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**Manipulation of vegetation succession in
forestry and applications for sustainable
forest management**

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Thesis submitted for the Degree of Doctor of Philosophy

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Declaration

This thesis is a record of my original work and has not been submitted as an exercise for a degree at this or any other university. Some of the field work for this thesis was carried out jointly and is duly acknowledged in the text. All sources of information have been appropriately acknowledged. Trinity College Library may lend or copy this thesis upon request.

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Summary abstract

This thesis contributes to an improved understanding of how vegetation succession of forestry plantations can be manipulated so that the subsequent successional trajectories contribute to the enhancement of biodiversity as part of Sustainable Forest Management (SFM). Many European countries have shown a net increase in forest area over the past several decades with almost half of this increase due to plantations and the rest from natural expansion of forests into former agricultural land and the restoration or creation of semi-natural planted forests using native species. As well as being managed for timber production plantations are increasingly under SFM that supports the provision of other environmental, economic, and social benefits from plantations. Research has shown that, with appropriate planning and management, forestry plantations have the potential to add to the landscape quality and local biodiversity of an area. Due to the currently high and increasing plantation cover in many countries it is important that their successional processes and, particularly, how these can be manipulated to contribute to the enhancement of biodiversity are investigated, especially in terms of informing SFM principles and practice. Ireland, with its very high non-native plantation cover relative to native woodland cover and the fact that the Irish forestry industry follows SFM policies, is particularly suitable for the investigation of management practices that may manipulate spontaneous succession during and after plantation rotations. The objective of this thesis was achieved by surveying the ground vegetation and natural tree regeneration in a range of forest types in Ireland chosen to represent the impacts of different management options on succession of vegetation communities, with particular regard to typical woodland species. Light availability (measured by proxies of canopy cover, canopy openness and stem density) was found to be an important driver of diversity and community differences in the different forest types in this thesis. This was in agreement with previous

research in plantations and in woodland restoration. Manipulating forest structure by earlier and more frequent thinning is recommended as a practical management tool to enhance ground vegetation diversity. Deadwood was found to be of importance to bryophyte species richness, as a bryophyte habitat and as an influence on community composition, in agreement with previous findings. Mixed plantations are often composed of two tree species as a crop- a main species forming the majority of the stand at planting and a secondary species which is planted to form a lesser component of the stand. The enhancement of ground vegetation diversity in mixed plantations would benefit from secondary species forming a substantial component of the mixed plantation in terms of canopy cover. This may be achieved by planting more compatible species in terms of, for example, growth rate, in an arrangement conducive to the establishment and maintenance of the secondary species in the canopy and undertaking appropriate management to ensure the secondary species thrives. We conclude that it may be preferable from both ecological and economic perspectives, to plant secondary species in a non-intimate mix arrangement (secondary species stands adjacent to the main species) rather than in an intimate mix configuration (secondary species dispersed as single stems throughout the crop). The influence, in terms of area and distance to, of either previous old woodland or existing semi-natural woodland surrounding the sites as a driver of diversity and community composition was evident in this research and in agreement with previous work. Soil type and pH were found important to diversity and composition and this research supports the assessment of soil type and properties as part of strategic forest planning. There were three methods of management recommended for enhancing ground vegetation diversity common to the four plantation types studied in this thesis Sitka spruce (*Picea sitchensis*) afforestation and reforestation and pure and mixed Norway spruce (*Picea abies*). These were: stand structure manipulation, alternatives to clearfell and deadwood retention. That these

management practices are recommended for all forest types in this thesis, emphasises non-intervention is not an option when enhancement of biodiversity is an expected outcome of a plantation rotation. This is particularly the case when woodland restoration is desired following clearfell. In conclusion, the forest types studied in this thesis have the potential to make an important contribution to the enhancement of biodiversity.

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1 General introduction

1.1 Successional studies

Studies of succession, the sequential replacement of species after a disturbance, are increasingly used to investigate modern environmental issues such as habitat restoration (Prach and Walker, 2011) as they help evaluate and predict the effects of change on successional trajectories (directions) of communities. How species assemble into communities following a disturbance is not fully understood and there is ongoing debate between those that argue that successional trajectories are predictable and those that understand the direction of vegetation succession to be a more random process (Prach and Walker, 2011, Weiher and Keddy, 2001). Succession is usually studied using either chronosequences or long-term studies. Chronosequencing, often termed as substituting space for time, uses a series of sites differing in age to form a time sequence of vegetation development from some initial condition (Johnson and Miyanishi, 2008), e.g. time since clearfell. Important assumptions include that each site has the same history, differ only in age and has the same initial environmental conditions. While long-term monitoring informs understanding of present, and helps predict future assembly of communities, long-term *experiments* can highlight the drivers of succession in communities (Silvertown et al., 2010). Chronosequencing is often preferred for successional studies as it is less resource intense than long-term monitoring. Funders of research may favour new findings over monitoring studies and often require easily definable outputs over a specified period of time, leaving long-term studies at a disadvantage (Silvertown et al., 2010). However, chronosequencing has been criticised as, in reality, the assumptions of these studies are often very difficult, if not impossible, to meet. The

assumption of the same initial conditions among sites is rarely ever met due to, for example, variations in edaphic conditions, the biotic environment and micro-climate between sites. The assumption that sites have the same history may appear to be satisfied; however, sites may have only a recent shared history, such as planted with same forestry species, but the longer term history of the sites may have been radically different, for example sites were originally woodland or moorland (Moola and Vasseur, 2004, Johnson and Miyanishi, 2008, Walker et al., 2010, French et al., 2008).

1.2 Successional experiments and restoration

Restoration is essentially the manipulation of succession to restore degraded, damaged, or destroyed landscapes to a specified reference ecosystem that existed previously or exists near the site (Prach and Walker, 2011). Both the successes and failures of restoration can be used to test theories of succession (Prach and Walker, 2011) e.g. the failure of natural dispersal to bring in desired species may reveal the absence of key dispersal agents or seed sources (Brunet and von Oheimb, 1998). When information on natural succession is used to inform the restoration effort this should increase the success of the project (Hobbs et al., 2007).

Spontaneous restoration (natural regeneration) can be an option in areas where the site is, for example, small, relatively undisturbed, surrounded by natural vegetation of the desired community and not under threat from invasive species. Compared with actively managed restoration involving planting and fencing, not only is it less resource intensive (however it does require at least an initial site survey, monitoring and subsequent intervention if required) but it also can result in habitats closer to the natural state (Little et al., 2009, Prach and Pysek, 2001, Rodwell and Patterson, 1994). However, spontaneous restoration is not always practical,

for example, in areas lacking suitable seed sources, with high seed predation and grazing pressures and aggressively invasive species (Little et al., 2009). Both spontaneous and managed restoration are long-term approaches, and as mentioned previously, as for any long-term study, can be frustrated by availability and continuity of resources (Silvertown et al., 2010).

1.3 Development of sustainable forest management

Deciduous forest is generally accepted as the vegetation type that covered the lowlands of Central and Western Europe before clearance by humans began approximately 5,000 years (Vera, 2000). Many European countries have shown a net increase in forest area over the past several decades with slightly less than half of this increase due to plantations and the rest from natural expansion of forests into former agricultural land and the restoration or creation of semi-natural planted forests using native species (FAO, 2011, MCPFE Liaison Unit Warsaw, 2007). In this context, plantations are defined as forests established through planting or seeding of one or more tree species in the process of afforestation (first rotation) or reforestation (subsequent rotations) (FAO, 2006). Their main objective is often the production of timber and so many plantations are intensively managed via site preparation (e.g., ploughing, use of fertilizers and herbicides), thinning, and clearfell harvesting, often with short rotations of <50 years between planting and harvesting (Brockerhoff et al., 2008). Currently only 5% of forests in Europe are undisturbed (mainly in northern and eastern Europe), 8% are plantations and 87% are semi-natural (MCPFE Liaison Unit Warsaw, 2007). Recent research has shown that, with appropriate planning and management, forestry plantations have the potential to add to the landscape quality and local biodiversity of an area. This is especially in

regions where land management is intensive, natural forest cover is low, where conservation action is urgent or where mature non-native plantations can perform important ecosystem processes such as water and mineral cycling, community dynamics (succession) and supply of deadwood (Forest Service, 2000b, Humphrey et al., 2001, 2002b, 2003, Humphrey, 2004, Stephens and Wagner, 2007, Bockerhoff et al., 2008, Bremer and Farley, 2010, Hartley, 2002, Quine and Humphrey, 2010, Humphrey, 2005, Roche et al., 2009, Iremonger et al., 2007). Some countries in North-west Europe, for example, Denmark, Iceland and the UK, plantations form 60-70% of forest cover (MCPFE Liaison Unit Warsaw, 2007). Ireland has one of the lowest forest covers in Europe at 10% (Forest Service, 2007) and nearly 90% of that is non-native plantation, giving Ireland the second highest cover of forest dominated by non-native conifers in Europe (only behind Malta at 100%) (MCPFE Liaison Unit Warsaw, 2007). SFM plays a major role in forestry policy not only in Ireland but in many countries (Forest Service, 2000b, Forestry Commission, 1998, Christensen and Emborg, 1996, MCPFE Liaison Unit Warsaw, 2007, FAO, 2011). As well as being managed for timber production, plantations under Sustainable Forest Management support the provision of other environmental, economic, and social benefits (Farmer and Nisbet, 2004, McAree, 2002, UNEP, 1992).

1.4 Justification for research

Due to the currently high and increasing plantation cover in many countries it is important that their successional processes and, particularly, how these can be manipulated to contribute to the enhancement of biodiversity are investigated, especially in terms of informing SFM principles and practice. Ireland, with high plantation cover and SFM policies, is particularly suitable for the investigation of management practices that may manipulate spontaneous

succession during and after plantation rotations. As outlined by Brockerhoff *et al.* (2008) plantations can accelerate forest succession on previously deforested sites and abandoned agricultural areas where persistent ecological barriers to succession, such as the lack of a tree canopy, might otherwise prevent recruitment of species. Planted canopy trees impact understory microclimate conditions, thereby affecting vegetation structural complexity and the development of litter and humus layers. These changes can lead to increased recruitment from surrounding habitats, and importantly for conservation, if native woodlands are near, of typical woodland species (Peterken and Game, 1984, Brunet and von Oheimb, 1998, Humphrey *et al.*, 2003, Verheyen *et al.*, 2003, Ferris and Simmons, 2000, Smith *et al.*, 2005). There is potential for the wide application of the research presented in this thesis both within Ireland and across the temperate zone especially in countries such as Britain that practice clearfell management.

1.5 Approaches and objectives

Ground vegetation was surveyed and the results are included in all chapters of this thesis. Ground vegetation is an important element of forest biodiversity as it plays a role in ecosystem functioning e.g. by providing food and/or habitat to insects (Humphrey *et al.*, 1999), mammals (Carey and Harrington, 2001) and birds (Sweeney *et al.*, 2010a). According to Ferris *et al.* (2000) ground vegetation also influences shrub layer development and natural tree regeneration.

Following an extensive literature review I carried out (unpublished) on diversity indices, species turnover and species richness (number) were selected as measures of diversity for all

forest types. Species turnover was calculated according to β sim following Koleff *et al.* (2003) and can also be interpreted as a measure of species similarity. Species richness or species number (SR) was calculated for vascular and bryophyte species together. SR was also calculated for vascular and bryophyte species separately as it is well recognised that these two plant types are often adapted to respond differently to environmental factors such as light (Marschall and Proctor, 2004, Vanderpoorten and Goffinet, 2009). Richness of species that were typical of woodland was also measured in an attempt to capture the occurrence of these species that are often indicative of a habitat of conservation value. Whether a species was native or non-native was not a focus for ground vegetation because the potential for a species to perform ecosystem services rather than their native status may be regarded as more important in some instance of restoration and conservation (Warren, 2007, Ewel and Putz, 2004). However, the native status of the tree species was important here as there is a general acceptance that if one of the species in a mixed plantation is native this will impact positively on diversity (Bremer and Farley, 2010, Hartley, 2002, Stephens and Wagner, 2007, Barbier *et al.*, 2008) However, many biodiversity programmes remain focused on native versus non-native ecosystem components, for example, it is recommended that native species be used in sustainable forest management (Bremer and Farley, 2010, Hartley, 2002, Forest Service, 2000b, Forestry Commission, 2004). Drivers of diversity and composition were investigated not only to highlight factors important to ground vegetation diversity and those with a potential to be manipulated by management but to show those suitable for use as diversity indicators for assessing forest conditions and compliance with SFM policy (Lindenmayer *et al.*, 2000). Both chronosequences and long-term experimental monitoring were used in this thesis.

To measure canopy extent for both plantation studies hemispherical photographs were taken at 1.3m above ground. The images were analysed using Gap Light Analyzer 2.0 software (Frazer et al., 1999) and percentage canopy openness was calculated. Canopy cover was also estimated visually in the field by subjectively estimating the canopy foliage cover only in the 10 x 10 plots. This was done by the same observers at all sites, namely myself and co-author Linda Coote.

The research reported in Chapters 2 and 3 of this thesis was carried out as part of an Irish forest biodiversity research project FORESTBIO (<http://www.ucc.ie/en/planforbio>). Certain areas of the research for these chapters were undertaken by myself and others areas were carried out in conjunction with the team from the FORESTBIO project. **Table 1.1** clarifies the research components that were carried out independently by myself and those that were carried out in conjunction with other FORESTBIO researchers. Chapter 4 involved a resurvey of plots established for a previous PhD thesis (Smith et al., 2003) and so the work carried out by myself and that done by George Smith (GS) is also clarified below.

Table 1.1 Clarification of research undertaken independently by Karen Moore (KM) and research undertaken in conjunction with other researchers. “na” indicates that the research component is not applicable to this chapter.

