing stage in ash (pole stage was not analysed). In birds, the increase was only significant when analysed using the modified, three-level structural classification (see Section 7.3.2). The numbers of species associated with open habitats generally tend to decrease after the initial stages of structural development, but (e.g. for spiders in all sites, and vascular plants in Sitka spruce) may increase again at the mature stage.

8.2.3 Trends in biodiversity between ash and Sitka spruce

Overall, we found that total species richness of spiders and bryophytes was significantly higher in Sitka spruce compared to ash. There was also greater species richness of forest spiders in Sitka spruce. We did not find any overall differences in the species richness of the other major taxonomic groups between ash and Sitka spruce sites. Bryophytes are favoured by the cool, damp conditions and reduced competition from taller vascular plants that are found in older spruce stands. Also, the habitats frequently used for spruce afforestation, such as wet heathland and bog, tend to be more bryophyte-rich than the typical improved grassland or pasture ash site. Ash had greater overall species richness of vascular plants and saproxylic (i.e. dependent on dead or dying wood) hoverflies. There are more saproxylic hoverflies restricted to broadleaved woodland compared to conifer forests in Ireland.

8.2.4 The effect of adding ash to a Sitka spruce plantation

We did not find many differences in the species richness of the ash and Sitka spruce components of mixed plantations. However, at the age class 2 stage there was a greater species richness of forest specialist spiders in the Sitka spruce component, and greater species richness of hoverflies in the ash component. Both these differences reflect the generally faster structural development of Sitka spruce compared to ash: by age class 2, Sitka spruce has usually developed a closed canopy favouring the occurrence of forest specialist spiders, while the more open ash component allows hoverfly species associated with the pre-planting habitats to persist.

At the plantation scale, direct comparisons of species richness in mixed plantations (i.e., Sitka spruce with ash) and paired pure plantations (Sitka spruce only) did not reveal many differences. However, our failure to detect such differences may reflect the impossibility of finding perfectly matching sites (i.e. sites that differ only in the presence or absence of an ash component). Other comparisons suggest that adding ash to a Sitka spruce plantation will increase the overall biodiversity of the plantation. In spiders in age classes 2 and 4, the average pairwise similarity is lower between plots from the ash and Sitka spruce components compared to between plots that are both within the Sitka spruce component. In hoverflies in age class 2, the number of unique species (i.e. species caught in only one trap in a site) was higher in the trap from the ash component compared to the traps from the Sitka spruce component. Also, consideration of the known habitat associations of the Irish hoverfly fauna indicates that there are twelve widespread species associated with ash plantations, which do not occur in Sitka spruce plantations.

The distinctiveness of the plant, spider and hoverfly assemblages associated with ash of age class 5 suggest that mixed plantations that retain their ash component beyond the period when Sitka spruce stands are felled will enhance their biodiversity in two ways. These plantations will develop assemblages that do not normally occur in pure Sitka spruce plantations. They will also support assemblages associated with mature forests when the reforested parts of the plantation are at the pre-thicket stage. However, a caveat must be applied to the first point, as the age class 5 ash sites surveyed all had old woodland nearby. Although this may not be uncharacteristic of older broadleaf stands in the current forest estate, given the estate or woodland origin of many such stands, proximity to woodland may not be typical of the agricultural sites currently being afforested with ash.

8.2.5 Biodiversity indicators

When considering biodiversity over the forest cycle, the best indicator for the majority of taxonomic groups is stand structural stage. There are differences in resolution among different species groups in how they "perceive" forest structure. For example, vascular plants exhibit a marked response to small changes in canopy cover in reopening Sitka spruce stands (Section 4.3.6.2), whereas forest and tree/shrub specialist hoverfly species richness remains more or less constant from the thicket through to the mature stages (Section 6.3.6). A fundamental distinction in forest structure to which virtually all taxonomic groups respond is between the pre-thicket stage and structural stages post-canopy closure.

8.2.5.1 Pre-thicket stands

Pre-thicket stands have not completed the transition from an open environment to a wooded one, and therefore patterns of biodiversity largely reflect pre-afforestation habitat. In all taxa, species typical of open habitats tend to be lost from plantations after canopy closure, so indicators of biodiversity in pre-thicket plantations (Table 89) may therefore highlight habitats of conservation value that should not have been afforested. Such indicators identified here will be tested by BIOFOREST in the future, using the independent set of data being collected for Project 3.1.1, Biodiversity of Afforestation Sites.

Pre-thicket sites occupied by heath or bog plant species are more species-rich than formerly improved grasslands. Therefore, species that indicate such communities are the most appropriate indicators of biodiversity among plants (Table 89, Section 4.3.6.1). Stress-tolerant species that are better able to survive in such infertile sites are a particularly important group of vascular plants. Similarly, the best indicators of bryophyte species richness are soil variables reflecting more acidic, nutrient poor conditions, or structural indicators reflecting these environmental conditions.

The best indicator for ground-dwelling spider biodiversity is structural: cover of the lower field layer (i.e. vegetation 10-50 cm in height). This is in contrast to the results for plants where high vegetation cover does not necessarily indicate high species richness, and in the case of competitive grasses on fertile soils actually indicates species poverty. Correlation analyses were performed between spider species richness (total and that of the habitat groups) and vegetation structure in life-form categories (as used in the vegetation chapter, c.f. Section 4.2.1.2) at the site and plot levels. Spider species richness did not appear to respond differently to different types of vegetation that would mainly comprise the lower field layer, i.e. graminoid cover and subshrub cover. The significant correlation between spider species richness and soil organic content in the pre-thicket mix assemblage (Section 5.3.4.1) suggests a possible correspondence between bryophyte and spider species richness in afforested heath or bog sites. The nature of this potential correspondence is unclear. Because soil samples collected at the pitfall trap plots included the litter layer, however, spiders may simply be responding to differences in litter quality.

Table 89. Summary selection of biodiversity indicators for pre-thicket ash and Sitka spruce stands. The sign of the indicators' relationship with species richness for each taxonomic group is given in brackets.

	Compositional	Structural	Functional
Vascular Plants	*Molinia caerulea* (+) *Calluna vulgaris* (+) *Erica tetralix* (+) *Agrostis stolonifera* (-) *Dactylis glomerata* (-)		Available P (-)
Bryophytes		Bryophyte cover (+) Subshrub cover (+) Graminoid cover (-)	pH (-) Available P (-) Soil organic content (+) Exchangeable Ca (-)
Spiders		Lower field layer cover (+)	
Hoverflies			Drainage (-)
Birds	Dunnock (+) Blackbird (+) Stonechat (+)[ab] Goldfinch (+)[a] Grasshopper Warbler (+)[b] Redpoll (+)[b] Whitethroat (+)[b]	Herb and moss layer (+)[c] Canopy height (-)[c] Shrub layer (+)[c]	

[a] Indicator of open habitat species richness.

[b] Indicator of Amber/Red list species richness.

[c] Migrant insectivores only.

Drainage of pre-thicket plantations is an indicator of reduced hoverfly species richness, presumably due to drainage reducing the availability of wet larval habitats (Section 6.3.7). This is in contrast to bryophytes, where observations in the field suggest that drains in pre-thicket plantations represent microhabitats that can support an additional suite of species (Section 4.4.4.2). Site drainage, however, also has implications for vascular plants and perhaps other species groups that will be more fully explored under Project 3.1.1.

As with spiders and plants, indicators of bird diversity reflect pre-planting habitat. High abundances of Dunnock and Blackbird indicate higher total species richness (Table 85 and Table 89); these species are typical of scrub and hedgerows, which shrub layer cover explicitly indicates. (Species indicators designated here are a subset of species with the highest correlations with measures of bird diversity identified in Section 7.3.6). Shrub layer cover as defined for birds (i.e. woody vegetation 0.5-2 m tall, including brambles) largely corresponds with subshrub cover as defined for vegetation (i.e. woody vegetation up to 2 m tall, not including brambles), an indicator of bryophyte diversity. Diversity of open habitat species, which decline markedly in more mature forests (Section 7.3.4), is indicated by greater abundances of Stonechat and Goldfinch. Grasshopper Warbler, Redpoll and

Whitethroat indicate greater richness of Amber/Red-listed species, which are also associated with open habitats. The negative association between tree height and species richness of migrant insectivores indicates a loss of pre-afforestation species. This is also reflected by the positive association with ground cover and mirrors the spider indicator, high cover of the lower field layer.

Because pre-afforestation habitat was not explicitly considered in this study, these indicators are rather coarse, in that they are likely to be able to distinguish between the biodiversity value of markedly different habitats, but not between species-rich and species-poor examples of wet heath, for instance. The utility of these indicators will be tested in further work by the BIOFOREST project.

8.2.5.2 Thicket through mature Sitka spruce stands

The identification of indicators of biodiversity for the more mature Sitka spruce structural stages reflect the different scales of response exhibited by species groups to changes in forest structure. These are summarised in Table 90 and are generally applicable to Sitka spruce forests past the pre-thicket stage. However, as discussed below, the use of some indicators should be restricted to only one or two structural stages. Mature Sitka spruce stands in particular show interesting differences in biodiversity patterns from thicket, closed-maturing and reopening stages.

Canopy cover is a key biodiversity indicator for vegetation, particularly vascular plants. As discussed in Section 4.4.4.1, the relationship between bryophyte diversity and canopy cover appears to be asymptotic: beyond a certain threshold, further increases in canopy openness have little impact. Although the correlation between total plant species richness and canopy cover is statistically significant only for the reopening stage (Table 28), this is an artefact of the reduced variation in canopy cover within each of the structural types. Other indicators of plant diversity are associated with this key factor, such as cover of forbs and brambles and the intensity of thinning. Cover of forbs appears to be a particularly useful indicator for the thicket and closed-maturing stand types, where it may identify locations, probably under less than full canopy closure, where species present before afforestation have persisted. The two groups of plant species shown in Table 90 are indicators of two relatively species-rich communities occurring in Sitka spruce plantations. They are all common species, and therefore the groups are probably best employed as indicators of target communities to be achieved by management, rather than as tools for identifying high biodiversity stands. Bramble cover as an indicator of biodiversity should be employed with caution: in some plots, species richness was actually lower where cover of *Rubus fruticosus* agg. exceeded 30%. In mature Sitka spruce stands, higher available P indicates greater richness of vascular plants. It may be that while increased canopy openness in mature stands permits colonisation by species largely with woodland affinities, greater soil fertility permits coexistence of a wider range of species. It should be emphasised, however, that this finding is based on sites of low overall fertility and that the true relationship between fertility and vascular richness may be unimodal (or hump-shaped) rather than linear.

The two sets of plant species listed in Table 90 are indicators of the most speciose plant communities occurring in thicket to mature Sitka spruce forests. These assemblages are generally found in the mature and reopening stages of forest development and may be considered “target” plant communities to be achieved through forest management. The first four species are indicators of the community type supporting the highest total plant species richness, whereas the next four species indicate a bryophyte-rich community that may not necessarily support high vascular plant species richness (c.f. Table 31). The indicators in each set should be used as a group rather than in isolation. Additional species indicators are those illustrated in Figure 41: *Dryopteris dilatata* cover of 3% or more, *Thuidium* *tamariscinum* cover of 20% or more and *Polytrichum formosum* presence. Their presence (at the given abundances) is indicative of Sitka spruce stands supporting relatively high total plant species richness.

Table 90. Summary selection of biodiversity indicators for thicket through mature Sitka spruce stands. The sign of the indicators' relationship with species richness for each taxonomic group is given in brackets.

	Compositional	Structural	Functional
Vascular Plants & Bryophytes	*Rubus fruticosus* agg. *Dryopteris dilatata* *Agrostis capillaris* *Thuidium tamariscinum* and *Plagiothecium undulatum*[a] *Hypnum jutlandicum*[a] *Dicranum scoparium*[a] *Eurhynchium praelongum*[a]	Canopy cover (-) Forb cover (+) Bramble cover < 30% (+) Bryophyte cover (+) Needle/FWD cover (-) CWD (+)[a] Proximity to woodland (+)[b]	Thinning (+) Available P (+)[c]
Spiders		Canopy cover (-) Lower field layer cover (+)	Thinning (+)
Hoverflies		CWD (+)	Wet habitats (+)[d]
Birds	Dunnock (+) Robin (+)[c] Blackbird (+) Wren (+)[c] Redpoll (+)[e] Chaffinch (+)[e] Willow Warbler (+)[e] Blackcap (+)[e] Long-tailed Tit (+)[e]	Distance from edge (-) Shrub layer (+) Age (-)[e]	Elevation (-)

[a] Indicators of bryophyte diversity only.

[b] Indicator of woodland vascular plant species richness.

[c] Mature (or Old) stands only.

[d] Not including thicket stands.

[e] Intermediate stands only.

Indicators of total species richness of spiders in the later stages of Sitka spruce stand development generally correspond with those for plants. Thinning is an important factor in reducing canopy cover and thereby encouraging development of the lower field layer in the reopening and mature structural types. These indicators, however, do not reflect species richness of forest specialists, which is better indicated by cover of ground layer vegetation, fine woody debris (FWD) and the absence of an upper field layer.

For hoverflies, the best biodiversity indicators are the presence of specialised larval habitats: standing and fallen coarse woody debris (CWD) and the presence of wet areas, such as flushes and pools. The latter represent features present at a larger scale than was investigated for spiders and plants. However, the presence of such habitats would be expected to increase the species richness of these groups at the plantation scale as well. Presence of CWD in mature Sitka spruce stands has also been found to be an indicator of biodiversity for bryophytes.

As with hoverflies, canopy cover *per se* is a less important factor for birds than for plants and spiders. Reduced canopy cover appears to be a suitable indicator of biodiversity only for resident insectivorous bird species in Intermediate stage forests. Shrub layer cover is also a good indicator of species richness for resident insectivores in Intermediate forests, and is also an indicator of species richness for habitat generalists in Old forests. Significant shrub layers cannot develop under closed-canopy conditions so, in the absence of other strong influences on shrub layer (such as grazing, or clearing of bramble, gorse and other shrubs), canopy cover can be considered a surrogate indicator for generalists. Shrub cover (including brambles as defined for birds) corresponds to some extent with bramble cover as an indicator of vascular plant richness. Forest age is a negative indicator of total bird species richness and the richness of other bird groups, including Open species in Intermediate stands, where canopy closure tends to increase with age.

Other structural variables are indicators of species richness for certain groups of birds. Greater abundances of Dunnock and Blackbird in Old and Intermediate forests, as in Young forests, are associated with the presence of scrub within the ranges of these species, perhaps as a result of heterogeneity in forest structure or proximity to scrubby habitats outside the forest boundary. Abundances of Redpoll (associated with Young forests) and Chaffinch (associated with Old forests) may also indicate structural variability inside or near the forest. Proximity to the forest edge is a landscape scale indicator of bird diversity without real parallels in the other taxonomic groups. Higher elevation sites support fewer bird species, largely because of the scarcity of scrub habitats.

8.2.5.3 Pole through mature ash stands

In comparison with Sitka spruce forests, few indicators of biodiversity were identified for ash forests. Part of the reason may be that ash plantations exhibited less clearly defined structural stages through the forest cycle. The heterogeneity of the ash sites used in this study, particularly the mixed sites, may have also contributed. In particular, semi-mature and mature ash stands were associated with semi-natural or estate woodlands, whereas the majority of the sites in the younger structural stages were not. In addition, fewer ash stands than Sitka spruce stands were surveyed.

The only convincing indicator of total species richness of vascular plants and bryophytes was low abundance of *Agrostis stolonifera* (Table 91). *Agrostis stolonifera*, a competitive grass species that forms large patches by vegetative spread, is an indicator of species-poor conditions. It is characteristic of grassland communities rather than semi-natural woodlands.

While the plant communities of Sitka spruce plantations have no natural equivalents in Ireland, the flora of ash plantations may be reasonably compared with that of semi-natural ash and oak woodlands. Because of the rarity of semi-natural woodlands, the development of a woodland flora in ash plantations will have biodiversity and conservation value in addition to the number of species present. Species indicative of a rich woodland flora are shown in Table 32 and Table 91 and discussed in Section 4.3.7. It is notable that the community type that they indicate occurs in BARN, an old woodland site, and other sites adjacent to semi-natural woodland. Proximity to native woodland is therefore designated as a structural indicator of woodland species diversity.

Forest spider species richness is reduced by increased lower field layer vegetation cover in the mature ash habitats, and total species richness is reduced by higher cover of bare soil. This difference between the factors affecting total and forest specialist richness mirrors that occurring in Sitka spruce stands. The distinction between spider assemblages in more mature spruce and ash stands (Figure 58) suggests that the latter may represent a community characteristic of semi-natural ash woodlands. Accordingly, reduced cover of the lower field layer may be a better indicator of spider biodiversity in older ash plantations.

No suitable indicators of biodiversity for hoverflies in older ash stands were identified.

As no real differences between Sitka spruce and ash plantation bird diversity were detected, they share bird species richness indicators. Distance to edge as a bird diversity indicator is comparable to the woodland plant diversity indicator proximity to woodland; however, there were no good indicators for richness of bird species associated with woodland. In addition, distance to edge and elevation are probably better reflections of the availability of scrub and hedgerows than availability of woodlands.

Table 91. Summary selection of biodiversity indicators for pole through mature ash stands. The sign of the indicators' relationship with species richness for each taxonomic group is given in brackets.

	Compositional	Structural	Functional
Vascular Plants & Bryophytes	*Agrostis stolonifera* (-) *Thamnobryum alopecurum* (+)[a] *Polystichum setiferum* (+)[a] *Hedera helix* (+)[a] *Primula vulgaris* (+)[a]	Proximity to woodland (+)[ab]	
Spiders		Lower field layer cover (-)[a] Soil cover (-)	
Birds	Dunnock (+) Blackbird (+) Wren (+) Robin (+)[c] Redpoll (+)[d] Chaffinch (+)[d] Willow Warbler (+)[d] Blackcap (+)[d] Long-tailed Tit (+)[d]	Distance from edge (-) Shrub layer (+) Age (-)[d]	Elevation (-)

[a] Indicators of woodland species richness.
[b] Vascular plant species richness only.
[c] Mature (or Old) stands only.
[d] Intermediate stands only.

8.3 ANALYSIS OF SIMILARITY IN ASSEMBLAGE STRUCTURE AND TRENDS IN SPECIES RICHNESS

8.3.1 Methods

For these analyses we mainly used site (rather than plot or trap) data and combined the ash and Sitka spruce components of the mix sites. For the vegetation data, we used one plot from the ash component and two plots from the Sitka spruce component to produce the site data for the mixed sites. For the spider data we used two plots from the ash component and three plots from the Sitka spruce component. For the hoverfly data we used the data for the ash trap and the Sitka spruce trap closest to the ash. These adjustments were necessary to eliminate the effect of increasing species number with sampling effort. We classified the structural group of the mixed sites as the structural group of its Sitka spruce component. We also carried out a separate set of analyses between the vegetation and spiders using matching plot data.

We used Mantel tests to carry out pairwise analyses of assemblage similarity between the taxonomic groups included in our study. We carried out one set of analyses on all the sites and another set on a reduced group of sites (referred to hereafter as the "main group of sites"), excluding the groups of sites that generally have very distinctive assemblages in most of the taxonomic groups. For this second set of analyses, we excluded the pre-thicket ash and Sitka spruce sites and the age class 5 ash sites. We also excluded COOL, INCH and RATH because these sites tend to cluster with the afore-mentioned structural groups.

We used pairwise correlation analyses to compare the trends in species richness between the taxonomic groups included in our study. We compared total species richness (or main species richness in hoverflies) between the groups. We also compared vascular and bryophyte species richness with the total species richness (or main species richness in hoverflies) of the other groups. We also compared the species richness of forest-associated species between the groups. For this comparison we used the vascular plants and bryophytes with high affinity for woodland groups, the forest spider group, the hoverfly tree/shrub specialist group, and the forest specialist birds group. We carried out correlations across all sites, and plotted graphs of the relationships coded by structural groups. Where visual inspection indicated a potential relationship within a structural group we examined the form of this relationship further.

We also carried out correlation analyses at the plot scale to compare trends in species richness between vegetation and spiders within structural groups, or combinations of structural groups. We defined the following groupings based upon the main discontinuities in the vegetation and spider assemblages, and the need to have a sufficient number of plots for analysis. The groups were: pre-thicket ash and Sitka spruce; thicket Sitka spruce; closed-maturing Sitka spruce; mature Sitka spruce; closed-maturing, reopening and mature Sitka spruce combined; and age class 5 ash with the mature ash compartment of RATH.

For all pairwise comparisons we used data from all the sites/plots that were sampled for the two groups being compared. This means that the sample sizes of the pairwise comparisons vary. There were 31 sites compared between vegetation and spiders, 29 between vegetation and hoverflies, 43 between vegetation and birds, 29 between spiders and hoverflies, 31 between spiders and birds, and 29 between hoverflies and birds.

8.3.2 Results

8.3.2.1 Assemblage similarity

Across all sites, all taxa showed highly significant similarities in the patterns of species composition. Within the main group of sites (Table 92), vegetation, spiders and hoverflies showed significant similarities in patterns of species composition, while variation in vegetation and spider species assemblages was also correlated with variation in bird species densities. At the plot scale (Table 93), variation in vegetation and spider species assemblages was similar within the pre-thicket, thicket and closed-maturing stages. Comparing the species assemblages of vegetation and spiders in mature Sitka spruce and in age class 5 ash, patterns of variation in species composition of the two taxa (i.e. using presence/absence data) were similar, but patterns of relative species abundances were not.

8.3.2.2 Trends in species richness

There were few significant correlations between the total species richness of the various taxonomic groups (Table 94). The correlation between the total species richness of spiders and hoverflies is consistent across most of the structural groups with the exception of the pre-thicket and closed-maturing ash and Sitka spruce groups (Figure 69). The correlation between the total species richness of vascular plants and birds is almost significant, but does not seem to hold within most of the structural groups (Figure 70). The species richness of forest-associated species was significantly (or almost significantly) correlated in all the pairwise correlations between the taxonomic groups (Table 95). However, these correlations appear to be mainly due to the fact that all taxonomic groups have low species richness of forest associated species in the pre-thicket sites, and there were few indications of the correlations holding within the structural groups. However, the correlation between numbers of forest-associated spiders and hoverflies (Figure 71) remains strong when the analysis is restricted to Sitka spruce sites past the pre-thicket stage (r = 0.602, p = 0.006, n = 19).

At the plot scale, there were few significant correlations between vegetation and spider species richness within structural groups. At the pre-thicket stage, the species richness of forest spiders and bryophytes with high woodland affinity were correlated (Pearson's r = 0.507, n = 32, p = 0.003). However, the form of this relationship is not convincing (Figure 72). At the thicket stage, the total species richness of spiders was correlated with total vegetation species richness (r = 0.491, p = 0.045, n = 17) and bryophyte species richness (r = 0.496, p = 0.043, n = 17) while the species richness of forest spider and vascular plants with high woodland affinity were also correlated (r = 0.608, p = 0.010, n = 17). These correlations reflect the differences between the two spider assemblages (as defined by cluster analysis) that occur in plots in this structural group (Figure 73 and Figure 74). The plots from the open thicket/open mature spruce group have higher total species richness of spiders, vegetation and bryophytes and lower species richness of forest spiders and vascular plants with high woodland affinity. However, within the subgroup of thicket stage plots with open thicket/open mature spruce spider assemblages, the relationship between total species richness of spiders and vegetation remains strong (r = 0.752, p = 0.005, n = 12; Figure 73). In the other groupings that we examined (closed-maturing Sitka spruce; mature Sitka spruce; closed-maturing, reopening and mature Sitka spruce combined; and age class 5 ash with RATH) there were no significant correlations between the various measures of spider and vegetation species richness at the plot scale.

Table 92. Analysis of similarity between patterns of variation (Mantel test) in species assemblages of taxa in the main group of sites[1].

	Spiders	Hoverflies	Birds – presence	Birds - densities
Vegetation – presence	r = 0.225 p = 0.005	r = 0.369 p =0.001	r = 0.121 p = 0.126	
Vegetation - cover	r = 0.337 p =0.001	r = 0.478 p =0.001		r = 0.245 p = 0.001
Spiders		r = 0.56 p = 0.001	r = 0.115 p = 0.108	r = 0.373 p = 0.003
Hoverflies			r = 0.121 p = 0.126	r = 0.146 p = 0.088

[1] This group excludes the pre-thicket ash and Sitka spruce sites, the age class 5 ash sites and COOL, INCH and RATH.

Table 93. **Analysis of similarity between patterns of variation (Mantel test) in vegetation and spider species assemblages at the plot scale.**

		Pre-thicket ash and Sitka spruce (n = 30)	Thicket Sitka spruce (n = 17)	Closed-maturing Sitka spruce (n = 20)	Mature Sitka spruce (n = 13)	Age class 5 ash (n = 13)
Presence-absence	r	0.297	0.398	0.181	0.237	0.292
	p	0.001	0.002	0.059	0.056	0.017
Abundance	r	0.313	0.357	0.178	-0.093	0.205
	p	0.002	0.002	0.044	0.239	0.131

Table 94. **Correlations between total species richness.**

		Vascular plants	Bryophytes	Spiders	Hoverflies	Birds
Vegetation	r	**0.88**	**0.34**	0.15	0.14	0.14
	p	< 0.001	0.024	0.406	0.460	0.362
Vascular plants	r		-0.15	0.20	0.26	0.27
	p		0.350	0.286	0.171	0.077
Bryophytes	r			-0.11	-0.30	**0.44**
	p			0.565	0.109	0.003
Spiders	r				**0.67**	0.17
	p				< 0.001	0.370
Hoverflies	r					0.28
	p					0.144

Table 95. **Correlations between species richness of forest associated species.**

		Bryophytes	Spiders	Hoverflies	Birds
Vascular plants	r	**0.79**	**0.37**	**0.40**	**0.33**
	p	< 0.001	0.041	0.034	0.021
Bryophytes	r		**0.59**	**0.42**	**0.44**
	p		< 0.001	0.024	0.003
Spiders	r			**0.70**	**0.54**
	p			< 0.001	0.002
Hoverflies	r				0.35
	p				0.065

8.4 DISCUSSION

8.4.1 Limitations of this study

This study has documented the vegetation, spider, hoverfly and bird biodiversity of ash and Sitka spruce plantation forests over the forest cycle and has identified indicators that can be used as surrogate measures of that biodiversity. Inevitably, however, with a study of this nature we have not been able to address all the relevant issues. Therefore, in interpreting the results of this study it is necessary to bear in mind the caveats we discuss below.

Our study was limited to plantations dominated by ash and Sitka spruce. Therefore, our results do not say anything about the potential biodiversity effects of planting other broadleaved or coniferous tree species. For example, the number of plant-feeding invertebrate species associated with ash in Britain is relatively low compared to other native broadleaved trees (Key, 1995). Therefore, comparisons between Sitka spruce and plantations of other native broadleaved tree species might produce greater contrasts in biodiversity than those we found. Oak and birch would be particularly interesting to study in this context as they support high numbers of plant-feeding invertebrate species (Jones, 1959; Atkinson, 1992; Key, 1995). (European Commission, 1999)While there will be some invertebrate species that specialise on other conifer species, a more important potential effect on biodiversity of choice of conifer species would be its implications for the forest habitat structure. In particular pines and larches tend to allow greater light penetration through the canopy and therefore allow greater development of vascular ground flora during the middle part of the forest cycle (Hill, 1979; Ferris *et al.*, 2000).

Like any biodiversity study we have had to be selective about the taxonomic groups that we studied. While our study has covered a broad range of taxonomic and functional groups, there are important components of forest biodiversity that we have not sampled. We did not study lichens or fungi. (A study of the epiphytic lichen flora of Sitka spruce plantations forms a major component of Project 3.1.3, Investigation of Experimental Methods to Enhance Biodiversity in Plantation Forests.) Both these groups have strong associations with forest habitats and can be important indicators of forest habitat quality, particularly in relation to deadwood. British studies of these groups have produced important findings in relation to forest biodiversity. For example, Humphrey *et al.* (2002) found that forest plantations had significantly poorer lichen communities compared to semi-natural stands. By contrast, Ferris *et al.* (2000b) and Humphrey *et al.* (2000) found that forest plantations supported high biodiversity of macrofungi. Humphrey *et al.* (2000) did not find any difference in the species richness of macrofungi between Scots pine and Sitka spruce plantations and semi-natural oak woodlands, although there were substantial differences in community composition among forest types.

Among the invertebrate groups, we have studied one group of mainly ground-dwelling predators (spiders), and another group of trophically and functionally diverse species (hoverflies). Inevitably there are many biodiverse and forest-associated invertebrate groups that we did not survey. The important question is the extent to which the invertebrate groups that we have covered represents the range of functional diversity that exists in forest ecosystems. In this context, one significant gap is host-specific phytophagous invertebrates. While *Cheilosia* hoverflies are phytophagous, they are associated exclusively with herb layer forbs (Stubbs & Falk, 2002). Phytophagous insects associated with shrub and tree foliage (such as many Lepidoptera) could well show differences in species assemblages and biodiversity between different forest types that were not detected in this study. Some data on Lepidoptera are included in Appendix 5.

The only vertebrate group that we studied was birds. However, other Irish vertebrate groups are very species-poor and generally lack forest specialists. Bats are one group for which forests may be important habitat components in the Irish landscape, and red squirrels are forest specialists.

Our sampling design attempted to provide adequate levels of replication, and to reduce the confounding effects of environmental variation. However, due to logistical constraints, the design was better suited to detecting trends in biodiversity across the forest cycle than to analysing variation in biodiversity within one age class or structural group. While we have been able to identify potential biodiversity indicators within structural groups, these are often based on data from rather small numbers of sites. Our use of data at the plot/trap level runs the risk of pseudoreplication if the main source of variation is at the site level. While there is clearly significant variation within sites in, at least, vegetation and spider biodiversity, there are also clearly significant environmental differences between sites within the same structural group. Furthermore, we have not been able to carry out rigorous statistical tests of our proposed biodiversity indicators. Rigorous statistical testing would require identification of potential indicators prior to any analysis, followed by confirmatory statistical testing. In the near-absence of information on Irish plantation biodiversity, we have been limited to exploratory analyses which have identified provisional indicators that need to be tested with independent data. Other work within the BIOFOREST project will allow some of the indicators for pre-thicket and age class 4 Sitka spruce to be tested on independent datasets.