Research component	Chapters 2 and 3		Chapter 4	
	KM	FORESTBIO	KM	GS
Abstraction and collation of relevant afforestation site data	X			na
Research design		X		X
Site selection	X	X		X
Determination and collation of environmental and management info on sites	X			X
Ground vegetation surveys	X	X	X	X
Hemispherical photography	X	X	na	na
Species identification	X	X	X	X
Soil collection	X	X		X
Soil analysis (pH)	X	X		X
Data entry	X		X	X
Data collation	X		X	
Data analysis	X		X	

The main objective of this thesis is to contribute to an improved understanding of how vegetation succession of plantations can be manipulated and how this may contribute to Sustainable Forest Management practices. The chapters are outlined below.

- Chapter 2

Previous research has indicated a potential for afforestation to contribute to ground vegetation diversity in Ireland (French et al., 2008, Iremonger et al., 2007) and elsewhere in Europe (Humphrey et al., 2003, Peterken, 2001, Pitkänen, 1997). However, little research has been done on ground vegetation diversity and composition in reforestation (Eycott et al., 2006, Cooper et al., 2008, Ferris et al., 2000). To investigate the factors influencing ground vegetation diversity of reforestation (second rotation), surveys in Sitka spruce stands were carried out using a chronosequence approach and these results were quantitatively compared

with those from a previous survey in a chronosequence of Sitka spruce afforestation (Iremonger et al., 2007). This chapter also contributes to the evaluation of conceptual models of ground vegetation succession over sequential rotations of plantations (Peterken, 2001, Hill, 1979). The impact on succession by the planting of the same crop species after clearfell was investigated with particular reference to typical woodland community development.

- Chapter 3

There is a general acceptance that mixed species plantations support more species than monocultures, especially when one of the mixed species is native (Bremer and Farley, 2010, Hartley, 2002, Stephens and Wagner, 2007, Barbier et al., 2008). Although the effectiveness of non-intimate mixes in enhancing ground vegetation has been investigated (Smith et al., 2005, Ferris and Simmons, 2000, Kirby, 1988), the biodiversity of intimate mixes has received little attention in the scientific literature (Saetre et al., 1997). To investigate the ground vegetation diversity of these plantations types, surveys were carried out throughout the island of Ireland, comparing monocultures (pure stands) of Norway spruce with intimately mixed stands of Norway spruce and Scots pine and Norway spruce and oak (from here on referred to as mixed plantations or mixes). Mature stands were surveyed and are reported in Chapters 2 and 3 and so the results of chapter 3 from Norway spruce pure and mixed plantations can, at least qualitatively, be compared with those from Sitka spruce mature afforestation of Chapter 2 as both surveys contain data from commercially mature afforestation stands.

- Chapter 4

When plantations are clearfelled that prior to planting were in areas that hosted habitat of conservation value it may be of interest to the landowners to restore these areas to the pre-existing native habitat such as native woodland. There is detailed guidance on the establishment of woodlands on clearfelled conifer stands in Britain and Ireland (Harmer, 1999, Rodwell and Patterson, 1994, Little et al., 2009). In Britain the restoration of native woods, particularly in plantations established on ancient woodland, has been studied by Pryor *et al.* (2002) and Thompson *et al.* (2003). With regards to the areas under survey in this research oak-birch-holly woodland was deemed to be an appropriate community for restoration. Factors taken into account in this decision included the ecology of surrounding existing semi-natural woodlands, soil type, climate and historical evidence (Carey, 2009, Mitchell, 1988). The conservation value of these upland acid oakwoods in Ireland is recognized and they are included as “old sessile oak woods with *Ilex* and *Blechnum* in the British Isles” in Annex 1 of the EU Habitats Directive (91A0) (Fossitt, 2000). However, the only published empirical research on restoration of oak woods on conifer clearfell appears to be by Smith *et al.* (2003) and Truscott *et al.* (2004). To investigate how successional trajectories from conifer clearfell may be manipulated to move towards native woodland restoration (in this research to oak woodland), the vegetation of plots that were established on conifer clearfell and experimentally manipulated a decade previously by Smith (2003) were resurveyed by myself. The plots had been managed under the ‘clearfell and replacement’ method of restoration and the experimental manipulations of succession at time of plot establishment were by fencing, planting and weeding. The plots had been set up as a chronosequence with time since felling differing between sites but they had also been set up as long-term *experimental* sites. Thus, rather than relying solely on the chronosequence approach for this successional study, it was

possible to resurvey these sites after 10 years. Results from surveys at the time of plot establishment carried out by Smith (2003) were quantitatively compared with the resurvey carried out by myself and possible drivers of successional change were investigated. As time since the stands were felled differs among the plots surveyed in Chapter 4 (by up to 11 years) they were not directly comparable to either of the earlier stages of pre-thicket (surveyed 4-6 years after felling) or thicket (9 or 8-15 years after felling) in Chapter 2. However, Chapters 2 and 4 represent different possible outcomes from two management options open to foresters: one being a clearfell site is replanted with the same crop and the other being the clearfell site is restored to native woodland.

To summarise, the specific aims and layout of this thesis are as follows:

1. To compare quantitatively the ground vegetation communities of afforestation with second rotation reforestation and to identify factors important in determining the succession of vegetation communities over these rotations. To make SFM recommendations to, for example, promote the establishment of typical woodland ground vegetation communities over successive rotations. (Chapter 2).
2. To compare the ground vegetation communities of mature pure Norway spruce stands with intimately mixed stands of Norway spruce and native species (oak or Scots pine) and to identify factors important in determining the vegetation of these plantation types. To make SFM recommendations for enhancing diversity of ground vegetation, particularly of typical woodland species, in plantations with a mix canopy of non-native and native species. (Chapter 3).

3. To quantitatively compare the ground vegetation communities developed on conifer clearfell over a ten year interval and to identify factors important in determining vegetation succession after clearfell. To assess the conservation value of the vegetation communities that develop after a ten year interval and to make management recommendations for the restoration of native woodland on conifer clearfell (Chapter 4).

2 Factors influencing the ground vegetation diversity of two successive rotations of non-native conifer plantations

To be submitted as: Karen Moore, Linda Coote, Daniel L. Kelly, Fraser J.G. Mitchell.

Factors influencing the ground vegetation diversity of two successive rotations of non-native conifer plantations. Forest Ecology and Management.

2.1 Abstract

Forestry plantations have the potential to add to the biodiversity of an area and Sustainable Forest Management (SFM) promotes the enhancement and conservation of biodiversity in plantations. In Ireland and Britain afforestation rotation stands, the first plantation in a previously unwooded area, are increasingly reaching commercial maturity and being felled. Subsequent replanting of these areas means an increasing proportion of many forest estates are reforestation rotations, however, the biodiversity potential of reforestation is underrepresented in published literature. In this paper we presented results from the first Irish study on ground vegetation diversity over a whole reforestation forest cycle. Here these results were compared quantitatively with those from previous research on afforestation carried out by French *et al.* (2008). The plantation type was Sitka spruce (*Picea sitchensis*). Trends in total species richness were high during early stages, decreased to a minimum during closed canopy mid-rotation stages, but increased again as the canopy reopened during mature stages. Total typical woodland species richness increased significantly over each forest cycle; however, expected gains of typical woodland species richness in reforestation compared to afforestation were not found. Despite very different starting points for both rotations, in terms of community composition, there was floristic

convergence between them over the forest cycle. Diversity indicators identified for both rotations by modelling were canopy cover, rotational stage, area of old woodland within 1km and soil pH. Also for vascular diversity there was an interaction between canopy cover and area of old woodland and, for bryophytes between canopy cover and coarse woody debris volume. These results suggest that for plantations to support more typical woodland species thinning should occur earlier and more regularly preventing canopy closure and deadwood should be retained after thinning and felling.

2.2 Introduction

Recent research has shown that, with appropriate planning and management, forestry plantations have the potential to add to the landscape quality and local biodiversity of an area, especially in intensively managed regions (Forest Service, 2000b, Humphrey et al., 2001, 2002b, 2003, Humphrey, 2004, Stephens and Wagner, 2007, Iremonger et al., 2007). Sustainable Forest Management (SFM) incorporates the social, environmental and financial aspects of forest management in a holistic manner (Farmer and Nisbet, 2004, McAree, 2002, UNEP, 1992) and forms a major goal of forestry policy in many countries (Forest Service, 2000b, Christensen and Emborg, 1996, MCPFE Liaison Unit Warsaw, 2007). The conservation and enhancement of biodiversity is a core component of SFM. Ground vegetation is an important element of forest biodiversity and it has important roles in ecosystem functioning including the provision of food and/or habitat to insects (Humphrey et al., 1999), mammals (Carey and Harrington, 2001) and birds (Sweeney et al., 2010a). Various factors have an influence on ground vegetation diversity and some may be suitable for use as indicators, thus providing a basis for assessing forest conditions and compliance with SFM policy (Lindenmayer et al., 2000).

In the early 1900's Ireland's forest cover was approximately 1% (Neeson, 1991), and, although Ireland still has one of the lowest forest covers in Europe, it has now increased to 10% (Forest Service, 2007). This is primarily due to state afforestation with the non-native conifer Sitka spruce (*Picea sitchensis*) giving Ireland the highest proportion of forest dominated by non-native conifers in Europe (nearly 90%) and the majority of these (52%) are Sitka spruce (Forest Service, 2007). Denmark, Iceland and the UK have the next highest proportion of non-native plantations in Europe at 60-70% (MCPFE Liaison Unit Warsaw, 2007). Afforestation stands, i.e. the first rotation of a plantation on a previously unforested site, are increasingly reaching maturity. In countries such as Ireland and Britain where such stands are clearfelled, the subsequent replanting of these areas means an increasing proportion of many plantations are now reforestation rotations. The impacts of successive rotations on ground vegetation diversity have been little studied.

Although there has been significant research into the biodiversity implications of afforestation in Ireland (French et al., 2008, Iremonger et al., 2007) and elsewhere in Europe (Humphrey et al., 2003, Peterken, 2001, Pitkänen, 1997), little research has been done on factors affecting ground vegetation diversity in reforestation. In Britain, Eycott *et al.* (2006) related ground vegetation community composition in reforested pine plantations to environmental and ecological factors. Peterken (2001) and Hill (1979) developed conceptual models of ground vegetation development over successive rotations of plantations established on peatland or heath. Previous research on reforestation in Ireland by Cooper *et al.* (2008) investigated only the early stages of reforestation (0 – 11 years) established on dredged sediments along the banks of a river. Several factors may differ depending on the rotation, for example, the presence of deadwood after clearfell will be a factor in reforestation, but not in afforestation, while the soil seed banks may be very

different between rotations. In this paper we present results from the first Irish study on ground vegetation diversity over the whole reforestation forest cycle. These results are compared quantitatively with those of previous research on afforestation carried out by French *et al.* (2008). The key aims of this paper are:

1. to compare directly the species richness and vegetation community composition of afforestation with second rotation reforestation
2. to identify factors important in determining the vegetation communities and species richness of these rotations, particularly of typical woodland species, which could be used as diversity indicators
3. to recommend management practices for promoting typical woodland ground vegetation communities over successive rotations

The results from this research will increase our understanding of how ground vegetation diversity can be enhanced in reforestation to inform the management of successive rotations of non-native conifer plantations. It will add to the quantitative data available to investigate under what circumstances plantations may have positive or negative outcomes for ground vegetation diversity. In this thesis different possible outcomes of two management options are presented according to whether the clearfell site is replanted with the same crop (this chapter) or managed to succeed to native woodland (Chapter 4). The afforestation mature stands surveyed in this Chapter can be, at least qualitatively, compared with the mature stands in Chapter 3 (refer to **section 5.2.**).

2.3 Materials and methods

2.3.1 Site selection

Sites were selected where Sitka spruce was the primary crop tree (> 80% cover) and individual stands of different ages were sampled to create a chronosequence that allowed ‘monitoring’ over a short time period of two consecutive rotations. Four age classes were delineated: Age class I - tree establishment at 4-6 years; Age class II - canopy closure at 9-16 years; Age class III - time of first thinning at 20-29 years; Age class IV - commercial maturity at 30-47 years. Thirty one afforestation sites were surveyed during the summer of 2001 for a research programme on the biodiversity of afforestation plantations (French et al., 2008). Twenty reforestation sites were surveyed during the summer of 2007 that, as closely as possible, matched the habitat conditions of afforestation plantations in terms of characteristics such as stand size, soil type, and land use and management history. The sites in a chronosequence (one from each age class) were geographically clustered, where possible, to lessen the potential influence of environmental variation. **Fig. 2.1** shows the location of the sites. Sites that were established on or adjacent to areas of old woodland were, for reforestation, one re-opening and one mature site and for afforestation, one closed-maturing, one re-opening and two mature sites. Thus these sites were old woodland in at least 1900 and that they were, at the time of survey, nearing the end of their second rotation indicates that these sites may have been woodland directly prior to afforestation. One afforestation mature site was scrub prior to planting. Previous land use of afforestation sites by proportion in each rotation was 57.6% grassland or rough grazing, 39.6% unknown and 2.8% scrub and of reforestation sites (before afforestation) 92.8% grassland or rough grazing and 7.2% bog/heath.



Figure 2.1 Map of Ireland showing distribution of study sites. Grey symbols represent afforestation sites and black or symbols represent reforestation sites. (structural classes outlined in **Table 2.1**). ♦ Pre-thicket; ● Thicket; * Closed-maturing; ■ Reopening; + Mature.

2.3.2 Data collection

At each site, three 10 m x 10 m plots were positioned at least 50 m from the forest edge and 50 m from each other to reduce edge and pseudo-replication effects respectively. In each plot, percent cover of each species of ground vegetation was recorded to the nearest 5%. Cover below 5% was recorded either as 3% (indicating cover of 1–5%) or 0.5% (indicating cover <1%). Ground vegetation for this study was defined as vascular plants, mosses and liverworts growing on the forest floor and on microhabitats e.g. deadwood, rocks and tree bases. In reforestation only bryophyte species forming patches more than 10cm² were recorded (no minimum patch size was used for the afforestation sites). However, we considered that the difference in recording intensity was negligible in practice. Vascular plant nomenclature follows Stace (2010), mosses follow Smith (2004) and liverworts follow Paton (1999).

Vegetation structure was recorded in the 10m x 10m plots as the percentage cover of vegetation (as for species cover) in the following strata: canopy, understorey (≥ 2 m tall), shrub (woody species <2m tall, excluding brambles/briars but including climbing species), bramble/briar (*Rubus fruticosus* agg & *Rosa* spp), fern, graminoid (grass, rush and sedge), forb (broadleaved herbaceous plants) and bryophyte. Simpsons reciprocal index ($1/D$) was calculated as a measure of structural diversity, using these covers. The diameter at breast height (DBH) at 1.3 m of all planted trees ≥ 2 m tall and all unplanted trees of ≥ 5 cm DBH was recorded and the species of these trees was noted. The percentage cover of the following was also recorded: leaf litter (broadleaved tree and herbaceous litter); fine woody debris (FWD, <10cm diameter); needle litter; cover of brush piles (piles of deadwood left on site following thinning and/or clearfell, recorded in reforestation only).

Thinning status, type and intensity were recorded from field observations. The volume of coarse woody debris (CWD) maximum ≥ 10 cm diameter was recorded and categorised as follows: logs and large branches ($>45^\circ$ departure from vertical); snags (standing deadwood; $\leq 45^\circ$ and ≥ 1 m tall); stumps (< 1 m tall), and within three states of decay: sound (intact with very little evidence of decay); moderately decayed (crumbling in the hand); advanced decay (moist, rotten and sometimes hollow). Total CWD volume was also calculated. Five soil samples were collected to an approximate depth of 5 cm from near the corners and the centre of the 10 m x 10 m plot and bulked in the field. Soil pH was determined at the earliest opportunity, using a glass electrode pH meter on a suspension of soil and distilled water. Soil samples were air dried prior to analysis for organic matter content (LOI – $550^\circ\text{C} \times 5$ hrs). Information on previous land use (for reforestation sites this was land use before afforestation rather than before replanting), ground preparation for planting and thinning (type and year(s) carried out) was collected from forest managers but due to the variable quality of these data (and of soil type) these variables were not used in formal analysis. Stand age was determined from the management database. The distance to old woodland and area of old woodland (defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the third edition 6" O.S. maps, 1900-1913), within 1 km of sites were recorded (note: woodland may or may not be existing at time of field survey). Mean weighted Ellenberg values for vascular plants (Hill et al., 2004) and bryophytes (Hill et al., 2007) for adaptation to moisture (F) and nitrogen (N, essentially representing soil fertility) were calculated for each plot.

Previous research on afforestation sites in Ireland by Smith *et al.* (2005) found that stands within an age class varied greatly in structure. So although the sites had been selected on the basis of age class, they were reclassified for analysis according to their structure using

canopy cover, tree height and mean DBH. Five structural stages were selected based on these ranges: pre-thicket, thicket, closed-maturing, re-opening and mature (**Table 2.1**).

Table 2.1. Structural stages delineated over the forest cycle using canopy cover, tree height and DBH. Age range (years), structure and mean canopy cover (and range) of the structural stages and number of sites (n) surveyed in each rotation, afforestation - Affor, reforestation - Refor.

Stand structural stage	Age (yrs)	Forest structure	Canopy cover (%)	Affor n	Refor n
Pre-thicket	4 – 6	Open canopy	37.00 (11.74 - 58.32)	8	5
Thicket	8 – 15	Canopy closing	88.70 (71.71 – 90.00)	6	5
Closed-maturing	8-47	No thinning-results in closed canopy	81.50 (76.71 – 95.00)	7	5
Re-opening	20-47	Thinning results in re-opening of canopy	74.20 (63.34 – 83.35)	4	2
Mature	30- 47	Commercially mature	60.46 (40.07 – 80.00)	6	3

2.3.3 Data analysis

The following biodiversity metrics (excluding planted tree species) were calculated for each plot: total, vascular plant and bryophyte species richness (SR). Species richness is a widely accepted and intuitive method of measuring biodiversity (Magurran, 2004), previously found suitable for use in plantations (French et al., 2008). It does not, however, indicate whether the species involved are of conservation interest (Bremer and Farley, 2010) and may also underestimate the conservation value of important but naturally species-poor habitats (Magurran, 2004). Conservation of specialist species, for example, natives and typical woodland species are often the focus of management strategies for biodiversity conservation in plantations (Felton et al., 2010a, Hartley, 2002). In an attempt to capture the conservation interest of the habitats surveyed in this research, species recorded were classified according to their affinity for woodlands: low (not usually found in woodlands), moderate (frequently occurring in both woodlands and unwooded habitats) or high (typical woodland species) using information on habitat preferences from Irish and British floras for vascular plants (Hubbard, 1984, Jermy et al., 1982, Preston et al., 2002,

Webb et al., 1996, Grime et al., 2007, Hill et al., 2004) and for bryophytes (Hill et al., 2007, Paton, 1999, Purvis et al., 1992, Smith, 2004, Watson, 1981). (Refer to **Appendix 1** for details). β sim was calculated as a metric for species turnover following Koleff *et al.* (2003) with a maximum value of 1, indicating no species in common, and minimum value of 0, indicating all species common. Species turnover was measured among the three plots of a site. These values were averaged to give site values that indicated the heterogeneity of the sites species composition. These site values were then compared to give information on how species turnover varied among sites. For analysis FWD and needle litter covers were combined (FWD-needle litter) to make data sets from both afforestation and reforestation surveys comparable.

Both plot level and site level data were used in analysis. Site level data were calculated from plot level data by combining the variables from the three 10m x 10m plots and averaging. Plot level data are more sensitive to heterogeneity in richness and ecological processes, while site level data provide an overview of relationships between vegetation communities and factors that may impact on them (Smith et al., 2005). Prior to statistical testing data exploration for normality, heterogeneity of variances, outliers and collinearity was carried out using SPSS 16 (SPSS, 2007), Minitab 13 (2000) and R (R Development Core Team, 2010). Where outliers were detected the data were transformed as appropriate (detailed in results). Non-normal distribution and heterogeneity of variance was dealt with by transformation and if data still did not meet assumptions of parametric tests satisfactorily non-parametric statistics were employed.

To examine patterns in ground vegetation communities across afforestation and reforestation forest cycles, a non-metric multidimensional scaling (NMS) ordination was

used. This technique is based on ranked distances and has thus been found particularly suitable for the analysis of non-normal data from ecological communities (McCune and Grace, 2002). The “slow and thorough” autopilot settings in PC Ord version 5.26 (McCune and Mefford, 2006) were used which include the following parameters: Sorensen distance measure; 500 maximum number of iterations; Random Starting coordinates; 100 runs with real data; Step down in dimensionality (Initial step length = 0.2); 50 runs with randomized data. NMS axes are arbitrary (Legendre and Legendre, 1998), so varimax rotation was used to help interpret the ordination axes as it maximizes the variance of species correlations with the ordination axes, resulting in groups of sites with very high and very low axis correlations (Lichstein et al., 2002). Spearman’s rho (r) non-parametric correlation analysis was undertaken between site axis scores and environmental variables to aid interpretation of the ordination by indicating what axes may represent in terms of measured variables. It should be noted that varimax rotated NMS axes are still arbitrary so caution was used in interpreting correlations between NMS scores and environmental variables. Indicator species analysis using plot level data was used to highlight species associated with each structural stage of both rotations (McCune and Grace, 2002). A perfect indicator species with an indicator value of 100% would be one that was unique to one habitat and was observed in all samples from that habitat (Dufrêne and Legendre, 1997). Indicator values (IV) were derived for each species from the average abundance of each species in a given group of sites over the average abundance of that species in all the sites expressed as a percentage (McCune and Mefford, 2006). This value was tested for statistical significance using a Monte Carlo test. Only species with an indicator value greater than 25% and with $p \leq 0.05$ were considered as a species with an IV lower than 25% is not considered to be a good indicator (Dufrêne and Legendre, 1997). Information on the affinity for woodlands (as described previously), Ellenberg values (Hill et al., 1999, 2007, 2004) for light (L) soil moisture (F) and soil reactivity (R) and ecological strategies, of the indicator species

associated with each stage were used to highlight the environmental conditions prevalent during these stages. The ecological strategies of vascular plants were classified using the CSR model of Grime *et al.* (2007, 1988). Vascular species (not bryophytes) are classified as competitors (C), stress-tolerators (S), ruderals (R) or intermediates between any two or all three of these categories. In the CSR model species classification is based on plant life-history such as method of reproduction, nutrient requirements and size. As there were too many species in the data set (267 species) to display effectively on an ordination only the indicator species for the different forest types and the common species (occurring in 25 % or more of sites) are displayed. Ordinations and indicator species analysis were conducted using PC-Ord version 5.26 (McCune and Mefford, 2006).

Relationships between response and explanatory variables were examined using Spearman's ρ (r) non-parametric correlation analysis across both rotations at the plot level. The two most developed structural classes (re-opening and mature) were pooled to ensure there were a sufficient number of plots for correlation analysis. *Post hoc* p -value multiple comparisons corrections, such as Bonferroni or Dunn-Sidak, were not applied due to criticisms that they are too conservative as they reduce the level for significance below the usual 0.05 and thus significant relationships may be missed (Dytham, 2003).

Correlations were viewed with caution when they did not appear to be ecologically meaningful. Non-parametric Kruskal-Wallis tests followed by *post hoc* Mann-Whitney U tests (Dytham, 2003) were used to investigate differences in diversity metrics and environmental variables among and between structural stages in both rotations.

Using site level data, species richness and typical woodland species richness of vascular plants and bryophytes were modelled separately using Poisson distributed Generalized

Additive Models (GAMs), except for the vascular typical woodland SR model, where overdispersion was detected, thus the standard errors were corrected using a quasi-GAM model. To make an informed decision in choosing the variables for model analysis the influence on ground vegetation species richness of the variables measured was reviewed in the literature and is outlined below. Canopy cover has previously been found to be of paramount importance in driving species diversity in plantations (Eycott et al., 2006, Hill, 1986, Schoonmaker and McKee, 1988, Smith et al., 2005, Carnus et al., 2006) and has been used as a proxy for forest management since decreased canopy cover through thinning, planted spacing or species selection has been found to influence biodiversity (Bremer and Farley, 2010, Hartley, 2002). The rotational stage of a plantation may be important in determining the stands diversity and there are models for the cumulative effects of successive plantations on ground vegetation diversity and composition including those by Peterken (2001) Peterken and Game (1984) and Hill (1979). Peterken (2001) describes the possible succession of ground vegetation when bog and heath are afforested with conifers. The original moorland vegetation is eliminated during the thicket stage of the first rotation and gradually replaced with more typical woodland vegetation. When the afforestation plantations are felled, the ground vegetation develops vigorously containing a variety of typical woodland herbs, opportunist colonizers and heath species from the seed bank. With each rotation, it is proposed that the balance will shift from bog and heath species to typical woodland species. Area of previous (and existing) old woodland surrounding a site has been reported as influencing total and typical woodland ground vegetation species richness (Smith et al., 2005, Williams et al., 1998, Brockerhoff et al., 2008, Felton et al., 2010a, Bremer and Farley, 2010, Carnus et al., 2006). For example, Smith *et al.* (2005) reported the area (log-transformed) of old woodland or scrub within 1 km of sites to be positively significantly related to typical vascular woodland SR. Soil has been reported as impacting ground vegetation diversity (Eycott et al., 2006, Smith et al.,

2005, Kirby, 1988, Hardtle et al., 2003, Roche et al., 2009). For example Ferris *et al.* (2000) found plant community composition and diversity was closely related to soil fertility and pH. Deadwood is accepted as being of importance to bryophyte species richness (Márialigeti et al., 2009, Smith et al., 2005, Humphrey et al., 2002c) with, for example, Ferris *et al.* (2000) reporting a positive relationship between deadwood volume and bryophyte species diversity and so CWD volume was included in bryophyte models. Large complex brash piles were only recorded in reforestation and only found in pre-thicket sites so, although from field observations we observed a high number of species exploiting this unique niche in reforestation pre-thicket, there were too few sites in the data set with them present to statistically analyse their impact on SR confidently.

Proposed interactions investigated by modelling were: canopy cover interaction with area of woodland investigating the hypothesis that closed canopy sites would have low SR no matter what their site history was: canopy cover interaction with CWD volume investigating the hypothesis that no matter how large a resource of deadwood there was, its use as habitat by bryophytes may be curtailed if the canopy cover is too high (Humphrey et al., 2002a). Following the literature review a suite of variables thought, *a priori*, to be important influences on ground vegetation species richness were considered as candidates for inclusion in the global models and examined for correlation using Spearman rank analysis and for collinearity using Variance Inflation Factor (VIF) analysis (values > 3 were taken as indicating collinearity (Zuur et al., 2007)). When collinearity was detected the variable that was more ecologically meaningful, of most relevance to forestry management and that was the easiest and most cost efficient to measure, was included in the models (refer to **section 2.4.4** for correlation and VIF results and variables chosen for the global models).

Multimodel Inference (MMI) (Burnham and Anderson, 2002) was carried out on the global models (the model containing all chosen variables and interactions) using the MuMIn package (Barton, 2009) in R version 2.12.1 (R Development Core Team, 2010). An 'all combinations' scheme was selected i.e. all possible models were tested for the set of variables and interactions to quantify the relative importance of the variables compared to each other. AIC_c (Akaike's information criterion corrected for small sample size: $n/K < 40$ where n is number of samples and K is the number of parameters) was used to rank and weight the models (for the quasi-GAM model the QAIC_c was used). Akaike weights (ω_i) were calculated using AIC_c values and are a measure of how close model i is to approximating the best model, given the data and set of candidate models. Model sets were selected containing all models within 2 units of the lowest AIC_c or QAIC_c. The relative importance (R.I.) of each variable was calculated by summing the Akaike weights (ω_i) of all models containing the variable and gave a measure of support for the presence of a relationship between the variable or interaction and the response, relative to other variables and interactions tested. Model averaging was also undertaken, where parameters are averaged over each model set. Burnham and Anderson (2002) advise against interpreting averaged model parameters if an explanatory variable had a non-linear association with the response variable.