While we have sampled a wide range of Sitka spruce plantations, our sampling of ash plantations has been limited both by the nature of our survey design and by the availability of suitable sites. The semi-mature and mature ash stands that we sampled were on sites formerly occupied by scrub or woodland or were located adjacent to woodland and are unlikely to be representative of new ash afforestation of agricultural land (see Section 3.3.3.1). Half of the ash stands that we sampled were the ash component of mix sites. These stands usually contain small amounts of ash (typically c. 1 ha) and may be planted on sites that are not typical of those where ash would be planted as the main crop tree. Therefore, the biodiversity of these stands may not be representative of the biodiversity that will develop in sites where ash is the dominant crop tree. However, these mixed stands allow comparison of the biodiversity that occurs where ash and Sitka spruce are planted under similar conditions, so our results will inform decision-making about the implications of choice of crop species for biodiversity.

8.4.2 Assemblages of ash and Sitka spruce plantation forests

Over the forest cycle, ash and Sitka spruce plantations can support diverse vegetation, spider, hoverfly and bird assemblages. These assemblages contain a large proportion of generalist species and we recorded few species of conservation importance. However, mature stands can develop a characteristic woodland flora and support forest specialist spiders and hoverflies. It is important to note that in this context, “mature” refers to stand structure, not to commercial maturity. Stands, particularly those that are not thinned, may reach commercial maturity and may be felled in the closed-maturing or reopening stages without attaining structural maturity.

The results of the Mantel tests indicate that there is a broad similarity in assemblage variation across forest types and structural classes in the four taxonomic groups that we studied. This similarity remains even when the sites with the most distinctive assemblages are excluded from the analyses. This suggests that using an appropriately specified single structural classification as a framework for biodiversity conservation planning in ash and Sitka spruce plantations will adequately represent the broad variation in vegetation, spider, hoverfly, and bird assemblages. However, reviewing the results of the analyses of the individual taxonomic groups shows that there are some significant differences between the groups in the detail of assemblage variation across forest types and structural classes. In particular, birds do not show the marked distinctiveness of the assemblages in mature ash that is so noticeable in the other taxonomic groups, reflecting the poor sensitivity of the depauperate Irish woodland bird fauna to variation in forest habitat.

Within structural groups, the sampling design permitted us to examine similarity in assemblage structure between vegetation and spiders only. Again the results indicate that there is an overall broad similarity in assemblage variation between sites within structural groups. However, there is some indication that the similarity decreases with increasing structural development of the forest. These results indicate that selecting complementary sets of sites for conservation measures on the basis of their vegetation assemblages will tend to capture the range of assemblage variation in spiders. However, these patterns of assemblage similarity may reflect similar responses by vegetation and spider assemblages to major environmental differences between sites, so this conclusion may not apply if the range of sites is restricted to a narrow environmental range.

The various taxonomic groups studied generally showed different trends in total species richness across the forest cycle, so it is not surprising that there were few significant correlations among the species richness of these groups. There is, however, a general pattern of the highest species richness occurring either at the beginning or the end of the forest cycle. High species richness in the pre-thicket stage is probably associated with the persistence of species associated with the pre-planting habitats. The pre-planting habitats of the majority of our pre-thicket sites were semi-natural habitats: cutover blanket bog and unimproved wet grassland. The sites that had been improved grassland before planting (INCH, KILM, and KILW) had low vegetation and hoverfly species richness. In general, pre-thicket plantations on improved grassland sites would be expected to support low biodiversity of these groups in the pre-thicket stage, due to the low botanical diversity of such grasslands, and the lack of wet features for hoverflies. Therefore, if future afforestation trends result in increased planting on improved grassland, the biodiversity importance of the pre-thicket stage is likely to diminish. In any case, the opportunity for increasing biodiversity by forestry management at the pre-thicket stage may be quite limited due to the large influence of the pre-planting habitat type and the short duration of the pre-thicket phase. In the increasing proportion of Ireland's forest estate that is second rotation, species typical of open habitats are likely to be less conspicuous components of the pre-thicket forest biota than we found them to be in afforestation sites. These considerations emphasise the importance of the mature stages for biodiversity, especially as the biodiversity of forest-associated species tends to be highest in this stage.

The high biodiversity associated with the pre-thicket stage should not necessarily be interpreted as a positive contribution by plantation forestry to biodiversity conservation in Ireland. As discussed above, this high biodiversity probably results from the pre-thicket sites being, in the main, located on sites that had semi-natural habitats before planting. Therefore, the pre-planting habitat may already have had high biodiversity, and afforestation of such habitats will not necessarily result in a net increase in biodiversity, and may result in a net loss of biodiversity. These issues will be investigated in more detail in BIOFOREST Project 3.1.1, Biodiversity of Afforestation Sites.

Forest type generally did not have a major effect on biodiversity and there were few differences in overall species richness between ash and Sitka spruce (but see caveats below). The age class 5 ash sites, which showed some similarities to semi-natural woodlands, did have distinctive vegetation, spider and hoverfly assemblages. However, these sites did not tend to have higher species richness (even of forest-associated species) compared to the mature Sitka spruce sites, with the exception of saproxylic hoverflies. In fact, spider species richness was lowest in mature ash sites. Also, the comparison is biased towards ash, because these sites were older than any of the Sitka spruce sites studied, and also had more old woodland influence. Therefore, our results do not support the general perception that broadleaved plantations have higher biodiversity than conifer plantations. However, comparison of the assemblages in the ash and Sitka spruce components of mixed sites does indicate that adding ash to a Sitka spruce plantation increases biodiversity at the plantation scale. Therefore, our results support the requirement for grant applications to include a broadleaf component. The different ecological characteristics of various broadleaved tree species, as demonstrated by the variation in insect faunas discussed above, suggests that it would be worth investigating the biodiversity associated with plantations of other broadleaved tree species.

8.4.3 Biodiversity indicators

Our comparisons of variation in species richness between the different taxonomic groups produced few significant correlations. These results suggest that use of relatively easily surveyed groups (such as vascular plants and birds) as surrogates of biodiversity for other taxonomic groups is not justified. Therefore, it is probably necessary to cover a range of different taxonomic groups to make an adequate assessment of the biodiversity of a particular site. It is likely that inclusion of additional taxonomic groups in our study (see Section 8.4.1) would have revealed additional patterns of variation in biodiversity.

9 CONCLUSIONS AND RECOMMENDATIONS

9.1 IDENTIFICATION OF PROVISIONAL BIODIVERSITY INDICATORS

9.1.1 Application

The compositional, structural and functional indicators of biodiversity we have identified are summarised below. They are discussed in more detail in Section 8.2.5 and in the relevant sections of the chapters for each taxonomic group. These features can be used to assess the effect of site management practices on biodiversity and/or to identify sites that potentially are of high biodiversity value. Each of these indicators are applicable for one or more of the taxonomic groups covered in this report. If the indicators for particular subgroups of species, such as forest specialist spiders, are desired, those detailed in the appropriate taxonomic group chapter should be used rather than the summary lists of indicators below.

These indicators of biodiversity should be considered as provisional indicators only, until they are verified using independent data (Noss, 1999). In addition, the context in which they have been identified, i.e. pure stands and non-intimate mixes of Sitka spruce and ash, must be taken into consideration prior to their application. Unless otherwise noted, the below indicators should be employed at the site or stand level, rather than at the level of the whole plantation or landscape.

The various indicators should be used in conjunction; in general, it is misleading to label a stand as "biodiverse" (or not) on the basis of just one or two indicators. We recommend the presence of at least four indicators in two or more groups (compositional, structural and functional) as a general guideline for designating sites or stands as potentially having high biodiversity. The numbers and types of indicators that should be present in order to accurately categorise the biodiversity status of forest units should be investigated during the process of indicator verification. The indicators cannot substitute for thorough flora and fauna surveys, particularly when sites of potentially major biodiversity importance are involved, but can be employed as a first step in biodiversity management assessment or identifying sites of biodiversity value. In sites where few indicators are present, management practices can be reviewed and improved. Forest stands or plantations identified as being of potentially high biodiversity can be surveyed and assessed more thoroughly and management for biodiversity can be prioritised in forest planning and operations.

9.1.2 Pre-thicket plantations

These biodiversity indicators were developed for pre-thicket ash and Sitka spruce stands. The period that stands are in this growth stage (perhaps eight years at most) is brief, and therefore opportunities for biodiversity management of pre-thicket stands are limited. We therefore recommend that the below indicators will be best employed when planning afforestation. Sites where several indicators are present or have high or low values, as appropriate, should be subject to a more thorough ecological assessment to determine the biodiversity value of the site before the decision to grant-aid planting is made. See Section 8.2.5.1 for further details.

These validity of these indicators for selecting unafforested sites of high biodiversity will be tested by the BIOFOREST project in the near future using an independent set of data collected for Project 3.1.1, Biodiversity of Afforestation Sites.

Compositional

- Presence of *all* of the following: *Molinia caerulea* (purple moor grass), *Calluna vulgaris* (heather, ling) and *Erica tetralix* (cross-leaved bell-heather)

- High abundance of Dunnock
- High abundance of Blackbird
- High abundance of Stonechat
- High abundance of Goldfinch
- High abundance of Grasshopper warbler
- High abundance of Redpoll
- High abundance of Whitethroat

Structural

- High bryophyte cover
- High cover of woody vegetation < 2 m tall
- Low graminoid cover
- High cover of 10-50 cm tall broadleaved vegetation

Functional

- Low available phosphorus
- Low pH
- High soil organic content
- Low exchangeable calcium

These indicators can also be used for the provisional identification of plantations at the pre-thicket stage for which biodiversity management should be a priority. Two additional indicators for this purpose are:

- Poorly growing trees at the plantation scale (structural)
- Undrained plantations with wet microhabitats (functional)

9.1.3 Thicket and post-thicket Sitka spruce plantations

The following biodiversity indicators for Sitka spruce plantations at thicket stage and beyond should be used as tools to assess if current management practices are likely to conserve or enhance biodiversity.

Compositional

- High abundance of Dunnock
- High abundance of Robin in Old forests
- High abundance of Blackbird
- High abundance of Wren in Old forests
- High abundance of Redpoll in Intermediate forests
- High abundance of Chaffinch in Intermediate forests
- High abundance of Willow warbler in Intermediate forests
- High abundance of Blackcap in Intermediate forests
- High abundance of Long-tailed tit in Intermediate forests

Structural

- Low canopy cover
- Forb cover > 20%
- Bramble cover < 30%
- Bryophyte cover > 50%
- High cover of 10-50 cm tall vegetation
- Abundance of coarse woody debris
- Low needle and fine woody debris cover
- Low distance to forest edge
- High shrub layer cover at the plantation scale

Functional
- Heavy thinning

These indicators can also be used for the provisional identification of plantations at the thicket and post-thicket stages for which biodiversity management should be a priority. Additional indicators for this purpose are:

- Younger age in Intermediate forests (structural)
- High available P in mature stands (functional)
- Wet habitats in closed-maturing, reopening and mature forests (functional)
- Low elevation (functional)

The following two groups of plants are indicators of two relatively species rich plant communities occurring in Sitka spruce plantations. As they are all common species, the groups are best employed at the stand (not whole plantation) level as indicators of target communities to be achieved by management, rather than as tools for identifying high biodiversity stands (cf. Sections 4.4.4.3 and 8.2.5.2).

- Presence of *all* of the following: *Rubus fruticosus* agg. (bramble), *Dryopteris dilatata* (broad buckler fern), *Agrostis capillaris* (common bent grass) and *Thuidium tamariscinum* (tamarisk moss)
- Presence of *all* of the following: *Plagiothecium undulatum* (wavy flat-moss), *Hypnum jutlandicum* (cypress moss), *Dicranum scoparium* (fork moss) and *Eurhynchium praelongum* (feather moss)

9.1.4 Pole-stage and older Ash plantations

The following biodiversity indicators for ash plantations at pole stage and beyond should be used as tools to assess if current management practices are likely to conserve or enhance biodiversity, particularly of species associated with semi-natural woodland.

Compositional
- Presence of *all* of the following: *Thamnobryum alopecurum* (fox-tail feather-moss), *Polystichum setiferum* (soft shield fern), *Hedera helix* (ivy), and *Primula vulgaris* (primrose)
- High abundance of Dunnock
- High abundance of Robin in Old forests
- High abundance of Blackbird
- High abundance of Wren in Old forests
- High abundance of Redpoll in Intermediate forests
- High abundance of Chaffinch in Intermediate forests
- High abundance of Willow warbler in Intermediate forests
- High abundance of Blackcap in Intermediate forests
- High abundance of Long-tailed tit in Intermediate forests

Structural
- Low cover of 10-50 cm tall vegetation
- Low distance to edge
- High shrub layer cover at the plantation scale

These indicators can also be used to provisionally identify plantations at the pole and later stages for which biodiversity management should be a priority. Additional indicators for this purpose are:

- Proximity to semi-natural woodland (structural)
- Younger age in Intermediate forests (structural)
- Low elevation (functional)

9.2 MANAGEMENT RECOMMENDATIONS AND MODIFICATIONS TO THE *FOREST BIODIVERSITY GUIDELINES*

Several common themes emerge from comparing the management recommendations identified for each taxonomic group. Other management recommendations are specific to particular taxonomic groups, but in no cases do the management recommendations for one group conflict with those for another group. Table 96 contains a summary of the management recommendations that we have identified, indicates if modifications to the *Forest Biodiversity Guidelines* (Forest Service, 2000b) are required and lists the taxonomic group(s) that each recommendation arises from. Although a given recommendation may originate from the results of a particular taxonomic group, implementation of the recommendation will probably also benefit the biodiversity of other groups. For example, Recommendation 1 below would most likely benefit many other groups of invertebrates and vertebrates in addition to hoverflies and birds.

The specific management recommendations are outlined below. For each recommendation we have stated whether it is already included in the *Forest Biodiversity Guidelines* (Forest Service, 2000b), or whether a modification to these *Guidelines* is required. These management recommendations are discussed in more detail in the relevant sections of the chapters for each taxonomic group. In many cases, recommendations may be applied to parts of forests in addition to whole forests. All recommendations are made subject to the limitations of this study (Section 8.4.1). In particular, we emphasize that the only tree species studied were Sitka spruce and ash in pure stands and non-intimate mixtures. Extrapolation of our results and recommendations to other species and mixtures should be done with caution. Some of the forest planning recommendations may be applicable to reforestation projects as well as afforestation, but it should be recognised that these recommendations were developed based on results from first rotation forests only.

Table 96. Summary of management recommendations. Recommendations are further explained in text below.

Recommendation	Taxonomic groups that recommendation arises from	Modification to *Guidelines*[1] required?
Forest planning		
1. Choose improved grassland sites over semi-natural habitats for afforestation	Vegetation, Hoverflies, Birds	Yes
2. Establish plantations in close proximity to semi-natural woodland	Vegetation	Yes
3. Create mosaic of stands of different age and structure at the landscape scale	Vegetation, Spiders, Hoverflies, Birds	No
4. Include a mixture of canopy species when planting	Vegetation, Spiders, Hoverflies	No
5. Leave small unplanted areas to maintain gaps through the forest cycle	Vegetation, Spiders, Hoverflies	Yes
6. Leave small areas of wet habitat and avoid drainage where possible	Hoverflies	Yes
7. Include open space within broadleaved component of plantation	Hoverflies	Yes
8. Leave areas of scrub and hedgerows unplanted	Birds	No
9. Design complex edges to plantations to increase proportion of edge habitat	Birds	Yes
10. Leave boundaries unplanted to allow development of complex edge structure	Birds	Yes
Forest management		
11. Provide guidelines to help foresters to identify potentially important habitats for ground flora, spider and hoverfly diversity	Vegetation, Spiders, Hoverflies	Yes
12. Rigorously thin Sitka spruce forests to prevent canopy closure	Vegetation, Spiders, Hoverflies	Yes
13. Avoid removal of shrub layer during thinning	Birds	Yes
14. Retain mature Sitka spruce forests, where there is no risk of damage to adjoining semi-natural habitats	Vegetation, Spiders	Yes
15. Retain large diameter deadwood	Bryophytes, Hoverflies	Yes

[1] (Forest Service, 2000b).

9.2.1 Forest planning

Recommendation 1: Choose improved grassland sites over semi-natural habitats for afforestation.

This recommendation should be incorporated into the *Guidelines*.

Plantations on improved grassland are likely to result in lower impacts on vegetation, hoverfly and bird biodiversity compared to plantations established on unimproved wet grassland, heathland and bog habitats. The *Guidelines* recommend that "local biodiversity factors (including habitats and species of particular interest)" should be identified and incorporated into the site development plan, but do not explicitly consider the choice of sites for afforestation. Therefore, the *Guidelines* should recommend that, where possible, improved grassland or arable land should be used for afforestation instead of semi-natural habitats, including wet grasslands, particularly in landscapes dominated by intensive farming. In landscapes with extensive areas of semi-natural habitats, afforestation of small amounts of these habitats is unlikely to have significant negative effects on local biodiversity, providing the areas selected for afforestation are not habitats that are locally scarce or rare, and that the potential cumulative impacts of repeated small-scale afforestation in the same area are considered.

Recommendation 2: Establish plantations in close proximity to semi-natural woodland.

This recommendation should be incorporated into the *Guidelines*.

This study has shown that as forest plantations mature, they may become suitable habitats for characteristic woodland plants, particularly where they are near existing semi-natural woodland. We recommend that plantations be established in close proximity to semi-natural woodland. This will facilitate the establishment of woodland plant species in plantations, and also would be likely to benefit other taxonomic groups with poor dispersal abilities, such as molluscs. We recommend that new plantations close to semi-natural woodland should be established and managed under the *Native Woodland Scheme* (Forest Service, 2001). Failing that, plantations established under the normal afforestation grant scheme should be comprised of species also occurring in the existing woodland. Under no circumstances should a new plantation comprised of shade-tolerant, potentially invasive species, such as sycamore, beech, western hemlock, western red cedar or fir species, be placed in close proximity to semi-natural woodland.

Recommendation 3: Create mosaic of stands of different age and structure at the landscape scale.

No modification to the *Guidelines* is required for this.

The recommendation in the *Guidelines* to promote age and structural diversity at the landscape scale is supported by the results from all taxonomical groups. Different species assemblages are associated with each stand structural stage, so when there are a number of these close together, both open habitat specialists and forest specialists may coexist in a forest. A diverse forest structure should be implemented at the planning stage of afforestation. Planning a mosaic of stands of different ages and structural stages should not pose problems in large forests under a single owner. In a landscape where forest parcels are or are likely to be under several different owners, achievement of age and structural diversity will be more difficult.

Recommendation 4: Include a mixture of canopy species when planting.

No modification to the *Guidelines* is required for this.

The recommendation in the *Guidelines* for diversity of canopy species within a forest is supported by the results of this research. Only non-intimately mixed forests (i.e. adjacent single-species blocks) were studied, however, and therefore we can make no conclusions or recommendations on intimate mixtures of tree species (see Recommendation 17 below).

Recommendation 5: Leave small unplanted areas to maintain gaps through the forest cycle.

Recommendation 6: Leave small areas of wet habitat and avoid drainage where possible.

Recommendation 7: Include open space within broadleaved component of plantation.

These recommendations should be incorporated into the *Guidelines*.

Retention of open space and existing habitats at the planting stage is required in the *Guidelines* through the designation of *Areas of Biodiversity Enhancement* (ABEs). Our research supports this requirement. Open space within plantations promotes vegetation and spider biodiversity, wet habitats are important for hoverfly biodiversity and scrub/shrub layer habitats which can develop in open spaces are important for bird biodiversity. The specific guidance on the types of habitats that should be retained is currently weak. Therefore, the *Guidelines* should be modified to make specific recommendations about the type, size and configuration of open space and retained habitats that should be left unplanted. Results from BIOFOREST Project 3.1.3, Investigation of Experimental Methods to Enhance Biodiversity in Plantation Forests will provide further guidance for the incorporation of open space in forestry plantations.

Although there is no minimum size for ABEs, in practice this requirement is interpreted through the retention of one or a few discrete patches of habitat that, for ease of mapping, are usually a minimum of 0.16 ha. However, even very small areas of open space (e.g. less than 400 m^2) may promote biodiversity at the thicket stage by allowing persistence of ground flora and creating habitat for spiders and hoverflies. Such open spaces should be widely scattered through the forest and should be incorporated into plantations less than 10 ha in size.

Similarly, the wet habitat features used by hoverflies are often very small scale (e.g. wet flushes and seasonal brooks) and can easily be lost through drainage. Such small wet areas may also support unique assemblages of other invertebrate or plant species. Therefore, the *Guidelines* should highlight their importance, discourage ground preparation or other drainage in or near small wet areas and recommend that they be included in the ABE. In some cases, wet habitat features included in the ABE that do not support species dependent on open conditions may be planted (without ground preparation) with native tree species suitable for wet sites, such as willow or alder, to create a wet woodland. In sites where wet habitat features are widespread, the *Guidelines* should discourage drainage of the site and encourage the use of crop species suitable for wet sites, such as alder or birch.

Consideration of the recorded hoverfly fauna associated with ash plantations in Ireland suggests that where ash is the 10% broadleaved component of a conifer plantation, the inclusion of an area of open space large enough to allow the development of grassy clearings can potentially increase the biodiversity of the plantation by providing habitat for species that do not normally occur in conifer plantations. Therefore, the *Guidelines* should recommend that at least some of the open space and broadleaf components be placed together, where possible.

Recommendation 8: Leave areas of scrub and hedgerows unplanted.

No modification to the *Guidelines* is required for this.

The results of this research confirm the value of scrub for bird biodiversity. Scrub should not be removed or planted and should be included as a retained habitat in ABEs. Planting should be set back from retained scrub and hedgerows so that these habitats are not shaded-out by the trees as they mature.

Recommendation 9: Design complex edges to plantations to increase proportion of edge habitat.

Recommendation 10: Leave boundaries unplanted to allow development of complex edge structure.

These recommendations should be incorporated into the *Guidelines*.

The results of this research suggest that increasing the amount of edge habitat would increase bird diversity. Establishing irregular external and internal forest edges (e.g. along roads and rides) and encouraging heterogeneity of structure and species composition would improve the quantity and quality of edge habitat. Similarly, leaving a wide, unplanted margin between the forest edge and the forest boundary or fence, in which native trees, scrub and open habitats are allowed to develop, would increase the range of bird species supported by a forest. These recommendations are also included in the *Forestry and Bird Management and Planning Guide* (O'Halloran *et al.*, 2002), and are in broad agreement with existing recommendations of the *Forestry and the Landscape Guidelines* (Forest Service, 2000c).

Although the Irish avifauna lacks forest specialists, increases in edge habitat in small plantations can reduce available habitat for other species, such as some bryophytes, that favour the forest interior. Conflict between the goals of increasing edge habitat and increasing forest interior habitat should be resolved on a site-by-site basis, depending on such factors as the presence of forest specialist species, amounts of forest edge and interior available in the landscape and management objectives.

9.2.2 Forest management

Recommendation 11: Provide guidelines to help foresters to identify potentially important habitats for ground flora, spider and hoverfly diversity.

This recommendation should be incorporated into the *Guidelines*.

For sustainable forest management it is important for foresters to be able to identify potentially important habitats within established forests that need special consideration. At present, the *Guidelines* only contain guidance on identifying important habitats at the pre-planting stage, and even this guidance contains many flaws (Gittings *et al.*, 2002). We have identified biodiversity indicators that could be used by foresters to identify potentially important sites that should then be subject to more rigorous survey and evaluation (see Sections 8.2.5 and 9.1). While these indicators require further verification, they provide a basis for further development that could be informed by the experiences of their use on the ground by foresters. These indicators, by themselves, cannot substitute for thorough flora and fauna surveys when sites of potentially major biodiversity importance are involved. However, because most plantation forests are unlikely to be of biodiversity importance at a national or regional scale, and because of the considerable investment of time and expertise involved in detailed surveys of a site’s biota, the use of surrogate indicators as a first step in identifying sites of biodiversity value is probably justified even if there will be some degree of error involved in the resulting evaluation.

Recommendation 12: Rigorous thinning of Sitka spruce forests to prevent canopy closure.

This recommendation should be incorporated into the *Guidelines*.

Thinning of Sitka spruce forests should be early and rigorous so that complete canopy closure is prevented (i.e. before the thicket stage is reached). This will promote ground flora diversity and create habitat for spiders and hoverflies. Although this recommendation follows from our results which clearly show the negative impacts of closed-canopy spruce forests on the abundance and diversity of understorey flora, we recognise that it is contrary to what is considered to be silvicultural best practice. This recommendation may be applied to parts of larger forests or to the whole of particular forests, such as those with good biodiversity potential or those receiving significant amenity use. Implementation of this recommendation may not be feasible in sites with significant windthrow risk.

Recommendation 13: Avoid removal of shrub layer during thinning.

This recommendation should be incorporated into the *Guidelines*.

While thinning generally has a positive effect on the biodiversity of the groups studied, it does have the potential to have negative effects on bird biodiversity if shrub layer habitat is removed while thinning. Although this is not usual practice during thinning, significant damage may be caused to shrub layers or scrub that have developed in areas with open canopies, in rides or along roads. Thinning should avoid removal of native shrub layer habitat; of course, invasive exotic shrub species, such as *Rhododendron ponticum* and *Prunus laurocerasus* (cherry laurel), should be removed.

Recommendation 14: Retain mature Sitka spruce forests, where there is no risk of damage to adjoining semi-natural habitats.

This recommendation should be incorporated into the *Guidelines*.

Structurally mature plantations are a particularly important stage in the Sitka spruce cycle for vascular plants, bryophytes and spiders with strong woodland affinities. Therefore, the *Guidelines* should encourage the retention of some mature stands beyond the normal felling age. Selection of plantations for long-term retention should avoid sites where there is a risk of exotic tree regeneration in adjacent semi-natural habitats such as woodlands, bogs and heathlands. The plantations selected for retention should have indicators associated with high botanical and spider biodiversity, and should contain good amounts of large diameter deadwood. In small private plantations it may not be feasible to retain entire plantations; however, the retention of at least small groups of older trees should be actively encouraged. Remnant stands increase the age and structural diversity of forests (Recommendation 3) and can act as refugia for species with woodland affinities which may then colonise second and later-rotation stands. It is not possible to recommend a minimum duration for retention on the basis of our research, which did not focus on overmature forests (c.f. Recommendation 19).

Recommendation 15: Retention of large diameter deadwood.

This recommendation should be incorporated into the *Guidelines*.

Although the *Guidelines* recognise the importance of retaining dead wood, they do not specify the type(s) of deadwood that should be retained. Our results indicate that in Sitka spruce stands, large diameter deadwood supports a richer saproxylic hoverfly fauna than smaller diameter deadwood, although the total number of species involved is small. Mature spruce stands with greater volumes of large diameter deadwood supported higher species richness of bryophytes. Larger diameter deadwood tends to be a scarcer resource and is generally more important for the rarer saproxylic invertebrates and for bryophytes. Therefore, the *Guidelines* should emphasise the importance of large diameter deadwood and require that the specified volumes of deadwood (i.e. standing and fallen trees) retained after thinning and felling be comprised of trees greater than 7 cm diameter and preferably greater than 20 cm diameter.

9.3 RECOMMENDATIONS FOR FURTHER RESEARCH

Our research has led directly to the recommendations for forest planning and management detailed above. It has also highlighted additional information gaps that we were not able to fill in the course of our work. We recommend below some of the most notable subjects requiring further research. These recommendations are not inclusive- there are numerous areas of forest biodiversity and management that require more work- but we believe they are among the most urgent suggested by our present research.

Recommendation 16: Verification of the indicators developed in this study.

As has been stated several times in this report, the indicators developed here can only be considered provisional until they are verified by research using independent data. The process of verification should analyse and rank the predictive power of the indicators. The number and type of indicators required to accurately classify forest units according to biodiversity should also be examined.

Recommendation 17: A comprehensive national survey and classification of semi-natural grasslands.

While the ecology and conservation value of bogs, for example, is generally understood, there is little understanding of the biodiversity of semi-natural grasslands. Without baseline information on the variation among different grassland community types, their distribution and the diversity of flora and fauna they support, it is impossible to identify grasslands of conservation value that should not be subject to afforestation (or other intensive management). Wet grasslands in particular are frequently the subject of afforestation, and it is likely that many wet grasslands of high biodiversity have been planted because foresters, forest inspectors and bodies consulted prior to afforestation were unaware of their value. We therefore recommend that a comprehensive national survey, analysis and classification of semi-natural grasslands be undertaken as a matter of urgency. Such a survey should also produce biodiversity indicators that allow non-specialists to identify grasslands of potential conservation value.

Recommendation 18: An investigation of the implications for biodiversity of different tree species mixtures.

In this study, we were constrained by time and resources to investigate only non-intimate mixtures of Sitka spruce and ash. In the past, commercial forestry was largely dominated by pure forests of Sitka spruce. With changes in afforestation grants, more diverse mixtures of crop species are being planted, many of them intimate mixtures. The structures of mixed forests may differ significantly from monocultures, particularly with respect to canopy cover, and the biodiversity of mixed stands may also be different. We recommend that the effects on biodiversity of different tree species mixtures be researched. Such a project should compare mixed forests comprised of single species stands, intimate mixtures and intermediate situations such as where species alternate by one or more rows or are aggregated in small groups. The study should include one or more of the more popular conifer mixes, such as Sitka spruce and Japanese larch, as well as one or more conifer-broadleaf mixes, such as Scots pine and oak.

Recommendation 19: An investigation of the biodiversity of overmature commercial plantations.

This study has indicated that Sitka spruce forests retained beyond commercial maturity can develop desirable biodiversity features akin to those found in "old-growth" forests. Investigation of the biodiversity of overmature commercial forests and the relationship between species assemblages and old-growth structural characteristics will enhance sustainable forest management. The role of overmature plantations as a species source for colonisation of adjacent reforestation areas should also be studied.

Recommendation 20: A study of the biodiversity of second rotation forests.