2.4 Results

2.4.1 Species richness

A total of 267 ground vegetation species were recorded from both rotations in the 100m² plots, comprising 178 vascular plants and 89 bryophytes. Forty four typical woodland

species (as defined in **Section 2.3.3** those with a high woodland affinity) were recorded in afforestation and 58 in reforestation. Of the typical woodland species recorded in both rotations, 26 were bryophytes and 37 were vascular plants. Unique species recorded in afforestation numbered 113 (of which 14% were typical woodland species) and 31 species were unique to reforestation (38% of which were typical woodland species). There were no red data list species recorded (Curtis and McGough, 1988). *Stachys officinalis* (betony) was recorded in a mature reforestation stand that was established on old woodland and adjacent to existing woodland. It is on the Irish Flora Protection Order (Anon, 1999) list and is a 'notable' species, (rare species typically found in woodland, or species indicative of long-established woodland) of the 30 listed by Perrin *et al.* (2008).

For both rotations total species richness (SR) was high during the early pre-thicket stages and then decreased towards the closed-maturing stages (total SR of the closed-maturing stages are significantly lower than all other stages, except re-opening, **Table 2.2**). Total SR increased again during the mature stages; in afforestation this increase was to levels significantly higher than pre-thicket but in reforestation there was no significant difference between the pre-thicket and the mature stages. The only significant difference in total SR between rotations was in the closed-maturing stages where reforestation was lower than afforestation. For both rotations there were no more vascular species in the mature stages than pre-thicket stages and vascular SR followed the same trend for total SR. There was a significant difference in bryophyte SR over the afforestation cycle, but not over the reforestation cycle. The lowest bryophyte SR for afforestation was in the pre-thicket and re-opening stages while in reforestation it was in the closed-maturing stage. Bryophyte SR differed significantly between rotations where it was higher in reforestation pre-thicket than afforestation and lower in reforestation closed-maturing than afforestation. For both

rotations, the mature stages had significantly more total typical woodland species compared to all other stages (except for typical woodland vascular SR, where there was no significant difference between the re-opening and mature stages). In afforestation the pre-thicket was significantly lower than all the other stages, whereas in reforestation the pre-thicket is not significantly different to the thicket to re-opening stages. Typical woodland bryophyte SR followed the same trend as for total typical woodland SR over each rotation whereas for typical woodland vascular SR there were some deviations from this trend: in afforestation, re-opening was significantly higher than closed-maturing and in reforestation re-opening and mature were not significantly different. Significant differences in species richness were calculated between afforestation mature and reforestation pre-thicket as contiguous stages in a reforestation cycle to investigate what, if any, changes occurred. Between rotations, all of the SR metrics were significantly higher at the end of afforestation than at the beginning of reforestation except for vascular SR where there was no significant difference between rotations (**Table 2.2**). Species turnover calculated to measure within site heterogeneity was significantly higher in afforestation pre-thicket, thicket and mature stages compared with reforestation (**Table 2.2**).

Table 2.2. Median, interquartile diversity metrics for ground vegetation in each structural stage of afforestation (Affer) and reforestation (Refor). High TW = typical woodland species. Number in brackets after stage is number of observations (n) in Affer and Refor respectively. Significant differences between groups and within groups tested with non-parametric Mann Whitney (U). Differences between stages in an individual rotation ($p \leq 0.05$) are indicated with different capital letters before mean value; “*” indicates differences ($p \leq 0.05$) between the same stage of the two rotations; **a** ($p \leq 0.05$), **b** ($p \leq 0.001$) in final column indicate differences between contiguous stages in the second rotation cycle (afforestation mature and reforestation pre-thicket).

		Pre-thicket (22, 15)	Thicket (18, 15)	Closed- maturing (21, 15)	Re-opening (12, 6)	Mature (17, 9)
Total SR	Affer	^A 24.0, 14.50	^A 21.50, 8.50	^B 11.0, 8.0*	^{AB} 16.0, 12.50	^C 28.0, 12.0 a
	Refor	^A 31.0, 11.5	^B 15.0, 8.50	^C 7.0, 6.0*	^{BC} 10.50, 8.25	^A 28.0, 6.0
Vascular SR	Affer	^A 18.0, 9.0	^B 10.50, 5.25	^C 2.0, 4.0	^{BC} 7.0, 8.75	^A 18.0, 8.0
	Refor	^A 19.0, 7.50	^B 8.0, 5.0	^C 3.0, 4.0	^{BC} 2.0, 5.75	^A 19.0, 13.0
Bryophyte SR	Affer	^A 4.50, 5.0*	^B 10.0, 3.50	^B 9.0, 8.0 *	^{ABC} 7.50, 2.50	^C 13.0, 4.0 a
	Refor	^{AC} 9.0, 5.0 *	^A 8.0, 5.50	^B 4.0, 4.5*	^A 6.0, 2.25	^C 11.0, 4.0
Total TW SR	Affer	^A 2.0, 3.0 *	^B 6.50, 2.75	^B 6.0, 4.0	^B 7.9 ± 1.2	^C 11.0, 4.0 b
	Refor	^A 7.0, 4.0 *	^A 6.0, 3.0	^A 5.0, 3.5	^A 6.2 ± 1.1	^B 14.0, 7.0
TW vascular SR	Affer	^A 0.0, 1.50*	^B 2.0, 2.5	^C 1.0, 1.0	^D 4.0, 4.0	^E 5.0, 4.0 b
	Refor	^A 3.0, 2.0*	^A 2.0, 1.50	^A 2.0, 2.0	^{AB} 2.0, 2.0	^B 5.0, 6.0
TW bryophyte SR	Affer	^A 0.5, 2.0*	^B 4.0, 2.0	^B 4.0, 3.5	^B 4.0, 1.50	^C 6.0, 2.0 a
	Refor	^A 4.0, 2.0*	^A 4.0, 2.0	^A 3.0, 2.0	^A 4.50, 1.75	^B 7.0, 2.0
Species turnover	Affer	^{AB} 0.30, 0.21 *	^{A*} 0.40, 0.09	^B 0.29, 0.16	^B 0.25, 0.16	^B 0.32, 0.05 *a
	Refor	^{AB} 0.23, 0.04*	^A 0.33, 0.16 *	^B 0.17, 0.18	^{AB} 0.24, 0.07	^{AB} 0.24, 0.09 *

2.4.2 Structural, environmental and site history variables

Canopy cover was greater in reforestation than afforestation throughout the forest cycle, although only significantly so in the pre-thicket and mature stages (**Table 2.3**). For both rotations structural diversity followed a similar trend to that of total species richness over the forest cycle - high during early stages, lowest during the closed-maturing stages and increasing in the re-opening and mature stages: in afforestation this increase was to the highest levels of the cycle but in reforestation there was no significant difference between

pre-thicket and mature stages. Over the forest cycle CWD volume was significantly higher in reforestation compared to afforestation until the re-opening stages were differences became non-significant. Soil pH was lower in reforestation compared to afforestation, but only significantly so in the pre-thicket and thicket stages. Area of old woodland (in a 1km radius surrounding sites) was higher in reforestation than afforestation but only significantly so in the pre-thicket and re-opening stages. However, there was a significantly higher area of old woodland surrounding afforestation mature sites than reforestation pre-thicket.

Table 2.3. Median, interquartile for structural, and environmental variables in each structural stage of afforestation (Affor) and reforestation (Refor). Number in brackets after stage is number of plots (n) in Affor and Refor respectively. Significant differences between groups and within groups tested with non-parametric Mann Whitney (U) where applicable. Differences between stages in each rotation ($p \leq 0.05$) indicated with different capital letters before mean value; “*” differences ($p \leq 0.05$) between the same stage of the two rotations; **a** ($p \leq 0.05$) in final column indicate differences between contiguous stages in the second rotation cycle (afforestation mature and reforestation pre-thicket).

		Pre-thicket (22, 15)	Thicket (18, 15)	Closed- maturing (21, 15)	Re-opening (12, 6)	Mature (17, 9)
Canopy cover (%)	Affor	^A 32.50, 20.0 *	^{BC} 87.50,32.50	^B 90.0,11.25	^C 70.0, 26.25	^D 60.0, 5.0 * a
	Refor	^A 50.0, 17.50* a	^{BC} 85.0, 22.50	^B 95.0, 5.0	^C 80.0, 3.75	^C 75.0, 15.0 *
Structural diversity (1/D)	Affor	^A 2.48, 0.77 *	^{AB} 1.97, 1.52	^C 1.12, 0.55	^{BC} 1.58, 0.99	^D 3.01, 1.32
	Refor	^A 3.43, 0.85 *	^B 2.38, 0.81	^C 1.45, 0.73	^C 1.83, 0.38	^{AB} 2.42, 2.21
CWD m ³ /100m ²	Affor	^A 0.0, 0.0 *	^B 0.0, 0.0 *	^C 0.10, 0.11 *	^D 0.10, 0.13	^{CD} 0.24, 0.43
	Refor	^A 0.23, 0.12 *	^A 0.21, 0.24*	^B 0.48, 0.49 *	^{AB} 0.21, 0.26	^{AB} 0.27, 0.22
Soil pH	Affor	^A 5.10, 1.90 *	^A 5.10, 0.80 *	^B 4.40, 1.30	^B 4.20, 0.20	^B 4.50, 0.40
	Refor	^A 4.20, 0.90 *	^A 4 .0, 0.50 *	^A 4.30, 0.40	^A 4.10, 0.70	^A 4.30, 0.90
Area of old woodland (m ²)	Affor	^A 1.0, 2.70	^A 0.20, 3.50 *	^A 1.0, 4.0	^A 1.0, 5.0 *	^B 8.0, 17.0 a
	Refor	^A 0.0, 10.13 a	^A 0.85, 19.90 *	^A 3.55, 4.87	^B 65.78,71.03 *	^{AB} 1.58, 136.84

2.4.3 Community composition

In the ordination of the total vegetation composition of all sites combined a 3D solution was suggested and cumulative variation in the data explained by the ordination was 75.9% with Axis 1 accounting for 11.9%, Axis 2 for 32.3% and Axis 3 for 31.7 % (**Fig. 2.2 a, b and c**). Final instability = 0.00000 and the Monte Carlo test showed the stress was significantly different to that expected by chance: final stress = 12.09 ($p = 0.004$). Axes 2 and 3 together separated most of the afforestation sites from the reforestation sites apart from the mature sites from both rotations which ordinated closely. The most distinct group was the pre-thicket afforestation sites which were clearly separated from all of the other site types along axis 2; this axis also explained most of the variation in the data. Axis 2 was correlated negatively with canopy cover ($r_s = -0.631$, $p \leq 0.01$), CWD volume ($r_s = -0.659$, $p \leq 0.01$), pH ($r_s = -0.612$, $p \leq 0.01$), elevation ($r_s = -0.512$, $p \leq 0.01$) and positively with Ellenberg drainage ($r_s = 0.530$, $p \leq 0.01$). Axis 3 was positively correlated with canopy cover ($r_s = 0.528$, $p \leq 0.01$), and area of old woodland ($r_s = 0.356$, $p \leq 0.01$) and negatively with CWD volume ($r_s = -0.384$, $p \leq 0.01$). Axis 1 was correlated negatively with canopy cover ($r_s = -0.406$, $p \leq 0.01$), CWD volume ($r_s = -0.659$, $p \leq 0.05$), LOI ($r_s = -0.501$, $p \leq 0.01$) and positively with Ellenberg fertility ($r_s = 0.530$, $p \leq 0.01$) and distance to oldwood ($r_s = 0.444$, $p \leq 0.05$).

Afforestation pre-thicket sites were spread over a larger area in the ordination space than reforestation pre-thicket sites indicating that they had a higher variability in species composition. Moreover, although the pre-thicket stages of the two rotations were widely separated in ordination space especially on axis 2, the mature stages for both rotations ordinated relatively close. The extensive overlap among some structural stages in ordination space indicated heterogeneity in vegetation composition among sites within certain structural stages. The ordination also showed that reforestation communities were

more similar to each other (sites relatively clustered) compared to afforestation communities (sites more spread out). Although the afforestation mature and reforestation pre-thicket sites appeared to ordinate closely within dimensions 2 and 3 of the ordination (**Fig. 2.2a**), they were slightly separated along axis 1 (**Figs. 2.2b and c**). Axes 2 and 3 displayed together in **Fig 2.2a** showed most of the afforestation sites separated out except for the mature which ordinated closely to the reforestation sites.

The ordinations in **Fig. 2.2** suggested species turnover between afforestation and reforestation rotations as most reforestation stages occupied different areas of the ordination from their corresponding afforestation stage. Species turnover, formally assessed with β_{sim} was relatively low between rotations (**Table 2.4**, inter-rotational values), however, it was highest at earlier stages of the rotations, lowest at re-opening and increased slightly again at mature stages. Turnover was also calculated between the successive stages (in terms of the chronosequence) of each rotation and, for both rotations, higher species turnover occurred between earlier stages than at later stages (**Table 2.4**, intra-rotational values). The difference was more pronounced in afforestation. The highest turnover was between afforestation pre-thicket and reforestation mature i.e. the beginning of the first rotation and the end of the second ($\beta_{sim} = 0.55$). The turnover between afforestation mature and reforestation pre-thicket i.e. the end of one rotation and the beginning of the next, was relatively low ($\beta_{sim} = 0.35$).

Figure 2.2 a)

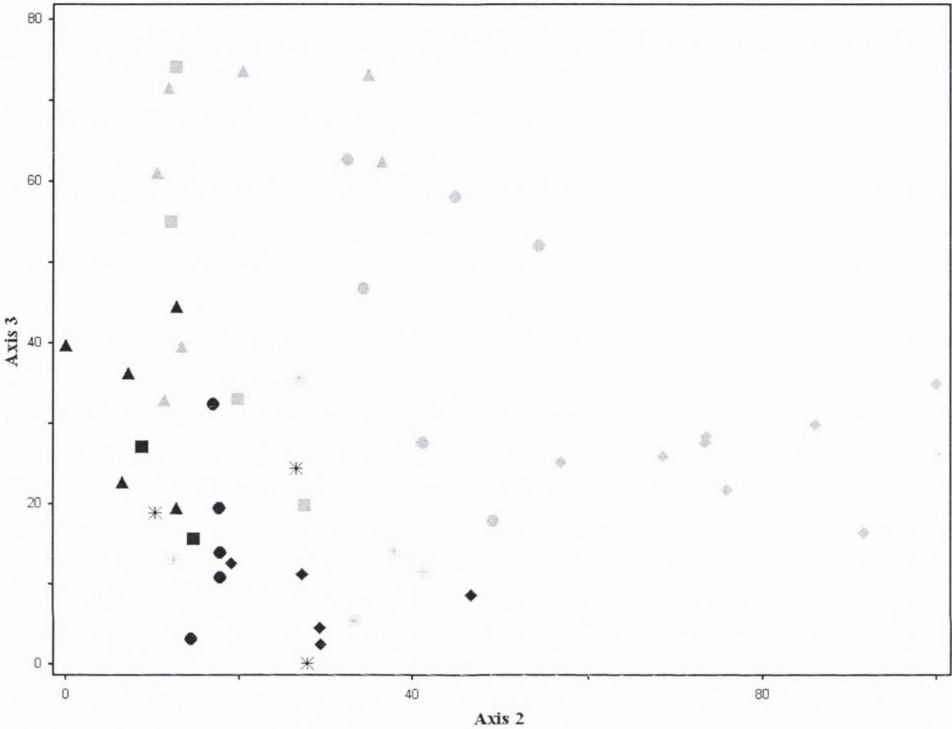
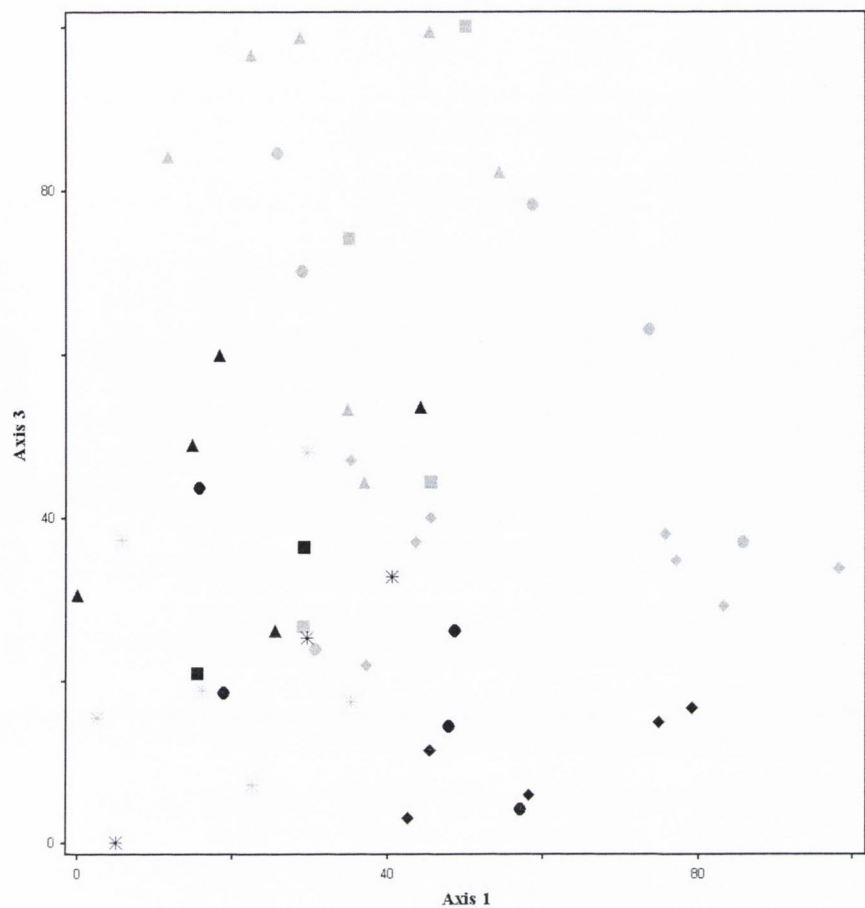


Figure 2.2 b)



c)

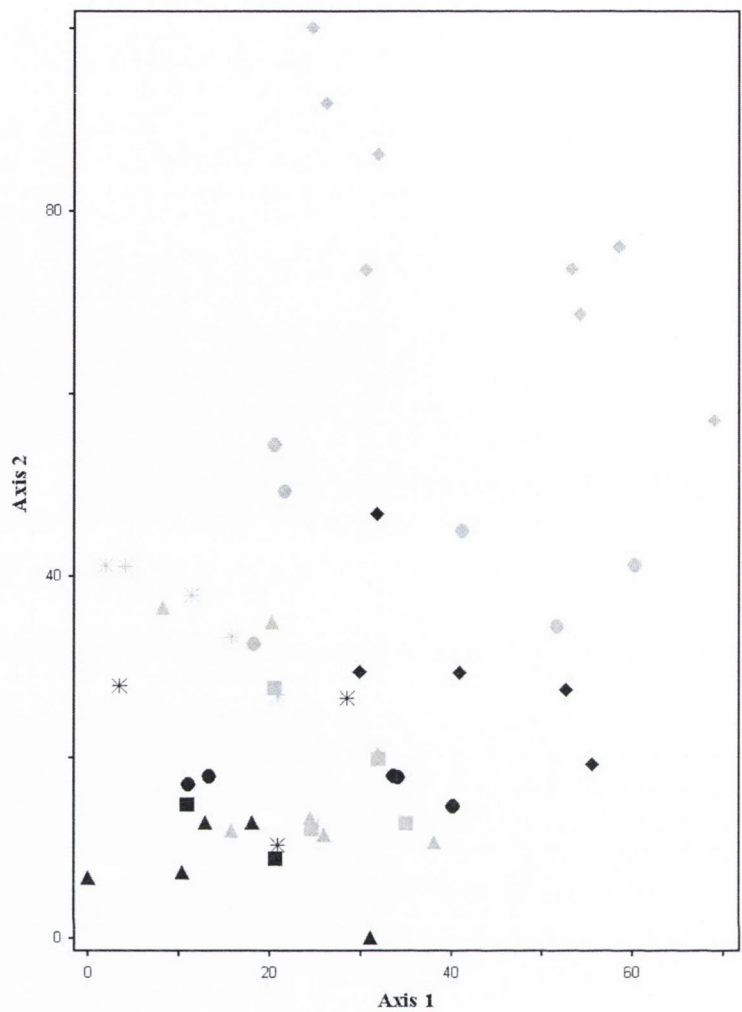


Figure 2.2a) Axes 2 and 3, **b)** axes 1 and 3 and **c)** axes 1 and 2 of varimax rotated NMS ordination of species composition and cover for afforestation (grey symbols) and reforestation (black symbols) sites at different stages of the forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; * Mature. Cumulative variation in the data explained by the ordination is 75.9% with Axis 1 accounting for 11.9%, Axis 2 for 32.3% and Axis 3 for 31.7%. Final stress =12.09 ($p=0.004$), Final instability = 0.00000.

Table 2.4. Species turnover (β_{sim}) on a scale representing no species turnover (0) to complete species turnover (1) between stages of rotations. Values in bold and italics are inter-rotational values for the same structural stage and bold, underlined values (along top and down left of table) are intra-rotational values for successive stages within each rotation.

		Reforestation								
		Pre-thicket			Closed-maturing					
Afforestation		<u>0.40</u>	Thicket	<u>0.37</u>		<u>0.37</u>	Re-opening	<u>0.20</u>	Mature	
Pre-thicket	<u>0.25</u>	0.39	0.45		0.45		0.50		0.55	
Thicket	<u>0.36</u>	0.43	0.35		0.25		0.25		0.45	
Closed-maturing	<u>0.32</u>	0.43	0.43		0.38		0.32		0.47	
Re-opening	<u>0.04</u>	0.46	0.40		0.29		0.19		0.37	
Mature		0.35	0.27		0.27		0.13		0.28	

Indicator species analysis (**Table 2.5**) identified the highest number of indicator species in the afforestation pre-thicket stage (13) with afforestation mature (10), reforestation pre-thicket (8) and reforestation mature (6) having the next highest numbers respectively. In the reforestation closed-maturing stages no indicator species were identified. In afforestation only the mature stage had indicator species with high woodland affinity such as the fern *Dryopteris dilitata* and the rush *Luzula sylvatica* whereas in reforestation pre-thicket only the moss *Polytrichastrum formosum* out of the eight indicator species had high woodland affinity and in the mature stage all indicator species had high woodland affinity. According to the Ellenberg light values in both rotations during the earlier stages indicator species were adapted to well lit places such as the grass *Festuca rubra* and the heather *Calluna vulgaris* while, in contrast in the later stages they were adapted to shade and semi-shade conditions (the herb *Oxalis acetosella* and the moss *Dicranella heteromalla* respectively). The stages with indicator species adapted to the lowest light levels were the re-opening stages of both rotations. According to Ellenberg moisture values indicator

species were adapted to differing soil drainage over both rotations with early stage species tolerating constantly moist or damp but not wet soils such as the fern *Athyrium filix femina* and the liverwort *Calypogeia fissidens*. In the later stages the species are moist to dry site indicators including the rush *Carex sylvatica* and the moss *Mnium horum* respectively. Comparing both rotations, in reforestation indicator species showed a tolerance for drier soils when compared with afforestation, especially at earlier stages of the rotations. According to the Ellenberg reactivity tolerances for indicator species there was more tolerance for acid soils in reforestation pre-thicket than afforestation pre-thicket, however, in later stages the differences in tolerances between rotations was not large. CSR values for ecological strategies were only available in pre-thicket and mature stages for both rotations as the other stages either had no indicator species or only had bryophyte ones. In afforestation pre-thicket sites most of the indicator species were intermediate between all ecological strategies such as the grass *Holcus lanatus* and the herb *Rumex acetosella* with all species following, at least to some extent, a competitive strategy. In reforestation pre-thicket most indicator species were intermediate between competitors and stress tolerators, there were no ruderals and again all species followed, at least to some extent, a competitive strategy. In the mature stages of both rotations all indicator species were stress-tolerant, either solely or in conjunction with another strategy and half of the indicator species were intermediate between the three strategies. In the afforestation pre-thicket stages eight of the thirteen indicator species were graminoids and in the reforestation pre-thicket stages two of the eight indicator species were heathers, *Calluna vulgaris* and *Ericia cinerea*.

Table 2.5. (next page) Percentage indicator values (IV) for significant indicator species in each structural group for both rotations (AFFOR afforestation and REFOR reforestation). Only species with a significant indicator value ($p \leq 0.05$) ≥ 25 are shown as values lower than this are not considered good indicators. Indicator species were not found for reforestation closed-maturing while reforestation thicket and afforestation closed-maturing had no species with an IV ≥ 25 . Mean $\pm$ s.e. of indicator species attributes for each stage also shown. AW, species affinity for woodlands (1 low, 2 moderate, 3 high) designated during this project. Ellenberg values are for light (L), soil moisture (F) and soil reactivity (R) according to Hill *et al.* (1999, 2007, 2004). L; 1, deep shade – 9, full light. F; 1, extreme dryness – 12, submerged. R; 1, extreme acidity - 9, basic. CSR ecological strategies (available for vascular plants) only are competitors (C), stress-tolerators (S), ruderals (R) or intermediates between any two or all three of these categories (1 – yes: 0 - no) according to Grime *et al.* (1988, 2007). Refer to **Section 2.3.3** for more detail on attribute classification.