Many commercial forests in Ireland are now up to half-way through their second rotation. There are no data on the biodiversity of these, and how it compares to the biodiversity of first rotation forests studied here. If Ireland is to continue its policy of clear-felling, it is vital to know how biodiversity changes with each felling cycle. The influence of factors relevant to the establishment of second rotation stands should be examined, including ground preparation, brash management, dead wood retention and proximity to retained first rotation stands.

Recommendation 21: A study of the biodiversity in forests under continuous cover management.

The BIOFOREST Project examined forests under a clearfell management regime, where forest blocks are clearfelled approximately every 35 years (for Sitka spruce). This represents the predominant management type in Irish forestry. However there is a trend in many parts of Europe, including parts of the UK, to transform clearfell regimes into continuous cover systems. Some research on silvicultural aspects of continuous cover systems is being carried out in Ireland, but the biodiversity implications of such management are not known. Research on the biodiversity of forests under different continuous cover systems should be carried out, perhaps using silvicultural forest plots already in existence if these are suitable.

Recommendation 22: Monitoring of forest biodiversity in permanent plots.

This study examined biodiversity over the forest cycle in different forest sites, using a chronosequence approach where sites in different stages of maturity were substituted for time. Although every effort was made to match site conditions among different growth stages, this was not always possible (e.g. pre-thicket ash established on grassland vs. semi-mature and mature ash established on or near scrub or woodland). The best method for understanding how forest biodiversity develops is through the establishment of permanent study sites where biodiversity can be monitored over the life cycle of the particular forest. A number of permanent biodiversity monitoring sites should be established around the country, carefully chosen to incorporate a range of climate conditions, soil types and canopy species. To ensure long-term continuity of this research, study sites should be state-owned, and appropriate project management and funding structures should be put in place.

Recommendation 23: Investigation of the inclusion of native woodland elements into commercial plantations.

One method of enhancing the native biodiversity of commercial forestry plantations could be the planting of small areas or copses of native woodland within the plantation. These areas of native woodland would be subject to long-term retention and would count towards the ABE requirement of grant-aided afforestation. Small areas of native woodland within plantations may enhance the woodland character of plantations by supporting woodland species that may not otherwise be able to exist in plantations of non-native species. Factors affecting the contribution of native copses to biodiversity should be studied, including the distance from sources of woodland species and location of copses within a plantation.

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Appendix 1 Vegetation species list

The vascular plant species recorded during this study are listed below. Their habitat preferences and ecological strategies are also indicated. Non-native species are marked with an asterisk (*). For details on species categorisation, see Section 4.2.3.3. Nomenclature follows Stace (1997).

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
*Acer pseudoplatanus**	High	Intermediate	Mesic	Yes	No	No
Achillea millefolium	Low	Intermediate	Mesic	Yes	Yes	Yes
Agrostis canina	Moderate	Acidophilic	Damp	Yes	Yes	Yes
Agrostis capillaris	Moderate	Acidophilic	Mesic	Yes	Yes	Yes
Agrostis gigantea	Low	Intermediate	Mesic	Yes	No	Yes
Agrostis stolonifera	Moderate	Intermediate	Damp	Yes	No	Yes
Ajuga reptans	High	Intermediate	Damp	Yes	Yes	Yes
Alnus glutinosa	High	Intermediate	Wet	Yes	Yes	No
Alopecurus geniculatus	Low	Intermediate	Wet	Yes	No	Yes
Alopecurus pratensis	Low	Intermediate	Mesic	Yes	No	No
Angelica sylvestris	Moderate	Intermediate	Damp	Yes	No	No
Anthoxanthum odoratum	Moderate	Acidophilic	Mesic	No	Yes	Yes
Arrhenatherum elatius	Low	Intermediate	Mesic	Yes	No	No
Arum maculatum	High	Basic	Mesic	No	Yes	Yes
Athyrium felix-femina	High	Intermediate	Damp	Yes	No	No
Bellis perennis	Low	Intermediate	Mesic	No	No	Yes
Betula pendula	Moderate	Intermediate	Mesic	Yes	No	No
Betula pubescens	Moderate	Intermediate	Damp	Yes	No	No
Blechnum spicant	High	Acidophilic	Mesic	No	Yes	No
Brachypodium sylvaticum	High	Intermediate	Mesic	Yes	Yes	No
Briza media	Low	Intermediate	Mesic	No	Yes	No
Calluna vulgaris	Moderate	Acidophilic	Mesic	Yes	Yes	No
Cardamine flexuosa	Moderate	Intermediate	Damp	No	Yes	Yes
Cardamine hirsuta	Low	Basic	Mesic	No	Yes	Yes
Cardamine pratensis	Moderate	Intermediate	Wet	Yes	Yes	Yes
Carex binervis	Low	Acidophilic	Mesic	No	Yes	No
Carex diandra	Low	Intermediate	Wet	No	Yes	No
Carex disticha	Low	Intermediate	Wet	Yes	Yes	No
Carex echinata	Moderate	Acidophilic	Wet	No	Yes	No
Carex flacca	Low	Basic	Damp	No	Yes	No
Carex hirta	Low	Intermediate	Damp	Yes	No	No
Carex hostiana	Low	Intermediate	Wet	No	Yes	No
Carex nigra	Low	Acidophilic	Wet	No	Yes	No
Carex ovalis	Low	Intermediate	Damp	No	Yes	No
Carex panicea	Low	Acidophilic	Wet	No	Yes	No
Carex pilulifera	Low	Acidophilic	Mesic	No	Yes	No
Carex pulicaris	Low	Intermediate	Wet	No	Yes	No

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
Carex remota	High	Intermediate	Damp	Yes	Yes	Yes
Carex sylvatica	High	Basic	Mesic	No	Yes	No
Carex vesicaria	Moderate	Intermediate	Wet	Yes	Yes	No
Carex viridula	Low	Intermediate	Damp	No	Yes	No
Centaurea nigra	Low	Intermediate	Mesic	No	Yes	No
Centaurea scabiosa	Low	Basic	Dry	No	Yes	No
Cerastium fontanum	Low	Intermediate	Mesic	No	No	Yes
Chamerion angustifolium	Moderate	Intermediate	Mesic	Yes	No	No
Chrysosplenium oppositifolium	High	Intermediate	Damp	Yes	Yes	Yes
Cirsium arvense	Low	Intermediate	Mesic	Yes	No	No
Cirsium dissectum	Low	Acidophilic	Wet	Yes	Yes	No
Cirsium palustre	Moderate	Intermediate	Damp	Yes	Yes	Yes
Cirsium vulgare	Low	Intermediate	Mesic	Yes	No	Yes
Corylus avellana	High	Basic	Mesic	Yes	Yes	No
Crataegus monogyna	Moderate	Intermediate	Mesic	Yes	Yes	No
Crepis capillaris	Low	Basic	Dry	No	Yes	Yes
Cynosurus cristatus	Low	Intermediate	Mesic	Yes	Yes	Yes
Dactylis glomerata	Moderate	Intermediate	Mesic	Yes	No	No
Dactylorhiza incarnata	Low	Intermediate	Wet	No	Yes	No
Dactylorhiza maculata	Moderate	Intermediate	Mesic	No	Yes	No
Daucus carota	Low	Basic	Dry	No	Yes	Yes
Deschampsia cespitosa	Moderate	Intermediate	Damp	Yes	Yes	No
Deschampsia flexuosa	Moderate	Acidophilic	Mesic	Yes	Yes	No
Digitalis purpurea	Moderate	Acidophilic	Mesic	Yes	Yes	Yes
Dryopteris aemula	High	Acidophilic	Mesic	Yes	Yes	No
Dryopteris affinis	High	Acidophilic	Mesic	Yes	Yes	No
Dryopteris carthusiana	High	Intermediate	Damp	Yes	Yes	No
Dryopteris dilitata	High	Acidophilic	Mesic	Yes	Yes	No
Dryopteris filix-mas	High	Acidophilic	Mesic	Yes	Yes	No
Elytrigia repens	Low	Intermediate	Mesic	Yes	No	No
*Epilobium brunnescens**	Low	Intermediate	Damp	No	Yes	Yes
Epilobium montanum	Moderate	Intermediate	Mesic	Yes	Yes	Yes
Epilobium obscurum	Low	Intermediate	Wet	Yes	Yes	Yes
Epilobium palustre	Low	Acidophilic	Wet	No	Yes	No
Epilobium parviflorum	Low	Intermediate	Wet	Yes	Yes	Yes
Epipactis helleborine	High	Basic	Mesic	No	Yes	No
Equisetum arvense	Low	Intermediate	Mesic	Yes	No	Yes
Equisetum palustre	Low	Intermediate	Wet	Yes	Yes	Yes
Equisetum sylvaticum	Moderate	Acidophilic	Damp	Yes	Yes	No
Erica cinerea	Low	Acidophilic	Mesic	No	Yes	No
Erica tetralix	Low	Acidophilic	Damp	No	Yes	No
Eriophorum vaginatum	Low	Acidophilic	Damp	No	Yes	No
*Fagus sylvatica**	High	Intermediate	Mesic	Yes	Yes	No

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
Festuca arundinacea	Low	Intermediate	Damp	Yes	Yes	Yes
Festuca ovina	Low	Intermediate	Mesic	No	Yes	No
Festuca rubra	Low	Intermediate	Mesic	Yes	Yes	Yes
Festuca tenuifolia	Low	Acidophilic	Mesic	No	Yes	No
Filipendula ulmaria	Moderate	Intermediate	Damp	Yes	No	No
Fragaria vesca	High	Basic	Mesic	Yes	Yes	Yes
Fraxinus excelsior	High	Basic	Mesic	Yes	No	No
*Fuchsia magellanica**	Low	Acidophilic	Mesic	Yes	No	No
Galeopsis tetrahit	Low	Acidophilic	Damp	No	No	Yes
Galium aparine	Moderate	Basic	Mesic	Yes	No	Yes
Galium palustre	Moderate	Intermediate	Wet	Yes	Yes	Yes
Galium saxatile	Low	Acidophilic	Mesic	No	Yes	No
Geranium dissectum	Low	Intermediate	Mesic	No	No	Yes
Geranium robertianum	Moderate	Intermediate	Mesic	Yes	Yes	Yes
Geum urbanum	High	Intermediate	Mesic	No	Yes	No
Glechoma hederacea	High	Intermediate	Mesic	Yes	Yes	Yes
Glyceria fluitans	Low	Intermediate	Wet	Yes	No	Yes
Hedera helix	High	Intermediate	Mesic	Yes	Yes	No
Heracleum sphondylium	Moderate	Intermediate	Mesic	Yes	No	Yes
Holcus lanatus	Low	Intermediate	Damp	Yes	Yes	Yes
Holcus mollis	Moderate	Acidophilic	Mesic	Yes	No	No
Hyacinthoides non-scripta	High	Intermediate	Mesic	Yes	Yes	Yes
Hypericum androsaemum	High	Intermediate	Mesic	No	Yes	No
Hypericum humifusum	Low	Acidophilic	Mesic	No	Yes	No
Hypericum perforatum	Low	Basic	Dry	Yes	No	Yes
Hypericum pulchrum	Low	Acidophilic	Dry	No	Yes	No
Hypericum tetrapterum	Low	Intermediate	Damp	Yes	Yes	Yes
Hypochoeris radicata	Low	Intermediate	Mesic	Yes	Yes	Yes
Ilex aquifolium	High	Acidophilic	Mesic	Yes	Yes	No
Iris pseudacorus	Moderate	Intermediate	Wet	Yes	Yes	No
Juncus acutiflorus	Moderate	Acidophilic	Damp	Yes	Yes	No
Juncus articulatus	Low	Intermediate	Damp	Yes	Yes	Yes
Juncus bufonius	Low	Intermediate	Damp	No	No	Yes
Juncus bulbosus	Low	Acidophilic	Wet	No	Yes	Yes
Juncus conglomeratus	Low	Acidophilic	Damp	Yes	Yes	No
Juncus effusus	Low	Acidophilic	Damp	Yes	No	No
Juncus inflexus	Low	Basic	Damp	Yes	Yes	No
Juncus squarrosus	Low	Acidophilic	Damp	No	Yes	No
Juncus subnodulosus	Low	Basic	Wet	Yes	Yes	No
Lathyrus linifolius	Moderate	Acidophilic	Damp	No	Yes	No
Lathyrus pratensis	Low	Intermediate	Mesic	Yes	Yes	Yes
Leontodon autumnalis	Low	Intermediate	Mesic	Yes	Yes	Yes

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
Leucanthemum vulgare	Low	Basic	Dry	Yes	Yes	Yes
Lolium perenne	Low	Intermediate	Mesic	Yes	No	Yes
Lonicera periclymenum	High	Intermediate	Mesic	Yes	Yes	No
Lotus corniculatus	Low	Intermediate	Dry	No	Yes	No
Lotus pedunculatus	Low	Intermediate	Damp	Yes	Yes	No
Luzula campestris	Low	Intermediate	Mesic	No	Yes	No
Luzula multiflora	Moderate	Acidophilic	Mesic	No	Yes	No
Luzula pilosa	High	Acidophilic	Damp	No	Yes	No
Luzula sylvatica	High	Acidophilic	Damp	Yes	Yes	No
Lychnis flos-cuculi	Low	Intermediate	Damp	Yes	Yes	Yes
Lysmachia nemorum	High	Intermediate	Mesic	No	Yes	No
Lythrum salicaria	Moderate	Intermediate	Wet	Yes	Yes	Yes
Mentha aquatica	Moderate	Intermediate	Wet	Yes	No	No
Molinia caerulea	Moderate	Acidophilic	Damp	Yes	Yes	No
Myosotis laxa	Low	Intermediate	Wet	Yes	No	Yes
Myrica gale	Low	Acidophilic	Wet	Yes	Yes	No
Ophioglossum vulgatum	Moderate	Intermediate	Damp	No	Yes	No
Oxalis acetosella	High	Acidophilic	Mesic	No	Yes	No
Phleum pratense	Low	Basic	Mesic	Yes	Yes	Yes
Phyllitis scolopendrium	High	Basic	Mesic	No	Yes	No
*Picea sitchensis**	High	Acidophilic	Damp	Yes	Yes	No
Plantago lanceolata	Low	Intermediate	Mesic	Yes	Yes	Yes
Poa annua	Low	Intermediate	Mesic	No	No	Yes
Poa pratensis	Low	Intermediate	Mesic	Yes	Yes	Yes
Poa trivialis	Moderate	Intermediate	Damp	Yes	No	Yes
Polygala serpyllifolia	Low	Acidophilic	Mesic	No	Yes	No
Polypodium cambricum	Moderate	Basic	Dry	No	Yes	No
Polystichum aculeatum	Moderate	Basic	Mesic	No	Yes	No
Polystichum setiferum	High	Intermediate	Mesic	Yes	Yes	No
Potentilla anglica	Low	Intermediate	Dry	Yes	Yes	Yes
Potentilla anserina	Low	Intermediate	Mesic	Yes	No	Yes
Potentilla erecta	Moderate	Acidophilic	Mesic	No	Yes	No
Potentilla palustris	Low	Intermediate	Wet	No	Yes	No
Potentilla reptans	Low	Basic	Dry	Yes	No	Yes
Potentilla sterilis	High	Intermediate	Mesic	No	Yes	No
Primula vulgaris	High	Intermediate	Mesic	Yes	Yes	Yes
Prunella vulgaris	Low	Intermediate	Mesic	Yes	Yes	Yes
*Prunus laurocerasus**	High	Intermediate	Mesic	Yes	Yes	No
Prunus spinosa	Moderate	Intermediate	Mesic	Yes	Yes	No
Pteridium aquilinum	Moderate	Acidophilic	Mesic	Yes	No	No
Quercus petraea	High	Acidophilic	Mesic	Yes	Yes	No
Quercus robur	High	Intermediate	Mesic	Yes	Yes	No
Ranunculus acris	Low	Intermediate	Mesic	Yes	Yes	Yes

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
Ranunculus flammula	Low	Intermediate	Wet	Yes	Yes	Yes
Ranunculus repens	Moderate	Intermediate	Damp	Yes	No	Yes
Rhianthus minor	Low	Intermediate	Mesic	No	Yes	Yes
*Rhododendron ponticum**	High	Acidophilic	Mesic	Yes	Yes	No
Rosa species	Moderate	Intermediate	Mesic	Yes	Yes	No
Rubus caesius	Low	Basic	Mesic	Yes	Yes	No
Rubus fruticosus agg.	Moderate	Intermediate	Mesic	Yes	Yes	No
Rubus idaeus	Moderate	Intermediate	Mesic	Yes	Yes	No
Rumex acetosa	Low	Intermediate	Mesic	Yes	Yes	Yes
Rumex acetosella	Low	Acidophilic	Mesic	No	Yes	Yes
Rumex conglomeratus	Low	Intermediate	Damp	Yes	No	Yes
Rumex obtusifolius	Low	Intermediate	Mesic	Yes	No	Yes
Rumex sanguineus	Moderate	Intermediate	Damp	Yes	Yes	Yes
Salix aurita	Low	Acidophilic	Damp	Yes	Yes	No
Salix cinerea	Moderate	Intermediate	Damp	Yes	No	No
Salix pentandra	Low	Intermediate	Damp	Yes	Yes	No
Salix repens	Low	Intermediate	Damp	Yes	Yes	No
Salix x *multinervis*	Moderate	Acidophilic	Damp	Yes	Yes	No
Salix x *reichardtii*	Moderate	Intermediate	Damp	Yes	No	No
Sambucus nigra	Moderate	Basic	Mesic	Yes	No	No
Sanicula europaea	High	Basic	Mesic	No	Yes	No
Schoenus nigricans	Low	Intermediate	Wet	Yes	Yes	No
Senecio aquaticus	Low	Intermediate	Damp	No	No	Yes
Senecio jacobaea	Low	Basic	Mesic	No	No	Yes
*Senecio squalidus**	Low	Basic	Dry	No	No	Yes
Senecio vulgaris	Low	Intermediate	Mesic	No	No	Yes
*Solanum nigrum**	Low	Intermediate	Mesic	No	No	Yes
Sonchus asper	Low	Intermediate	Mesic	No	No	Yes
Sorbus aucuparia	Moderate	Acidophilic	Mesic	Yes	Yes	No
Stachys palustris	Low	Intermediate	Damp	Yes	No	Yes
Stachys sylvatica	High	Intermediate	Mesic	Yes	No	No
Stellaria graminea	Low	Acidophilic	Damp	Yes	Yes	Yes
Stellaria holostea	Moderate	Intermediate	Mesic	Yes	Yes	Yes
Stellaria media	Low	Intermediate	Mesic	No	No	Yes
Stellaria uliginosa	Low	Acidophilic	Wet	Yes	No	Yes
Succisa pratensis	Low	Intermediate	Damp	No	Yes	No
Taraxacum species	Low	Intermediate	Mesic	No	No	Yes
Teucrium scorodonia	Moderate	Intermediate	Dry	Yes	Yes	Yes
Trichophorum cespitosum	Low	Acidophilic	Damp	No	Yes	Yes
Trifolium pratense	Low	Intermediate	Mesic	Yes	Yes	Yes
Trifolium repens	Low	Intermediate	Mesic	Yes	No	Yes
*Tsuga heterophylla**	High	Acidophilic	Damp	Yes	Yes	No
Ulex europaeus	Low	Intermediate	Mesic	Yes	Yes	No

Species name	Affinity for woodland	Substrate pH	Moisture	Competitor	Stress-tolerant	Ruderal
Ulex gallii	Low	Acidophilic	Mesic	Yes	Yes	No
Urtica dioica	Moderate	Intermediate	Mesic	Yes	No	No
Vaccinium myrtillus	Moderate	Acidophilic	Mesic	Yes	Yes	No
Veronica beccabunga	Low	Intermediate	Wet	Yes	No	Yes
Veronica chaemedrys	Moderate	Intermediate	Mesic	No	Yes	No
Veronica montana	High	Intermediate	Damp	No	Yes	No
Veronica officinalis	Low	Acidophilic	Dry	No	Yes	No
Veronica serpyllifolia	Low	Intermediate	Mesic	No	No	Yes
Viburnum opulus	High	Intermediate	Damp	Yes	Yes	No
Vicia cracca	Low	Intermediate	Mesic	Yes	No	No
Vicia sepium	Moderate	Intermediate	Mesic	Yes	No	No
Viola canina	Low	Acidophilic	Mesic	No	Yes	No
Viola palustris	Moderate	Acidophilic	Wet	No	Yes	No
Viola reichenbachiana	High	Basic	Mesic	No	Yes	No
Viola riviniana	Moderate	Intermediate	Mesic	No	Yes	No

The bryophyte species recorded during this study and their habitat preferences are listed below. Non-native species are marked with an asterisk (*). For details on species categorisation, see Section 4.2.3.3. Nomenclature follows Smith (1978) for mosses and Smith (1990) for liverworts.

Species name	Affinity for woodland	Substrate pH	Moisture
Atrichum undulatum	High	Acidophilic	Mesic
Aulocomnium palustre	Low	Acidophilic	Wet
Brachythecium rutabulum	Moderate	Basic	Mesic
Breutelia chrysocoma	Low	Intermediate	Wet
Bryum pseudotriquetrum	Low	Intermediate	Wet
Bryum rubens	Moderate	Basic	Mesic
Calliergon cordifolium	Moderate	Intermediate	Wet
Calliergon cuspidatum	Moderate	Basic	Damp
Calypogeia fissa	Moderate	Acidophilic	Damp
Calypogeia muelleriana	Moderate	Acidophilic	Damp
Campylopus atrovirens	Low	Acidophilic	Damp
*Campylopus introflexus**	Low	Acidophilic	Mesic
Campylopus paradoxus	Moderate	Acidophilic	Mesic
Campylopus pyriformis	Moderate	Acidophilic	Mesic
Cephalozia bicuspidata	Moderate	Acidophilic	Damp
Cephaloziella divaricata	Moderate	Acidophilic	Mesic
Cephaloziella hampeana	Moderate	Acidophilic	Damp
Conocephalum conicum	Moderate	Intermediate	Damp
Cryphaea heteromalla	Moderate	Basic	Dry
Dicranella heteromalla	Moderate	Acidophilic	Mesic
Dicranum majus	High	Acidophilic	Mesic
Dicranum scoparium	Moderate	Acidophilic	Mesic

Species name	Affinity for woodland	Substrate pH	Moisture
Diplophyllum albicans	Moderate	Acidophilic	Mesic
Drepanocladus revolvens	Low	Basic	Wet
Eurhynchium praelongum	High	Intermediate	Mesic
Eurhynchium striatum	High	Basic	Mesic
Eurhynchium swartzii	Moderate	Basic	Mesic
Fissidens bryoides	Moderate	Acidophilic	Mesic
Fissidens taxifolius	Moderate	Basic	Mesic
Frullania dilatata	Moderate	Intermediate	Dry
Frullania tamarisci	Moderate	Intermediate	Dry
Funaria obtusa	Low	Acidophilic	Damp
Homalia trichomanoides	Moderate	Basic	Mesic
Hookeria lucens	Moderate	Acidophilic	Damp
Hylocomium splendens	Moderate	Acidophilic	Mesic
Hypnum cupressiforme	Moderate	Acidophilic	Mesic
Hypnum jutlandicum	Moderate	Acidophilic	Mesic
Hypnum mammillatum	High	Acidophilic	Dry
Isopterygium elegans	High	Acidophilic	Mesic
Isothecium myosuroides	High	Acidophilic	Dry
Jungermannia atrovirens	Moderate	Basic	Damp
Kurzia pauciflora	Low	Acidophilic	Wet
Leucobryum glaucum	Moderate	Acidophilic	Mesic
Lophocolea bidentata	Moderate	Intermediate	Damp
Lophocolea heterophylla	High	Acidophilic	Mesic
Lophozia ventricosa	Moderate	Acidophilic	Mesic
Metzgeria furcata	High	Intermediate	Dry
Mnium hornum	High	Acidophilic	Mesic
Neckera crispa	Low	Basic	Dry
Odontoschisma sphagni	Low	Acidophilic	Wet
Pellia epiphylla	Moderate	Acidophilic	Damp
Philonotis fontana	Low	Intermediate	Wet
Plagiochila asplenoides	High	Basic	Mesic
Plagiomnium rostratum	Moderate	Basic	Mesic
Plagiomnium undulatum	High	Basic	Mesic
Plagiothecium denticulatum	High	Acidophilic	Mesic
Plagiothecium nemorale	High	Acidophilic	Mesic
Plagiothecium undulatum	Moderate	Acidophilic	Mesic
Pleurozium schreberi	Moderate	Acidophilic	Mesic
Pohlia carnea	Low	Basic	Wet
Polytrichum commune	Moderate	Acidophilic	Wet
Polytrichum formosum	High	Acidophilic	Mesic
Pseudephemerum nitidum	Moderate	Acidophilic	Mesic
Pseudoscleropodium purum	Moderate	Intermediate	Mesic
Racomitrium lanuginosum	Low	Acidophilic	Mesic
Radula complanata	High	Intermediate	Damp
Rhizomnium punctatum	Moderate	Intermediate	Wet

Species name	Affinity for woodland	Substrate pH	Moisture
Rhytidiadelphus loreus	Moderate	Acidophilic	Damp
Rhytidiadelphus squarrosus	Moderate	Intermediate	Mesic
Rhytidiadelphus triquetrus	Moderate	Basic	Mesic
Riccardia chamedryfolia	Moderate	Intermediate	Wet
Riccardia multifida	Moderate	Intermediate	Wet
Scapania gracilis	Moderate	Acidophilic	Mesic
Sphagnum auriculatum	Moderate	Acidophilic	Wet
Sphagnum capillifolium	Moderate	Acidophilic	Damp
Sphagnum cuspidatum	Low	Acidophilic	Wet
Sphagnum palustre	Moderate	Acidophilic	Wet
Sphagnum recurvum	Moderate	Acidophilic	Wet
Sphagnum squarrosum	Moderate	Intermediate	Wet
Sphagnum subnitens	Low	Acidophilic	Wet
Sphagnum subsecundum var *auriculatum*	Low	Intermediate	Wet
Thamnobryum alopecurum	High	Basic	Mesic
Thuidium tamariscinum	High	Intermediate	Mesic
Ulota bruschii	Moderate	Intermediate	Dry
Ulota crispa	Moderate	Intermediate	Dry

Appendix 2 Spider species list

The spider species recorded during this study and their ecological characteristics are listed below. Nomenclature follows (Roberts, 1993).

Family	Species name	Vegetation preference	Hunting strategy	Habitat preference	Hunting strategy
Clubionidae	*Agroeca proxima*	Low vegetation	Active hunter	Generalist	Generalist
Clubionidae	*Clubiona compta*	Trees and bushes	Active hunter	Generalist	Generalist
Clubionidae	*Clubiona diversa*	Low vegetation	Active hunter	Generalist	Generalist
Clubionidae	*Clubiona lutescens*	Low vegetation	Active hunter	Generalist	Wet
Clubionidae	*Clubiona neglecta*	Low vegetation	Active hunter	Generalist	Generalist
Clubionidae	*Clubiona reclusa*	Low vegetation	Active hunter	Generalist	Generalist
Clubionidae	*Clubiona stagnatilis*	Low vegetation	Active hunter	Generalist	Wet
Clubionidae	*Clubiona trivialis*	Low vegetation	Active hunter	Generalist	Dry
Gnaphosidae	*Drassodes lapidosus*	Ground layer	Active hunter	Generalist	Generalist
Gnaphosidae	*Micaria pulicaria*	Ground layer	Active hunter	Open	Generalist
Hahniidae	*Antistea elegans*	Ground layer	Web dweller	Open	Wet
Hahniidae	*Hahnia nava*	Ground layer	Web dweller	Open	Generalist
Linyphiidae	*Agyneta conigera*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Agyneta decora*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Agyneta olivacea*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Agyneta ramosa*	Ground layer	Web dweller	Generalist*	Wet*
Linyphiidae	*Agyneta subtilis*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Allomengea scopigera*	Low vegetation	Web dweller	Generalist	Wet
Linyphiidae	*Allomengea vidua*	Low vegetation	Web dweller	Generalist	Wet
Linyphiidae	*Alopecosa pulverulenta*	Ground layer	Active hunter	Open	Generalist
Linyphiidae	*Aphileta misera*	Unknown	Web dweller	Generalist*	Wet
Linyphiidae	*Asthenargus paganus*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Baryphyma gowerense*	Unknown	Web dweller	Open	Unknown
Linyphiidae	*Baryphyma maritinum*	Low vegetation	Web dweller	Open*	Unknown
Linyphiidae	*Bathyphantes approximatus*	Unknown	Web dweller	Generalist*	Wet*
Linyphiidae	*Bathyphantes gracilis*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Bathyphantes nigrinus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Bathyphantes parvulus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Centromerus dilutus*	Ground layer	Web dweller	Forest	Generalist*
Linyphiidae	*Ceratinella brevipes*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Ceratinella brevis*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Ceratinella scabrosa*	Ground layer	Web dweller	Generalist*	Generalist
Linyphiidae	*Cnephalocotes*	Ground layer	Web dweller	Generalist*	Generalist

Family	Species name	Vegetation preference	Hunting strategy	Habitat preference	Hunting strategy
	obscurus				
Linyphiidae	*Dicymbium nigrum*	Generalist	Web dweller	Generalist	Generalist*
Linyphiidae	*Dicymbium tibiale*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Diplocephalus latifrons*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Diplocephalus permixtus*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Diplocephalus picinus*	Ground layer	Web dweller	Generalist*	Generalist*
Linyphiidae	*Diplostylor concolor*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Dismodicus bifrons*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Erigone arctica*	Unknown	Web dweller	Generalist	Wet
Linyphiidae	*Erigone atra*	Generalist	Web dweller	Open	Wet
Linyphiidae	*Erigone dentipalpis*	Generalist	Web dweller	Open	Wet
Linyphiidae	*Erigone longipalpis*	Unknown	Web dweller	Generalist	Wet
Linyphiidae	*Erigonella hiemalis*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Gnathornarium dentatum*	Unknown	Web dweller	Generalist	Wet
Linyphiidae	*Gonatium rubens*	Ground layer	Web dweller	Open	Generalist
Linyphiidae	*Gongylidiellum vivum*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Gongylidum rufipes*	Low vegetation	Web dweller	Forest	Wet
Linyphiidae	*Hilaira excisa*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Hypomma bituberculatum*	Unknown	Web dweller	Generalist	Wet
Linyphiidae	*Hypomma cornutum*	Unknown	Web dweller	Generalist	Generalist
Linyphiidae	*Kaestneria pullata*	Low vegetation	Web dweller	Generalist	Wet
Linyphiidae	*Lepthyphantes alacris*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Lepthyphantes cristatus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes ericaeus*	Unknown	Web dweller	Generalist	Dry
Linyphiidae	*Lepthyphantes flavipes*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes mengei*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes nebulosus*	Other	Web dweller	Other	Generalist
Linyphiidae	*Lepthyphantes obscurus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes pallidus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes tenebricola*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Lepthyphantes tenuis*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Lepthyphantes zimmermanni*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Leptorhoptrum robustrum*	Unknown	Web dweller	Open	Wet
Linyphiidae	*Linyphia hortensis*	Low vegetation	Web dweller	Forest	Generalist
Linyphiidae	*Linyphia triangularis*	Low vegetation	Web dweller	Generalist	Generalist