Pre-thicket				Thicket		Re-opening				Mature			
AFFOR	IV	REFOR	IV	AFFOR	IV	AFFOR	IV	REFOR	IV	AFFOR	IV	REFOR	IV
<i>Holcus lanatus</i>	77	<i>Polytrichum communeae</i>	60	<i>Fissidens bryoides</i>	39	<i>Calypogeia fissidens</i>	25	<i>Dicranella heteromalla</i>	44	<i>Dryopteris dilitata</i>	48	<i>Oxalis acetosella</i>	41
<i>Festuca rubra</i>	75	<i>Camppylopus introflexus</i>	60	<i>Rhytidiadelphus squarosum</i>	28					<i>Campylopus flexuosus</i>	37	<i>Athyerium filix femina</i>	39
<i>Anthoxanthum odoratum</i>	58	<i>Calluna vulgaris</i>	58	<i>Brachythecium rutabulum</i>	27					<i>Atricum undulatum</i>	35	<i>Metzgeria temperata</i>	39
<i>Juncus acutiflora</i>	51	<i>Chamerion angustifolium</i>	58							<i>Teucrium scordonia</i>	35	<i>Blecnum spicant</i>	34
<i>Juncus effusus</i>	47	<i>Ericia cinerea</i>	45							<i>Digitalis purpurea</i>	35	<i>Carex sylvatica</i>	32
<i>Rumex acetosella</i>	45	<i>Salix cinerea</i>	44							<i>Carex pilulifera</i>	32	<i>Pseudotaxiphyllum elegans</i>	31
<i>Agrostis stolonifera</i>	43	<i>Rubus frutosis</i>	41							<i>Acer pseudoplatanus</i>	27		
<i>Calliergonella cuspidata</i>	36	<i>Polytrichastrum formosum</i>	36							<i>Hypnum cupressiforme</i>	26		
<i>Lotus pedunculatus</i>	35									<i>Mnium hornum</i>	25		
<i>Epilobium brunesscens</i>	33									<i>Luzula sylvatica</i>	25		
<i>Cirisium palustre</i>	32												
<i>Carex ovalis</i>	27												
<i>Dactylis glomerata</i>	27												
<u>Attributes</u>													
AW	1.46±0.14		2.0±0.27		2.0±0		2.0		3.0		2.2±0.25		3.0±0
Light	7.01±0.14		6.0±0.46		5.33±0.67		3.0		4.0		5.50±0.31		4.38±0.26
Moisture	6.62±0.33		5.88±0.35		5.67±0.33		7.0		6.0		5.20±0.25		5.88±0.23
Reactivity	5.38±0.33		3.75±0.67		5.33±0.33		3.0		3.0		4.20±0.57		4.63±0.42
Competitor	1.0±0		1.0±0		na		na		na		0.83±0.17		0.75±0.25
Stress tolerant	0.92±0.08		0.80±0.20		na		na		na		1.0±0		1±0
Ruderal	0.83±0.11		0		na		na		na		0.50±0.22		0.75±0.25

Figure 2.3 c)

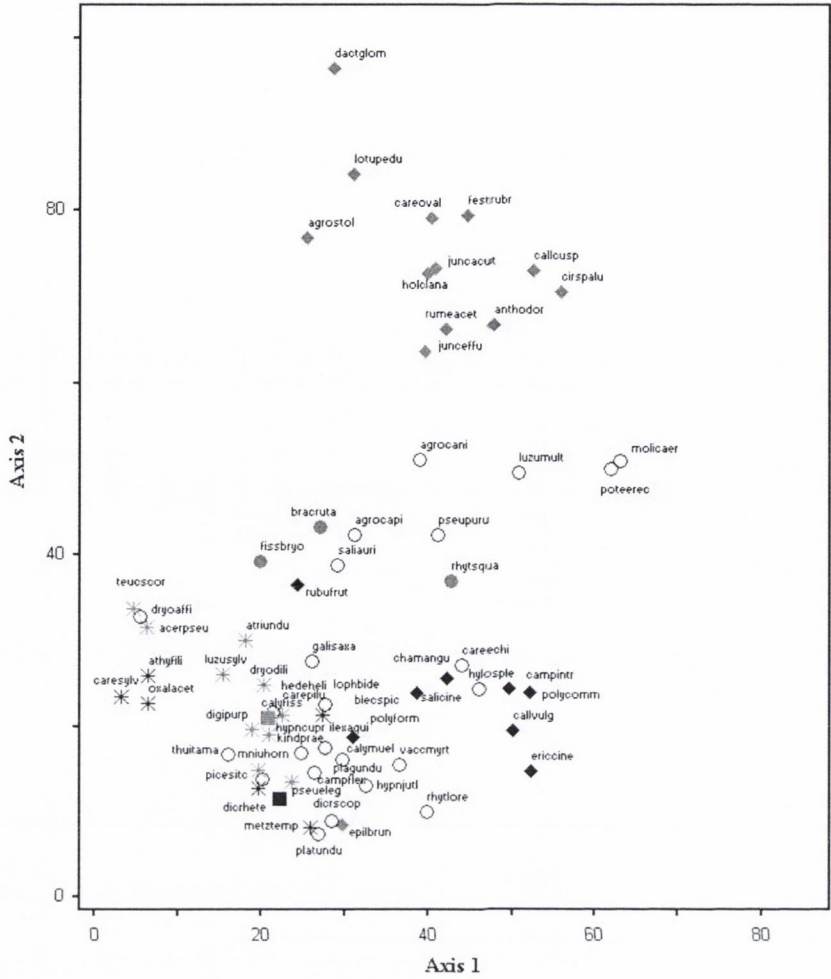


Figure 2.3 (inc. previous page) **a)** axes 3 and 2 **b)** axes 3 and 1 and **c)** axes 2 and 1 of the species plots for the varimax rotated NMS ordination of species composition and cover. Afforestation (grey symbols) and reforestation (black or open symbols) sites at different stages of the forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; * Mature; O common species in $\geq 25\%$ of plots. Cumulative variation in the data explained by the ordination is 75.9% with Axis 1 accounting for 11.9%, Axis 2 for 32.3% and Axis 3 for 31.7%. Final stress = 12.09 ($p=0.004$), Final instability = 0.00000. Species codes are first 4 letters of genus and first 4 letters of species name (refer to **Appendix 1** for details).

2.4.4 Drivers of diversity

Correlation analysis showed canopy cover was positively correlated highly with FWD-needle litter ($r_s = 0.822$, $p \leq 0.01$) and weakly with canopy height ($r_s = 0.390$, $p \leq 0.01$), DBH ($r_s = 0.308$, $p \leq 0.01$), age ($r_s = 0.339$, $p \leq 0.01$). Canopy cover was also highly

negatively correlated with structural diversity ($r_s = -0.620$, $p \leq 0.01$). Soil pH was weakly positively correlated with LOI ($r_s = 0.387$, $p \leq 0.01$), Ellenberg F ($r_s = 0.249$, $p \leq 0.01$) and Ellenberg N ($r_s = 0.383$, $p \leq 0.01$). Structural diversity was positively correlated ($p \leq 0.01$) with all vegetation structure covers. CWD volume was positively correlated ($p \leq 0.01$) with all other types and decay classes of deadwood (except sound and moderate snags). Distance to old woodland and area of old woodland within 1km were highly positively correlated with each other ($r_s = 0.821$, $p \leq 0.01$). Elevation and annual precipitation were moderately positively correlated with each other ($r_s = 0.485$, $p \leq 0.01$). The variables canopy cover, FWD- needle litter, canopy height, DBH, age, structural diversity, soil pH, LOI, Ellenberg F, Ellenberg N, structural diversity, CWD volume, distance to old woodland, area of old woodland within 1km, elevation and annual precipitation were tested for collinearity using VIF. When the VIF value for the group of variables was < 3 (Zuur et al., 2007) the global models were compiled using these variables. All global models contained the variables canopy cover, rotation, soil pH, log area of old woodland and the interactions ‘canopy cover x soil pH’ and ‘canopy cover x area of old woodland within 1km’. The global models for bryophyte SR and typical woodland bryophyte SR also contained CWD volume and the interaction of ‘canopy cover x CWD volume’. To reduce the influence of outliers, CWD volume was square root transformed and area of old woodland within 1km was log transformed.

Multimodel inference for the four species richness metrics (**Table 2.6**) showed canopy cover was of high relative importance across all model sets (R.I. = 1.00) while the ‘canopy cover x CWD volume’ interaction did not appear in any model set. Rotation was among the variables of high relative importance for vascular plant SR, but was less important for bryophyte SR and was of low importance for both typical woodland metrics. Soil pH was

of high relative importance for bryophyte SR, was less important for typical woodland bryophyte SR, and for both vascular metrics it was of low importance. Log area of old woodland within 1km was among the most important variables for both vascular SR metrics but was of relatively low importance for both bryophyte SR metrics. CWD volume was only important for the two bryophyte SR metrics but at a relatively low level. The averaged model parameters for the six bryophyte SR and the eleven typical woodland bryophyte SR models predicted higher SR in afforestation compared to reforestation and at sites with lower pH, higher CWD volumes and sites with smaller areas of old woodland within 1k. The averaged parameters for the three vascular SR models predicted higher vascular SR at lower canopy cover, in reforestation compared with afforestation and in areas with larger areas of old woodland within 1km. The averaged parameters for the three typical woodland vascular SR models predicted, as for vascular SR, higher SR at sites with larger areas of old woodland within 1km but differed from vascular SR models in predicting higher SR at more calcareous sites and higher SR in afforestation compared with reforestation.

Table 2.6. Akaike weights (ω_i) are a measure that the model i is the best model, given the data and set of candidate models. Model sets contain all models within 2 units of the lowest AICc (QAICc for vascular SR) for species richness of a) bryophytes, b) vascular plants c) typical woodland bryophytes and d) typical woodland vascular plants Every variable and interaction term in each model set is quantitatively ranked across all models in that set according to their relative importance (R.I.). Averaged Model Parameters (MP) are shown in terms of the directional association between the explanatory variable and the response averaged over each model set (“na” indicates the averaged model parameters are not interpretable as the variable had a non-linear association with the response i.e. smoother applied (Burnham and Anderson, 2002). Model number identifies the different models in a set.

a) Bryophyte SR								
Model number	1	2	3	4	5	6	R.I.	MP
Canopy cover	X	X	X	X	X	X	1.00	na
Soil pH	X	X	X	X			0.84	-ve
Rotation	X	X	X				0.75	-ve
Log area of old woodland			X		X		0.21	-ve
CWD volume		X					0.18	+ve
Akaike weights (ω_i)	0.44	0.18	0.13	0.09	0.08	0.07		

b) Vascular SR					
Model number	1	2	3	R.I.	M.P.
Canopy cover	X	X	X	1.00	-ve
Log area of old woodland	X	X	X	1.00	+ve
Rotation			X	1.00	+ve
Canopy cover x log area of old woodland		X		0.23	-ve
Soil pH	X	X	X	0.18	na
Akaike weights (ω_i)	0.60	0.23	0.18		

c) Typical woodland bryophyte SR													
Model number	1	2	3	4	5	6	7	8	9	10	11	R.I.	MP
Canopy cover	X	X	X	X	X	X	X	X	X	X	X	1.00	na
Soil pH	X			X	X	X				X		0.51	-ve
CWD volume			X	X					X	X	X	0.32	+ve
Rotation					X			X		X	X	0.20	-ve
Log area of old woodland						X	X		X			0.19	-ve
Akaike weights (ω_i)	0.24	0.17	0.11	0.09	0.08	0.07	0.07	0.06	0.05	0.04	0.03		

d) Typical woodland vascular SR					
Model number	1	2	3	R.I.	MP
Canopy cover	X	X	X	1.00	na
Log area of old woodland	X	X	X	1.00	+ve
Soil pH		X		0.20	+ve
Rotation			X	0.19	-ve
Akaike weights (ω_i)	0.62	0.20	0.19		

Burnham and Anderson (2002) advise against interpreting averaged model parameters if variable y is non linear with response x so in **Table 2.6** the directional relationship of the averaged model parameters with the responses, x were shown (+ve increase in y and increase in x ; -ve decrease in y and increase in x or *vice versa*). As the model parameters fitted with smoothers were not readily interpretable, as an aid to discerning the association between smoothed parameters (those non-linearly associated with response) and species metrics, best fit lines from polynomial regressions (order 4) were plotted (**Fig 2.3**). The scatter plots of both bryophyte SR (**Fig. 2.3 a**) and typical woodland bryophyte SR (**Fig. 2.3 b**) against canopy cover showed curvilinear relationships with relatively strong R^2 of 0.46 and 0.48 respectively. At low canopy covers (0~50%) there was a positive association between increasing canopy cover and both bryophyte SR metrics, but above a threshold of about 60% this association became negative. The scatter plot of typical woodland vascular SR against canopy cover (**Fig. 2.3 c**) showed a similar, but much weaker ($R^2 = 0.33$), relationship to that seen in the plots for both bryophyte SR metrics. From a linear regression applied to the vascular SR and canopy cover plot (result not shown) $R^2 = 0.51$. The higher R^2 for the regression between vascular SR and canopy cover indicated that canopy cover was a better predictor of this species metric than the other two bryophyte SR metrics and typical woodland vascular SR. The scatter plots for bryophyte SR and typical woodland bryophyte SR interestingly showed similar relationships with canopy cover although it may be expected that typical woodland plant species are more shade tolerant (Thomas and Packham, 2007, Hardtle et al., 2003). Investigation of the woodland affinity of the bryophytes recorded and their Ellenberg L values for adaptation to light revealed that the majority of bryophytes (55.68%) had intermediate affinity for woodland (high and low affinity 29.55% and 14.77% respectively). However, most of the bryophytes recorded were adapted to shade conditions (77.54% had Ellenberg L values of between 1 and 6) whereas those adapted to well lit places with values 7-9 were 24.0%). However, the scatter

plot of vascular SR against pH (**Fig. 2.3 d**) showed weak a non-linear association ($R^2 = 0.22$) and at low pH (<5.0) there was a slight positive association between increasing pH and vascular SR until above a threshold of about pH 5.0 this association became negative. Plots of vascular SR against area of old woodland conditional on differing levels of canopy cover (canopy cover levels of $< 50\%$, $50-65\%$ and $> 65\%$ - results not shown) did not help to further clarify the relationship of the interaction present in the model set.