Family	Species name	Vegetation preference	Hunting strategy	Habitat preference	Hunting strategy
Linyphiidae	*Lophomma punctatum*	Ground layer	Web dweller	Open	Wet
Linyphiidae	*Macrargus rufus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Maro minutus*	Ground layer	Web dweller	Generalist	Generalist*
Linyphiidae	*Maso sundervalli*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Meioneta saxatilis*	Low vegetation	Web dweller	Generalist	Generalist
Linyphiidae	*Meta mengei*	Trees and bushes	Web dweller	Generalist	Generalist
Linyphiidae	*Meta merianae*	Trees and bushes	Web dweller	Generalist	Wet
Linyphiidae	*Meta segmentata*	Trees and bushes	Web dweller	Generalist	Generalist
Linyphiidae	*Metopobactrus prominulus*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Micrargus herbigradus*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Micrargus subaequalis*	Ground layer	Web dweller	Open*	Generalist
Linyphiidae	*Microlinyphia pusilla*	Low vegetation	Web dweller	Open	Generalist
Linyphiidae	*Microneta viaria*	Ground layer	Web dweller	Forest*	Generalist*
Linyphiidae	*Monocephalus casteneipes*	Generalist	Web dweller	Forest	Generalist
Linyphiidae	*Monocephalus fuscipes*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Neriene clathrata*	Low vegetation	Web dweller	Generalist	Generalist
Linyphiidae	*Neriene montana*	Low vegetation	Web dweller	Generalist	Generalist
Linyphiidae	*Neriene peltata*	Low vegetation	Web dweller	Forest	Generalist
Linyphiidae	*Oedothorax fuscus*	Generalist	Web dweller	Generalist	Wet
Linyphiidae	*Oedothorax gibbosus*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Oedothorax retusus*	Generalist	Web dweller	Generalist	Wet
Linyphiidae	*Pelecopsis nemoralis*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Pelecopsis parallela*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Pocadicnemis juncea*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Pocadicnemis pumila*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Porrhomma campbelli*	Ground layer	Web dweller	Generalist	Generalist*
Linyphiidae	*Porrhomma convexum*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Porrhomma egeria*	Other	Web dweller	Other	Generalist*
Linyphiidae	*Porrhomma pallidum*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Porrhomma pygmaeum*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Saaristoa abnormis*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Saaristoa firma*	Generalist	Web dweller	Generalist	Generalist
Linyphiidae	*Saloca diceros*	Ground layer	Web dweller	Generalist*	Wet
Linyphiidae	*Savignya frontata*	Generalist	Web dweller	Generalist*	Generalist
Linyphiidae	*Silometopus elegans*	Ground layer	Web dweller	Open	Wet
Linyphiidae	*Tallusia experta*	Ground layer	Web dweller	Generalist*	Generalist
Linyphiidae	*Tapinocyba insecta*	Ground layer	Web dweller	Generalist	Generalist

Family	Species name	Vegetation preference	Hunting strategy	Habitat preference	Hunting strategy
Linyphiidae	*Tapinocyba pallens*	Ground layer	Web dweller	Forest	Generalist
Linyphiidae	*Tapinocyba praecox*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Taranucnus setosus*	Low vegetation	Web dweller	Generalist*	Wet
Linyphiidae	*Tiso vagans*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Walckenaeria acuminata*	Ground layer	Web dweller	Generalist*	Generalist*
Linyphiidae	*Walckenaeria atrobtibialis*	Unknown	Web dweller	Open*	Generalist
Linyphiidae	*Walckenaeria cuspidata*	Ground layer	Web dweller	Generalist	Wet
Linyphiidae	*Walckenaeria dysderoides*	Ground layer	Web dweller	Forest*	Generalist*
Linyphiidae	*Walckenaeria nodosa*	Generalist	Web dweller	Generalist	Wet
Linyphiidae	*Walckenaeria nudipalpis*	Ground layer	Web dweller	Generalist	Generalist
Linyphiidae	*Walckenaeria vigilax*	Ground layer	Web dweller	Generalist	Wet
Lycosidae	*Pardosa amentata*	Ground layer	Active hunter	Generalist	Wet
Lycosidae	*Pardosa lugubris*	Ground layer	Active hunter	Forest	Generalist
Lycosidae	*Pardosa nigriceps*	Low vegetation	Active hunter	Generalist	Generalist
Lycosidae	*Pardosa palustris*	Ground layer	Active hunter	Open	Generalist
Lycosidae	*Pardosa pullata*	Ground layer	Active hunter	Open	Wet
Lycosidae	*Pirata latitans*	Ground layer	Active hunter	Generalist	Wet
Lycosidae	*Pirata piraticus*	Ground layer	Active hunter	Generalist	Wet
Lycosidae	*Pirata uliginosus*	Ground layer	Active hunter	Generalist	Dry
Lycosidae	*Trochosa ruricola*	Ground layer	Active hunter	Generalist	Generalist
Lycosidae	*Trochosa terricola*	Ground layer	Active hunter	Open	Dry
Mimetidae	*Ero cambridgei*	Low vegetation	Web dweller	Generalist	Generalist
Segestriidae	*Segestria senoculata*	Other	Web dweller	Generalist	Generalist
Tetragnathidae	*Pachygnatha clercki*	Generalist	Active hunter	Generalist	Wet
Tetragnathidae	*Pachynatha degeeri*	Generalist	Active hunter	Generalist	Generalist
Theridiidae	*Enoplognatha ovata*	Low vegetation	Web dweller	Generalist	Generalist
Theridiidae	*Robertus lividus*	Ground layer	Web dweller	Generalist	Generalist
Theridiidae	*Robertus neglectus*	Ground layer	Web dweller	Generalist	Generalist
Theridiidae	*Theonoe minutissima*	Ground layer	Web dweller	Generalist	Generalist
Theridiidae	*Theridion bimaculatum*	Low vegetation	Web dweller	Generalist	Generalist
Theridiidae	*Theridion instabile*	Low vegetation	Web dweller	Generalist	Generalist
Theridiidae	*Theridion pallens*	Generalist	Web dweller	Generalist	Generalist
Thomisidae	*Oxyptila trux*	Low vegetation	Active hunter	Generalist	Generalist
Thomisidae	*Xysticus cristatus*	Low vegetation	Active hunter	Open	Generalist
Zoridae	*Zora spinimana*	Ground layer	Active hunter	Generalist	Generalist

* Classification was made on the basis of UK records only.

Appendix 3 Hoverfly species list

The hoverfly species recorded during this study and their ecological characteristics are listed below. Nomenclature follows Speight (2001a).

Species	Number of traps - all	Number of traps - main	Forest specialist	Tree/shrub specialist	Anthropophobic
Arctophila superbiens	3	3			1
Baccha elongata	39	39		1	
Chalcosyrphus nemorum	1	1	1	1	1
Cheilosia albitarsis	3	3			
Cheilosia bergenstammi	1	1			
Cheilosia illustrata	2	2			
Cheilosia pagana	3	3			
Cheilosia variabilis	2	1	1	1	1
Chrysogaster solstitialis	2	2			
Chrysotoxum bicinctum	22	22			
Chrysotoxum fasciatum	6	6			1
Criorhina berberina	4	4	1	1	1
Didea fasciata	2	2		1	1
Episyrphus balteatus	47	47			
Eristalis abusivus	3	2			1
Eristalis arbustorum	1	1			
Eristalis horticola	1	1			
Eristalis interruptus	7	6			
Eristalis intricarius	7	6			1
Eristalis pertinax	36	27			
Eumerus strigatus	1	1			
Eupeodes bucculatus	1	0		1	1
Eupeodes corollae	3	2			
Eupeodes latifasciatus	3	3			
Eupeodes luniger	2	1			
Ferdinandea cuprea	3	3			
Helophilus hybridus	4	3			1
Helophilus pendulus	69	52			
Lejogaster metallina	2	2			
Leucozona laternaria	1	0			
Leucozona lucorum	18	18			
Melangyna arctica	4	4			1
Melangyna lasiophthalma	3	3			
Melanogaster hirtella	8	4			
Melanostoma mellinum	27	26			
Melanostoma scalare	76	76			
Meligramma cincta	2	2		1	1
Meliscaeva auricollis	23	23			
Meliscaeva cinctella	44	44			
Myathropa florea	12	7			
Neoascia podagrica	23	20			

Species	Number of traps - all	Number of traps - main	Forest specialist	Tree/shrub specialist	Anthropophobic
Parasyrphus punctulatus	3	3		1	
Platycheirus albimanus	58	57			
Platycheirus amplus	1	0			1
Platycheirus angustatus	10	7			1
Platycheirus clypeatus	23	18			
Platycheirus fulviventris	1	0			
Platycheirus granditarsus	24	15			
Platycheirus immarginatus	1	0			1
Platycheirus manicatus	1	1			
Platycheirus nielseni	10	10			1
Platycheirus occultus	12	8			1
Platycheirus rosarum	7	5			
Platycheirus scutatus	25	25			
Rhingia campestris	47	0			
Riponnensia splendens	3	2			
Scaeva pyrastri	3	0			
Sericomyia lappona	13	13			1
Sericomyia silentis	66	56			
Sphaerophoria fatarum	3	3			1
Sphaerophoria interrupta	2	2			
Sphegina clunipes	61	61	1	1	1
Syrphus ribesii	10	10			
Syrphus torvus	6	5			
Syrphus vitripennis	7	7			
Trichopsomyia flavitarsis	3	3			
Volucella bombylans	15	15			
Volucella pellucens	13	13			
Xylota florum	1	0	1	1	1
Xylota jakutorum	16	15	1	1	1
Xylota segnis	54	54			
Xylota sylvarum	15	8	1	1	1

Species	Foliage	Herb layer	Timber	Ground debris	Root zone	Wet substrates	Dead wood
Arctophila superbiens						1	
Baccha elongata	1	1					
Chalcosyrphus nemorum			1			1	1
Cheilosia albitarsis		1			1		
Cheilosia bergenstammi		1			1		
Cheilosia illustrata		1			1		
Cheilosia pagana		1			1		
Cheilosia variabilis		1			1		
Chrysogaster solstitialis						1	
Chrysotoxum bicinctum					1		
Chrysotoxum fasciatum					1		
Criorhina berberina			1				1
Didea fasciata	1						
Episyrphus balteatus	1	1					
Eristalis abusivus						1	
Eristalis arbustorum				1		1	
Eristalis horticola						1	
Eristalis interruptus				1		1	
Eristalis intricarius				1		1	
Eristalis pertinax				1		1	
Eumerus strigatus		1			1		
Eupeodes bucculatus	1						
Eupeodes corollae	1	1					
Eupeodes latifasciatus				1	1		
Eupeodes luniger	1	1					
Ferdinandea cuprea					1		1
Helophilus hybridus						1	
Helophilus pendulus				1		1	
Lejogaster metallina						1	
Leucozona laternaria	1	1					
Leucozona lucorum		1			1		
Melangyna arctica	1						
Melangyna lasiophthalma	1						
Melanogaster hirtella						1	
Melanostoma mellinum		1		1	1		
Melanostoma scalare		1		1	1		
Meligramma cincta	1						
Meliscaeva auricollis	1						
Meliscaeva cinctella	1						
Myathropa florea				1		1	1
Neoascia podagrica				1		1	
Parasyrphus punctulatus	1						
Platycheirus albimanus	1	1		1	1		
Platycheirus amplus		1					

Species	Foliage	Herb layer	Timber	Ground debris	Root zone	Wet substrates	Dead wood
Platycheirus angustatus		1				1	
Platycheirus clypeatus		1		1	1		
Platycheirus fulviventris		1				1	
Platycheirus granditarsus				1	1		
Platycheirus immarginatus		1				1	
Platycheirus manicatus		1					
Platycheirus nielseni	1	1					
Platycheirus occultus		1				1	
Platycheirus rosarum				1	1		
Platycheirus scutatus	1	1					
Rhingia campestris				1		1	
Riponnensia splendens						1	
Scaeva pyrastri	1	1					
Sericomyia lappona						1	
Sericomyia silentis						1	
Sphaerophoria fatarum		1					
Sphaerophoria interrupta		1					
Sphegina clunipes			1			1	1
Syrphus ribesii	1	1					
Syrphus torvus	1	1					
Syrphus vitripennis	1	1					
Trichopsomyia flavitarsis		1					
Volucella bombylans							
Volucella pellucens							
Xylota florum							1
Xylota jakutorum			1				1
Xylota segnis			1		1		1
Xylota sylvarum			1				1

Appendix 4 Birds

A4.1 LIST OF BIRD SPECIES RECORDED AND THEIR CLASSIFICATION FOR THE PURPOSES OF ANALYSIS.

KEY:
A = Amber listed, R = Red-listed (Newton *et al.*, 1999)
Functional group: forest use: 1 = Forest species; 2 = Generalists; 3 = Open species
Functional group: food: 1 = Seedeater passerines; 2 = Resident insectivores; 3 = Migrant insectivores; all others blank.
Functional group: nest site: 1 = Hole nesting; 2 = Ground nesting; 3 = Canopy nesting; all others blank.