Figure 2.3 a)

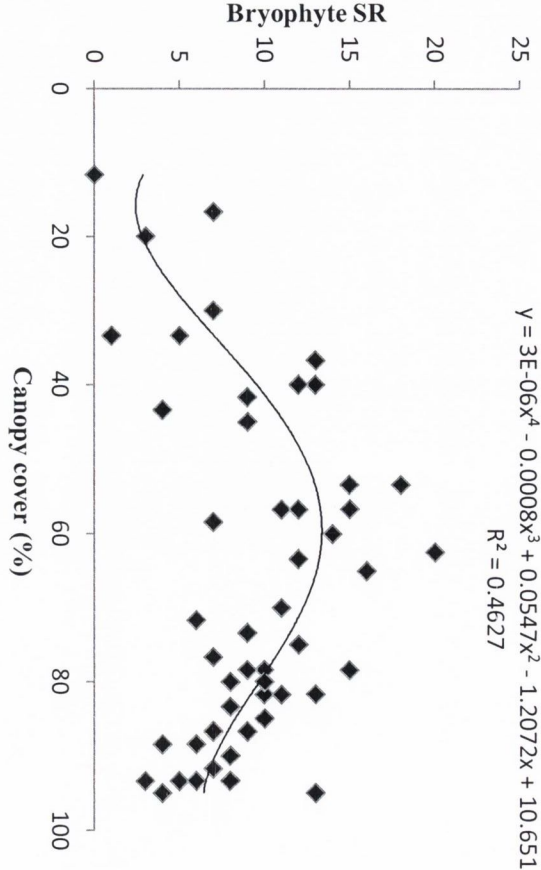


Figure 2.3 b)

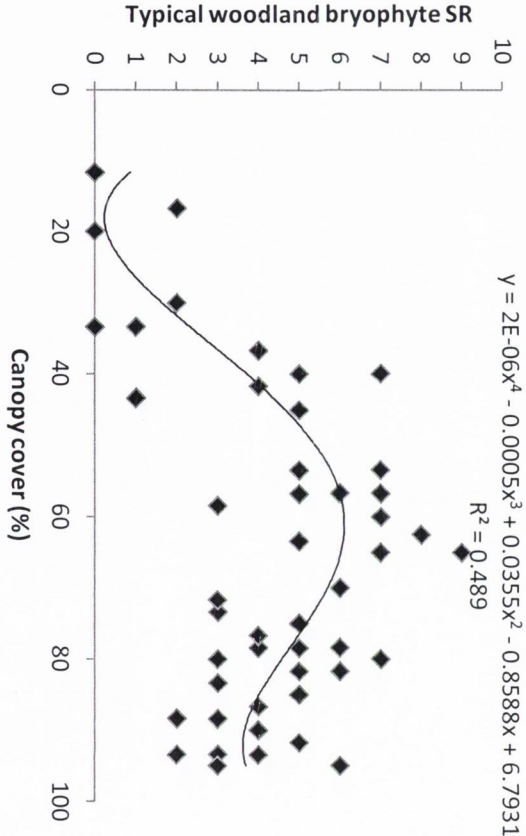


Figure 2.3 c)

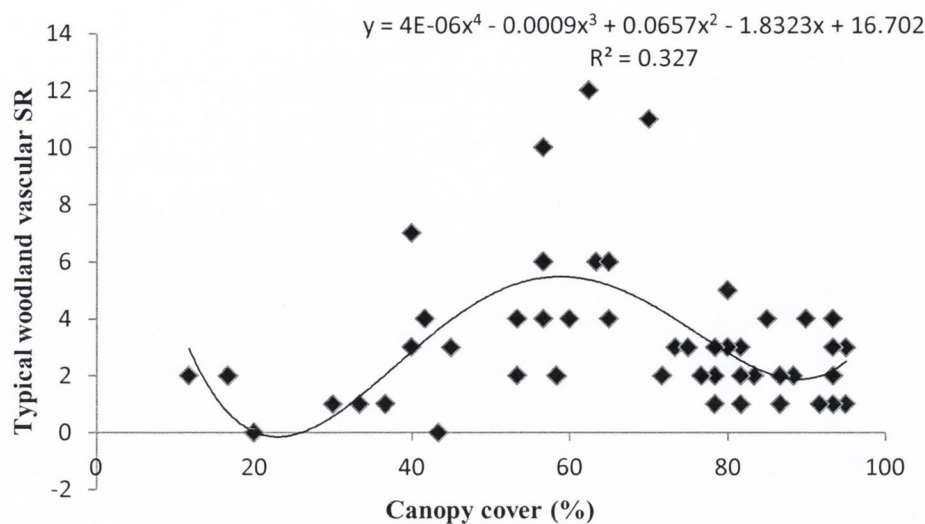


Figure 2.3 d)

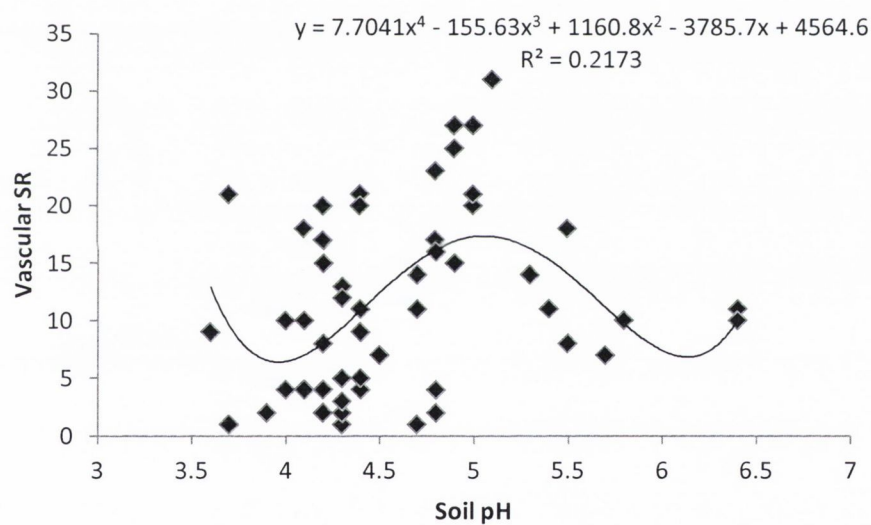


Figure 2.3. (this and previous page) **a)** Bryophyte SR versus canopy cover **b)** typical woodland bryophyte SR versus canopy cover **c)** typical woodland vascular SR versus canopy cover **d)** vascular SR versus soil pH (to aid interpretation the scale for soil pH only shows the range of values within which vascular SR was recorded).

2.5 Discussion

2.5.1 Comparison of ground vegetation diversity and composition over each rotational cycle and between afforestation and reforestation

Diversity was high during early pre-thicket stages, was at a minimum during the dense mid-rotation stages of closed-maturing and re-opening, but increased again after thinning (whether through natural die back or management) during the mature stage. This trend in total species richness agreed with previous work investigating the dynamics of ground vegetation diversity in plantations (Franklin, 1988, Hill, 1979, Hill, 1986, Humphrey et al., 2003, Williams et al., 1998, Kirby, 1988, Smith et al., 2005, Eycott et al., 2006, Fahy and Gormally, 1998, French et al., 2008). The afforestation chronosequence followed by the reforestation chronosequence can be considered a single continuum of plantation vegetation succession across two rotations. Some authors have predicted that ground vegetation diversity should continue to increase through these successive rotations (Peterken, 2001, Hill, 1979, Williams et al., 1998). The results of this current study, however, demonstrated no such increase. Both SR and species turnover results suggested that the development of ground vegetation diversity through the afforestation cycle was maintained in the reforestation cycle but it was not substantially enhanced. It appears that this may have been contributed to by the significantly higher canopy cover of the mature reforestation stage, compared with that of afforestation, restricting the development of a diverse ground vegetation (Eycott et al., 2006, Hill, 1986, Schoonmaker and McKee, 1988, Smith et al., 2005, Fahy and Gormally, 1998, French et al., 2008). Cooper *et al.* (2008) reported a decrease in typical woodland species richness in pre-thicket stages of Sitka spruce reforestation with increasing age (oldest sites were 11 years planted), and suggested that the ground vegetation diversity gains of afforestation were not sustained over even the early stages of reforestation. However, the results of this present research found the mature stage was the only significantly different stage over the reforestation cycle and that, over a

longer time scale, the diversity levels of afforestation were indeed maintained during reforestation.

Between rotations the significantly lower total SR and total typical woodland SR in pre-thicket reforestation compared with mature afforestation may reflect a loss of species numbers during the clearfell and replanting processes (Eycott et al., 2006, Cooper et al., 2008). This decrease in SR between rotations appeared to be due to a loss of bryophytes for total SR and, for total typical woodland SR, to loss of both typical woodland vascular plants and bryophytes. The lower light levels in mature afforestation may have favoured total bryophyte diversity over that of vascular plants and also favoured typical woodland species (Ferris et al., 2000, Schoonmaker and McKee, 1988, Hill, 1986, Fahy and Gormally, 1998, Marschall and Proctor, 2004). The relatively low species turnover ($\beta_{sim} = 0.35$) between mature afforestation and pre-thicket reforestation, and the ordination of these two stages close together, suggests that certain species may also be retained between rotations. One of the most important influences on vegetation succession in reforestation following clearfell is whether a species can establish before the canopy closes, either having persisted through the forest cycle vegetatively (perhaps in nearby refugia) and/or in the soil seed bank (Hill, 1986, Brunet and von Oheimb, 1998, Eycott et al., 2006, Ferris and Simmons, 2000, Humphrey et al., 2003, Williams et al., 1998). Importantly the retention, or indeed loss, of species between rotations could not, however, be quantitatively verified during this present research on a site by site basis as different afforestation and reforestation sites were studied rather than following individual sites through the two forest cycles with long-term monitoring. For example, by influencing the suite of species in soil seed bank or in refugia in surroundings, the previous land use of the sites before afforestation e.g. whether they were old woodland or open heath habitat, may have an

influence on species diversity (Cooper et al., 2008, Peterken, 1993, Williams et al., 1998, Bremer and Farley, 2010, French et al., 2008). In this study data collated on this was not definitive enough (i.e. previous land use for 39% of afforestation sites was unknown) to draw conclusions from.

Total SR was significantly higher in mature than pre-thicket in afforestation but not in reforestation. A possible cause of this difference in rotations was that canopy cover was significantly higher in mature of reforestation than afforestation. Total SR was higher in afforestation than reforestation in all stages (except pre-thicket) but the only significant difference in total SR between rotations was between the closed-maturing stages. Between these stages it was bryophyte, not vascular, SR that was significantly higher. Canopy cover was not significantly different between these stages but perhaps the afforestation sites had more penetration of light from the sides thus allowing sufficient light for bryophyte development. Factors influencing the higher total SR of pre-thicket in reforestation compared with afforestation (non significant) could include species being retained from the previous rotation either in remnants or seed bank (Hill, 1986, Brunet and von Oheimb, 1998, Eycott et al., 2006, Ferris and Simmons, 2000, Humphrey et al., 2003, Williams et al., 1998), ground disturbance during clearfell and replanting offering germination sites (Eycott et al., 2006, Williams et al., 1998) and the possible positive influence of large complex brash piles providing additional habitat observed during this research.

A theory of vegetation development over successive rotations established on peatland and heath developed by Hill (1979) and later extended by Peterken (2001) proposed that vegetation will shift from species of the original open habitat to species typical of woodland over each rotation and increasingly so over successive rotations. As the majority

of study sites in this present research with known previous land use were formerly rough grazing or unimproved grassland this model seems appropriate. This research found in agreement with this theory that there was a significant increase in typical woodland SR over each forest cycle, however, contrary to the theory there was no increase in typical woodland diversity over the two successive rotations. Indeed modelling showed that rotation, although important for all SR metrics, was relatively less important for typical woodland SR when compared with total SR metrics. Modelling predicted higher typical woodland SR in afforestation than reforestation, and for several stages this was the trend (**Table 2.2**). Development of a typical woodland vegetation is considered to be mainly a function of stand age (increasing time for woodland species, that are often slow colonizers, to disperse to a site and establish (Hill, 1979, Peterken, 1993, Cooper et al., 2008, Verheyen and Hermy, 2001)) and site history (whether the stand was established on a site sufficiently close to semi-natural woodland for woodland species to colonise, or indeed, on a site that was itself previously semi-natural woodland (Peterken and Game, 1984, Brunet and von Oheimb, 1998, Humphrey et al., 2003, Verheyen et al., 2003, Ferris and Simmons, 2000)). In this current research, stand age was not modelled directly as it was correlated with canopy cover; site history was modelled with the variable area of old woodland within 1km (highly positively correlated with distance to old woodland) and this variable was taken as an indication of the source of propagules for woodland species (they can remain viable in seed banks for long periods of time (Ferris and Simmons, 2000, Williams et al., 1998)). Area of old woodland within 1km was found to be relatively more important for both vascular SR metrics than the two bryophyte SR metrics. This concurs with the findings of Smith *et al.* (2005) who reported the typical woodland vascular SR of plantations was significantly positively correlated with log area of old woodland within 1km and the relationship with typical woodland bryophyte SR was positive but non-significant. Most bryophyte spores are wind dispersed resulting in many species being

spatially aggregated, whereas vascular seeds can have animal/insect facilitated dispersal mechanisms over wider areas (Vanderpoorten and Goffinet, 2009). The greater influence of area of old woodland on typical woodland vascular plants compared with typical woodland bryophytes may be due to the more restricted dispersal range of bryophytes. It would appear that vegetation with restricted dispersal capabilities would benefit from a higher area of old woodland around a site, however, it seems that typical woodland bryophytes are so restricted that they do not disperse from a given area of woodland to surrounding new forest as efficiently as typical woodland vascular plants. The interaction of canopy cover with area of old woodland was in the model set for vascular SR at a low relative importance. This could indicate that no matter how near or large the area of old woodland in the surroundings, a high canopy cover could reduce its potential positive influence on vascular SR. There was a significantly higher typical woodland SR in pre-thicket reforestation compared to afforestation, and it appears that this may reflect the retention of certain woodland species accumulated over the preceding rotation (Hill, 1986, Brunet and von Oheimb, 1998, Eycott et al., 2006, Ferris and Simmons, 2000, Humphrey et al., 2003, Williams et al., 1998) and/or differences in previous land use between the pre-thicket sites of each rotation. However, as outlined above, these hypotheses could not be adequately investigated without studying individual sites through the two forest cycles with long-term monitoring. The influence of site history on the development of a typical woodland vegetation was supported by the fact that a 'notable' woodland species of Perrin *et al.* (2008) (also on the Irish Flora Protection Order (Anon, 1999)) occurred in a mature plantation that was previously old woodland and was adjacent to existing woodland at time of survey.