Species	Latin name	Amb/Red	Forest use	Food	Nest site
Blackbird	*Turdus merula*		2	2	2
Blackcap	*Sylvia atricapilla*		1	3	
Blue tit	*Parus caeruleus*		2	2	1
Bullfinch	*Pyrrhula pyrrhula*		2	1	
Chaffinch	*Fringilla coelebs*		2	1	
Chiffchaff	*Phylloscopus collybita*		1	3	2
Coal tit	*Parus ater*		1	2	1
Collared dove	*Streptopelia decaocto*		3		
Crossbill	*Loxia curvirostra*		1	1	3
Cuckoo	*Cuculus canorus*	A	3	3	
Dunnock	*Prunella modularis*		2	2	
Goldcrest	*Regulus regulus*		1	2	3
Goldfinch	*Carduelis carduelis*		3	1	3
Grasshopper warbler	*Locustella naevia*	A	3	3	
Great tit	*Parus major*		2	2	1
Greenfinch	*Carduelis chloris*		3	1	
Grey wagtail	*Motacilla cinerea*		3	2	
Hen harrier	*Circus cyaneus*	R	3		2
Hooded crow	*Corvus corone*		3		3
House sparrow	*Passer domesticus*		3	1	
Jackdaw	*Corvus monedula*		3		
Jay	*Garrulus glandarius*		1		3
Kestrel	*Falco tinnunculus*		3		1
Linnet	*Carduelis cannabina*		3	1	
Long tailed tit	*Aegithalos cardatus*		2	2	
Magpie	*Pica pica*		3		
Meadow pipit	*Anthus pratensis*		3	2	2
Mistle thrush	*Turdus viscivorus*		3	2	
Peregrine	*Falco peregrinus*	A	3		
Pheasant	*Phasianus colchicus*		2		2
Pied wagtail	*Motacilla alba*		3	2	
Raven	*Corvus corax*		3		
Redpoll	*Carduelis flammea*	A	1	1	3
Reed bunting	*Emberiza shoeniclus*		3	1	2
Robin	*Erithacus rubecula*		2	2	2
Rook	*Corvus frugilegus*		3		3
Sand martin	*Riparia riparia*	A	3	3	
Sedge warbler	*Acrocephalus schoenobaenus*		3	3	
Siskin	*Carduelis spinus*		1	1	3
Skylark	*Alauda arvensis*	A	3	1	2
Snipe	*Gallinago gallinago*	A	3		
Song thrush	*Turdus philomelus*		2	2	
Sparrowhawk	*Accipiter nisus*		1		
Spotted flycatcher	*Musciapa striata*	A	2	3	3

Starling	*Sturnus vulgaris*		3	2	
Stock dove	*Columba oenas*	A	3		3
Stonechat	*Saxicola torquata*	A	3	2	2
Swallow	*Hirundo rustica*	A	3	3	
Swift	*Apus apus*		3	3	
Treecreeper	*Certhia familiaris*		1	2	1
Wheatear	*Oenanthe oenanthe*		3	3	
Whinchat	*Saxicola rubetra*	A	3	3	2
Whitethroat	*Sylvia communis*		3	3	
Willow warbler	*Phylloscopus trochilus*		2	3	2
Woodpigeon	*Columba palumbus*		2		3
Wren	*Troglodytes troglodytes*		2	2	2
Yellowhammer	*Emberiza citrinella*	R	3	1	

A4.2 DETERMINATION OF DETECTION FUNCTIONS

Table 97. Classification of sites into groups for detection function

Site group 1	Site group 2	Site group 3	Site group 4
LURG spruce	MUNG spruce	SAGG spruce	UNIO spruce
LACK spruce	MONT spruce	MARY spruce	SUNS spruce
KILM spruce	MOAN spruce	KDUF spruce	SINB spruce
CUMM spruce	FURY spruce	GLYN spruce	RATH spruce
COO spruce	COOA spruce	GFIN spruce	MSOP spruce
COOA spruce	COOA spruce	DOOG spruce	KILA spruce
BRAC spruce	SUNS ash	DERR spruce	RINC ash
BEND spruce	SINB ash	CUMM spruce	RATH ash
BALE spruce	KILA ash	CORR spruce	DEME ash
AREEN ash	GFIN ash	COON spruce	
MVAN ash	COOL ash	CONA spruce	
LURG ash	COMM ash	COMM spruce	
KILW ash	BARN ash	CLYD spruce	
KILM ash	BALY ash	BRAC spruce	
KESH ash		BOKY spruce	
INCH ash			
HIGG ash			
DOOG ash			
CUMM ash			
CORB ash			
COOA ash			
BALE ash			

Table 98. Classification of species into groups for detection function

Species Group 1	Species Group 2	Species Group 3	Species Group 4	Species Group 5
Willow warbler	Whinchat	Sand martin	Siskin	Woodpigeon
Wren	Wheatear	Swallow	Reed bunting	Long-tailed tit
Whitethroat	Treecreeper	Rook	Pied wagtail	Goldcrest
Sedge warbler	Sparrowhawk	Magpie	Redpoll	Coal tit
Song thrush	Spotted flycatcher	Mistle thrush	Linnet	Blue tit
Skylark	Stonechat	Kestrel	Great tit	
Pheasant	Robin	Jackdaw	Greenfinch	
Grasshopper warbler	Meadow pipit	Hooded crow	Goldfinch	
Chiffchaff	Jay	Cuckoo	Grey wagtail	
Blackcap	Dunnock		Crossbill	
Blackbird			Chaffinch	
			Bullfinch	

Table 99. Combinations of sites and species used to determine detection functions, and the detection function keys fitted to each combination (full detection functions given in Buckland et al. 2001)

Site	Species	Key	Scale Parameter	Shape Parameter	Adjustment term (order2)	Adjustment term (order4)	h(0)	S.E. h(0)
1	1	Uniform					8.01E-04	0
1	2	Neg. Exponential	115.1				1.08E-03	2.25E-04
1	3	Neg. Exponential	64.63				1.32E-03	4.50E-04
1	4	Half-normal	29.45		0.3131		2.10E-03	4.15E-04
1	5	Half-normal	30.45				1.50E-03	3.02E-04
2	1	Uniform			-0.3305		9.70E-04	1.01E-04
2	2&3	Uniform			-0.7718		1.30E-03	1.03E-04
2	4	Hazard Rate	13.53	1	0.1424		2.49E-03	1.96E-03
2	5	Uniform			-2.03	1.129	2.28E-03	1.73E-04
3	1	Half-normal	50.76				1.01E-03	8.21E-05
3	2	Half-normal	23.19				2.06E-03	1.76E-04
3	3&4	Hazard Rate	11.7	1			2.40E-03	1.07E-03
3	5	Half-normal	26.14			-0.8455	2.09E-03	2.04E-04
4	1	Uniform					8.12E-04	0
4	2	Neg. Exponential	158.2				9.93E-04	3.11E-04
4	3&5	Half-normal	22.72162		5.60E-02		2.28E-03	3.50E-04
4	4	Neg. Exponential	32.96				2.06E-03	1.05E-04

A4.3 REGRESSION EQUATIONS USED TO STANDARDISE SITE SPECIES RICHNESS VALUES

Table 100. Regression equations and r^2 values for relationships between number of species seen in all three visits (y), and numbers seen in visit 2 only (a), visits 1 and 2 (b), and visits 2 and 3 (c), for the 25 sites that were surveyed on all three rounds of visits.

Species richness value	y=total, a=visit2	y=total, a=visit2	y=total, a=visit2
Total	$y = 0.933a + 6.333; r^2=0.538$	$y = 0.956b + 2.500; r^2=0.838$	$y = 1.064c + 2.586; r^2=0.737$
Forest	$y = 0.628a + 2.893; r^2=0.383$	$y = 0.849b + 1.203; r^2=0.853$	$y = 0.910c + 1.183; r^2=0.584$
Generalist	$y = 0.896a + 3.254; r^2=0.461$	$y = 1.048b + 0.337; r^2=0.822$	$y = 0.910c + 2.232; r^2=0.676$
Open	$y = 1.029a + 2.014; r^2=0.418$	$y = 0.887b + 1.075; r^2=0.691$	$y = 0.987c + 1.064; r^2=0.684$
Red/Amber	$y = 1.028a + 0.170; r^2=0.553$	$y = b + 0.280; r^2=0.740$	$y = 1.071c + 0.509; r^2=0.853$
Migrant insectivores	$y = 0.923a + 0.942; r^2=0.627$	$y = 0.977b + 0.412; r^2=0.693$	$y = 0.811c + 0.857; r^2=0.786$
Resident insectivores	$y = 0.917a + 0.382; r^2=0.580$	$y = 0.873b + 1.460; r^2=0.923$	$y = 0.963c + 2.009; r^2=0.566$
Seedeaters	$y = 0.819a + 1.609; r^2=0.555$	$y = 0.853b + 0.893; r^2=0.788$	$y = 0.925c + 0.800; r^2=0.719$
Hole nesters	$y = 0.749a + 1.361; r^2=0.420$	$y = 0.861b + 0.598; r^2=0.798$	$y = 0.769c + 0.936; r^2=0.566$
Ground nesters	$y = 0.830a + 1.440; r^2=0.552$	$y = 0.831b + 1.004; r^2=0.851$	$y = 1.044c + 0.302; r^2=0.680$
Canopy nesters	$y = 0.331a + 0.246; r^2=0.182$	$y = 0.733b + 1.088; r^2=0.761$	$y = 0.625c + 1.500; r^2=0.367$

Appendix 5 Lepidoptera Species List

Table 101. List of the 46 Macrolepidoptera species identified from malaise trap catches, and the number of traps from which each species was recorded for each structural class. Data for traps situated in rides of post-thicket spruce are given in separate columns, as these traps caught many more species than traps situated under the forest canopy. Structural class codes are as follows: pta=pre-thicket ash, cma=closed maturing ash, sma=semi-mature ash, maa=mature ash, pts=pre-thicket spruce, ths=thicket spruce, cms=closed maturing spruce, ros=reopening spruce, mas=mature spruce. Nomenclature follows Emmet and Heath (1991).

	ASH				SITKA SPRUCE					
Structural class code	pta	cma	sma	maa	pts	ths	cms	ros	mas	mas ride
Total number of traps	2	1	4	4	1	5	8	4	4	1
Amphipyra pyramidea				2						
Apamea monoglypha	1	1	1		1	3	7	1	1	1
Aphantopus hyperantus							1			1
Cabera exanthemata							1			
Celaenia haworthii	1									
Celaenia leucostigma	1					2	1			
Chloroclysta sp. *		1	1		1	2			1	1
Chloroclystis v-ata							1			
Colostygia pectinataria							1		1	
Crocallis elinguaria			1							
Deileptenia ribeata										1
Diarsia brunnea					1	3				
Ecliptopera silaceata				1			1			1
Ennomos quercinaria			1							
Epione repandaria	1					1	1			
Epirrhoe alternata		1								
Eupithecia virgaureata			1							
Gymnoscelis rufifasciata										1
Hepialus hecta	1					2	5	3	3	1
Herminia grisealis										1
Herminia tarsipennalis									1	
Hydriomena furcata	2	1			1	2	5	1	4	1
Hypena proboscidalis		1					1			
Idaea aversata		1								
Idaea biselata	1	1	2			2	3	1	3	
Maniola jurtina										1
Mesapamea sp. †	2	1			1	1	2		3	1
Mesoleuca albicillata										1
Mniotypa adusta						1				
Mythimna impura							1			1
Noctua comes			1		1	1			1	
Noctua pronuba	1	1	1		1	1	4	1	2	1
Oligia latruncula										1
Opisthograptis luteolata							1			
Pararge aegeria										1
Peribatodes rhomboidaria							1			
Perizoma didymata							1			
Photedes pygmina	1				1	2				1
Pieris napi	1					1	2			1
Plusia festucae						1				
Rivula sericealis							1			1
Schrankia costaestrigalis	1				1	1	1	1		

	ASH				SITKA SPRUCE					
Structural class code	pta	cma	sma	maa	pts	ths	cms	ros	mas	mas ride
Selenia dentaria	1		1	1		1	2		1	
Sesia bembeciformis	1									
Xanthorhoe designata	1						2		1	
Xestia xanthographa	1									

* includes specimens of *Chlorocysta citrata* and *truncata*
† includes specimens of *Mesapamea didyma* and *M. secalis*

Table 102. List of the 77 Microlepidoptera species identified from malaise trap catches, and the number of traps from which each species was recorded for each structural class. Data for traps situated in rides of post-thicket spruce are given in separate columns, as these traps caught many more species than traps situated under the forest canopy. Structural class codes are as follows: pta=pre-thicket ash, cma=closed maturing ash, sma=semi-mature ash, maa=mature ash, pts=pre-thicket spruce, ths=thicket spruce, cms=closed maturing spruce, ros=reopening spruce, mas=mature spruce. Nomenclature follows Emmet and Heath (1991).

	ASH				SITKA SPRUCE							
	pta	cma	sma	maa	pts	ths	cms	cms ride	ros	ros ride	mas	mas ride
Total number of traps	2	1	4	4	1	5	8	1	4	1	4	1
Acleris aspersana						1						
Acleris laterana							1					
Agonopterix forsterana	1											
Agonopterix nervosa		1					1		1		2	1
Agriphila straminella	2	1	1			3	5	1	1	1	2	1
Agriphila tristella			1	1							1	
Alucita hexadactyla											1	
Anthophila fabriciana		1										
Aphelia paleana							1					
Apotomis semifasciana							1					
Argyresthia bonnetella			1									
Argyresthia semitestacella			1									
Blastobasis lignea	2	1	2	2	1	3	5	1	2		3	1
Borkhausenia fuscescens			2						1			
Calybites auroguttella												1
Carycolum tricolorella		1										
Coleophora glaucicolella	2				1		1					1
Coleophora serratella									1			
Cosmiotes freyerella				2								
Cosmopterix orichalcea												1
Digitivalva pulicariae			1									
Dipleurina lacustrata									1			1
Elachista albifrontella							1	1		1	2	1
Elachista apicipunctella			1				2				1	
Elachista bisulcella			1	1			1					
Elachista canapennella		1					1	1				
Elachista humilis	1					1	2					
Elachista luticomella	1											
Elachista regificella								1				
Endrosis sarcitella			1		1							
Epagoge grotiana			1									
Epiblema uddmanniana			1									
Epinotia nanana							2					1
Epinotia tedella							3		2		1	

	ASH				SITKA SPRUCE							
	pta	cma	sma	maa	pts	ths	cms	cms ride	ros	ros ride	mas	mas ride
Epinotia tenerana							1					
Eudonia mercurella	1	1	3	2		2	2	1	2		3	1
Eudonia truncicolella												1
Gracillaria syringella	1	1	2	2			2					
Helcystogramma rufescens		1					1					
Lampronia luzella									1			
Leucoptera laburnella			1									
Lozotaenia forsterana			1								1	
Micropterix aruncella							1					
Mirificarma mulinella	2	1	1									
Mompha propinquella												1
Mompha subbistrigella	1											
Nemapogon cloacella		1	1									1
Nemapogon ruricolellus							1					
Ochsenheimeria urella												1
Olethreutes lacunana	2	1	4	4	1	5	8	1	4	1	4	1
Olindia schumacherana											2	
Pammene regiana							1					
Pandemis heparana		1										
Parornix anglicella				1								
Phyllonorycter maestingella			1								1	
Phyllonorycter oxyacanthae	1					1	1	1				
Phyllonorycter salicicolella							1	1				1
Phyllonorycter spinicolella	1											
Phyllonorycter sorbi				1			1					
Phylloporia bistrigella						1						
Pseudargyrotoza conwagana		1										
Psychoides filicivora			2	1			1				1	
Rhigognostis incarnatella											1	
Rhopobota naevana	1	1	4	2		1	1		1			
Schreckensteinia festaliella	2		1	1	1	2	2	1			1	
Scoparia ambigualis		1	1				3	1	1	1	2	1
Stigmella aurella	1		3			2	1	1				
Stigmella hemargyrella			2									
Stigmella hybnerella			1				2					
Stigmella salicis								1				
Tinea semifulvella			1									
Trifurcula immundella							1					
Udea lutealis	2	1								1		
Udea prunalis	2	1	2			1	1			1	1	
Ypsophola nemorella	1					1						
Zeiraphera ratzeburgiana						2	5	1	2		1	1
Zelleria heperella	1								2			

FIGURES