A change in species composition over the two successive rotations was illustrated in both the ordination, with a large separation between pre-thicket afforestation and mature reforestation sites, and in the highest inter-rotational turnover ($\beta_{sim} = 0.55$) being between these two stages. The ordination showed there was a higher variability among pre-thicket afforestation sites as they had a wider spread in the ordination space. This may reflect the different starting conditions for each rotation; for afforestation pre-plantation habitats can vary from, for example, peatland to improved grassland whereas land use directly prior to reforestation was, by definition, plantation. That most of the afforestation sites were relatively well separated out in the ordination (except for mature which ordinate closely with reforestation sites) illustrated that large changes in vegetation communities occurred over the afforestation cycle and by the reforestation cycle the communities were more established and did not change as much. Despite each rotation having very different starting points there was clear floristic convergence between both rotations as they mature, as indicated by the mature stages of both rotations ordinating relatively close in space and the lower species turnover between rotations in the later stages compared to earlier stages (**Table 2.4**). Results, both from the significant high correlations between NMS axis scores and measured variables and from the MMI model sets, indicated that this floristic convergence was driven by similarities in the variables influencing species diversity especially canopy cover, area of old woodland, soil pH and CWD volume. A difference in the community dynamics of the two rotations was evident from the ordination, as the reforestation sites were clustered in ordination space relative to the spread of afforestation sites. This was also evident in the significantly higher species turnover (β_{sim}) for several afforestation stages compared with reforestation. We proposed that these differences may again reflect the differing site conditions at the start of each rotation.

Examination of indicator species and their attributes in the different stages highlighted several interesting relationships between indicator species, site conditions, rotation and structural stage. The presence of relatively high numbers of indicator species in both the pre-thicket and mature stands suggests a more specialised vegetation community in these stages across both rotations. The indicator species attributes of the structural stages in not only suggested the type of specialist communities that had developed but also showed how the communities had changed as the plantations matured. The more specialised vegetation across both rotations appeared to be bogs that were grass or heather dominated in pre-thicket stages and woodland vegetation dominated in mature stages. It could be that the very high proportion (61.54%) of graminoid indicator species in afforestation pre-thicket compared to the relatively high proportion (25%) of heather indicator species in reforestation pre-thicket could indicate succession over the two rotations from a grass dominated open habitat of, for instance, bog to a small woody shrub dominated habitat such as heath. However, as the sites were in a chronosequence and not the actual same site in each rotation this proposal could not be definitively investigated.

There was no indicator species identified for reforestation closed-maturing possibly as there were only a few plots in that stage that had any one species cover above 0.5 %. (Those species that occurred at over 0.5 % in a few of the plots were the mosses *Hypnum jutlandicum*, *Thuidium tamariscinum*, *Rhytidiadelphus loreus* and *Kindbergia praelonga*). There was only one indicator species each for afforestation and reforestation re-opening with an IV > 25. These low numbers of indicator species suggested a generalist flora with high dissimilarity between the stands in those stages.

For both rotations the majority of indicator species in earlier stages had low affinity for woodland and their light requirements, according to their Ellenberg L values, were for well lit habitats, whereas in the later stages high woodland affinity indicator species that thrive in shade increased and in the reforestation mature stage all indicator species had high affinity for woodland. It was not surprising that the indicator species adapted to the lowest light levels were in the closed-maturing stages which also had, on average, the highest canopy covers (afforestation $86.2 \pm \text{s.e. } 2.4$ and reforestation $90.0 \pm \text{s.e. } 3.0$).

It may be expected that there would be increased soil drainage in the reforestation sites compared to afforestation sites due to ground preparation carried out for the afforestation rotation, for example, the creation of drainage channels (Williams et al., 1998, Iremonger et al., 2007). This was indicated in the slightly lower Ellenberg moisture values indicating adaption for drier soils by indicator species in reforestation when compared with afforestation, especially at earlier stages of the rotations. However, Ellenberg F values ranged from, on average, 5 (moist) to 7 (damp but not wet) and so no large difference in soil drainage between rotations was evident from the indicator species attributes. Again it may be expected that soil pH would be lower in reforestation sites due to acidification of the soil by conifer needle litter over successive rotations (Williams et al., 1998). According to the Ellenberg reactivity values for indicator species there was, indeed, more tolerance for acid soils in reforestation pre-thicket than afforestation pre-thicket, however, there were either zero to negligible differences in tolerances between rotations in later stages. Soil pH values were significantly higher in the two earlier stages of afforestation compared with reforestation but there was no difference between any of the later stages and although there was lower pH in the later stages of afforestation over the stages of the reforestation cycle there was no significant change in soil pH. These results suggest that differences in soil reactivity indicated by Ellenberg R and in soil pH between the early stages of the two

rotations may be due to pre-plantation site conditions rather than acidification of soil by conifers over successive rotations.

The changes in CSR ecological strategies of the indicator species indicated a shift in environmental pressures between structural stages and rotations. Grime *et al.* (1988, 2007) detailed the habitats that vascular plants with the different strategies may occupy and this is outlined below. Generally, both competitors and stress-tolerators can exploit habitats where disturbance is rare, however, competitors may be found in habitats where resources are abundant, while stress-tolerators are found in habitats where resources are scarce and/or conditions are harsh. Ruderals are often found in habitats where disturbance is common and resources are plentiful; they are often weeds which have high demands for nutrients and/or are intolerant of competition. In this research, the presence of indicator species intermediate between C and S and the absence of those with R strategy suggested that reforestation pre-thicket was less disturbed than afforestation pre-thicket and there was more competition for poorer resources. That the pre-thicket reforestation sites were not as disturbed may be due to the lesser change in habitat between successive rotations as opposed to the often drastic habitat change between pre-afforestation and afforestation (Eycott *et al.*, 2006, Williams *et al.*, 1998). The majority of indicator species in both rotations pre-thicket stages were competitive whereas in mature stages they were stress tolerant. Availability of light is well recognised as an important factor effecting vegetation community development (Eycott *et al.*, 2006, Hill, 1986, Schoonmaker and McKee, 1988, Smith *et al.*, 2005, Carnus *et al.*, 2006) and in the open habitats of pre-thicket light was not limited so the vegetation was generally competitive, whereas in mature stages with high canopy cover, light was limited and so stress tolerant species were better represented.

2.5.2 Drivers of diversity

Canopy cover was identified by modelling as being of high relative importance for all species richness metrics. For vascular SR the association was negative, agreeing with previous research in plantations (Eycott et al., 2006, Hill, 1986, Schoonmaker and McKee, 1988, Smith et al., 2005, Carnus et al., 2006, French et al., 2008). For both bryophyte metrics and typical woodland vascular SR the association was non-linear: positive at low canopy covers while above about 60% cover the association became negative. Canopy cover was best at predicting, in order of accuracy vascular SR, both bryophyte species metrics and lastly typical woodland vascular SR. Typical woodland species are, in general, adapted to the differing light levels in forests (Thomas and Packham, 2007, Hardtle et al., 2003) e.g. seasonal changes in canopy cover of deciduous trees and canopy gaps. Bryophytes are generally shade adapted as they make trade-offs between getting sufficient light to photosynthesise while not being exposed to excess light that may cause desiccation and, at extremes, cellular damage (Marschall and Proctor, 2004, Vanderpoorten and Goffinet, 2009). These adaptations may confer a competitive advantage to bryophytes and typical woodland species in shady conditions (French et al., 2008, Humphrey et al., 2002a, Ferris et al., 2000, Hill, 1986). However, even for shade adapted species, there are light levels below which they are unable to survive (French et al., 2008, Hill, 1979). The scatter plots for bryophyte SR and typical woodland bryophyte SR interestingly showed similar relationships for both metrics with canopy cover. Investigation of the woodland affinity of the bryophytes recorded and their Ellenberg L values for adaptation to light revealed that the similar associations seen in these scatter plots may have been a function of the data set reflecting a high tolerance for shade rather than a high affinity for woodland.

Previous research has shown that litter in conifer stands can negatively affect ground vegetation diversity (De Vries, 1995, Eycott et al., 2006, French, 2005). In this research canopy cover and FWD-needle cover were highly positively correlated and it is difficult to separate out the impacts of each factor individually; where canopy cover is high, needle litter is also high and less rain can penetrate through the canopy and needle litter cover (Hill, 1979). However, it is likely that the low species richness during the closed-maturing stages is most likely a result of the high canopy cover retarding ground vegetation development through the attenuation of light and rainfall, than the smothering and acidifying effects of FWD-needle cover. Canopy cover and structural diversity were highly negatively correlated, precluding the inclusion of structural diversity in the models. However, the positive correlations between structural diversity and SR metrics agree with previous findings of Peterken and Game (1984) and Munro (2009) in suggesting that structural diversity can be used in the field as an indicator for species richness and typical woodland species richness of bryophytes and vascular plants across both rotations.

Modelling parameters showed that increasing soil pH was a relatively important negative influence on bryophyte SR and, to a lesser extent, on vascular plant SR with a scatter plot showing a positive association at low pH (<5.0) but above a threshold of about pH 5.0 this association was weakly negative. Previous research in plantations has reported varying relationships between soil pH and species richness of the different ground vegetation types. Eycott *et al.* (2006) found in plantations of *Pinus sylvestris* (Scots pine) and *Pinus nigra* (Corsican pine) that pH was positively associated with higher annual vascular plant richness but negatively with bryophytes (and trees and shrubs). A positive association between pH and diversity has been reported in plantations on ancient woodland (Kirby, 1988) and in Scots pine woods (Roche et al., 2009). Ferris and Simmons (2000) reported

pH to be strongly negatively correlated with vascular SR. Ferris *et al.* (2000) found total SR was negatively (non-significantly) associated with increasing pH in Sitka spruce, Scots pine, Corsican pine and *Picea abies* (Norway spruce) plantations. Smith *et al.* (2005) reported significant negative correlations between pH and total and bryophyte SR and a non-significant correlation with vascular SR in afforestation Sitka spruce. In agreement with the previous findings for bryophyte SR of Eycott *et al.* (2006) and Smith *et al.* (2005) our modelling results showed it was associated with pH and of high relative importance (as was typical woodland bryophyte metric). Modelling also found typical woodland vascular SR was positively associated with soil pH but of low relative importance. The differing relationship of soil pH with the species richness metrics may be due to the influence soil pH has on vegetation nutrient uptake of, for example, nitrogen (Ferris *et al.*, 2000, Hardtle *et al.*, 2003, Wilson *et al.*, 2001) with many species being adapted to a certain range of soil pH and nutrient status (Grime *et al.*, 2007, Ellenberg, 1974, Hill *et al.*, 2007, Hill *et al.*, 2004).

As expected, CWD volume was higher in every stage of reforestation compared to afforestation, significantly so in the first 3 stages, due to deadwood being left on site after clearfell and stumps from the sites previous rotation remaining *in situ*. The lack of differences in the two last stages could be due to the previous rotations stumps being almost completely decayed, thus lowering the measureable CWD in reforestation.

Investigations into the potential value of conifer plantations for bryophyte diversity have focused on the value of deadwood as a habitat for bryophytes (Humphrey and Peace, 2003, Smith *et al.*, 2005). In this research the averaged model sets for both bryophyte SR metrics showed CWD volume, although low in relative importance, was positively associated with them, in agreement with previous research in plantations (Hodge and Peterken, 1998, Humphrey *et al.*, 2002a, Humphrey and Peace, 2003, Humphrey *et al.*, 2002c, Ferris *et al.*,

2000, French et al., 2008). Deadwood volumes were low in this study's sites when compared to those expected in unmanaged forests (Sweeney et al., 2010b, Kirby, 1998) and this may have contributed to the relatively low importance of CWD volume to bryophyte SR. The measure of CWD volume was chosen for modelling as it was significantly highly correlated with the majority of other deadwood measurements but it does not take into account the type of deadwood, its size or state of decay which have all been found to be important to bryophyte diversity (Humphrey et al., 2002a). CWD volume was found to be of relatively higher importance to typical woodland bryophyte SR compared with bryophyte SR and we propose this may be indicative of a convergence of specialization i.e. typical woodland bryophytes are perhaps also more likely to be adapted to exploiting deadwood. Although there was significantly higher CWD volume in the closed-maturing stages of reforestation compared with afforestation, there was significantly lower bryophyte SR, suggesting perhaps an interaction between canopy and deadwood in their impact on bryophyte SR e.g. no matter how much deadwood is available if the light environment is not favourable than this habitat will not be exploited to its fullest by the bryophyte community. However, the MMI results predicted that this proposed interaction is not important relative to the other variables.

2.5.3 Management implications

Although soil pH was in the set of models for all species richness metrics it is a difficult factor to manipulate in forest management but there is more scope for manipulating forest structure and deadwood to enhance diversity over successive rotations. Manipulating forest structure by thinning although usually undertaken to increase the size of the remaining trees (Booth et al., 2007), can also promote ground vegetation development by increasing

light availability and altering moisture and temperature conditions which in turn stimulate soil fauna productivity, decomposition processes and increases nutrient availability (French et al., 2008, Humphrey, 2004, Smith et al., 2005, Williams et al., 1998). The disturbance of the ground during thinning operations can also open up additional germination sites. The negative impact of canopy cover on species diversity found in this research supports thinning as a practical management tool to enhance ground vegetation diversity. Thinning is usually carried out on a 3 or 5 year cycle depending on growth rate, with three to four thinnings taking place over the forest cycle (Anon, 2002). Line thinning (e.g. 1 row of trees in 7 removed) is typically followed by selective thinning (removal of dead, suppressed or poorly formed trees). The recommended age for first thinning for normal production conifer sites in Ireland is nineteen years or a top height of 12 m, although it is acknowledged that canopy closure (indicated by branches dead up to 2m and suppression of ground vegetation) occurs at 7-9 m (Booth et al., 2007) so thinning is presently recommended *after* the canopy is expected to close. One reforestation site and several afforestation sites had been thinned 2 years prior to survey, yet structurally they were classified in this research as closed-maturing stages, suggesting thinning was not significant enough to prevent canopy closure. Management policy for earlier and more vigorous thinning to prevent canopy closure should be implemented where appropriate. However, caution should be applied in areas with high winds and shallow soils, as thinning can significantly increase the risk of windthrow in these areas (Dhubhain et al., 2001, Joyce and O'Carroll, 2002, Mason et al., 2005, Mason and Kerr, 2001). In order to maintain the biodiversity gains of afforestation over successive rotations, canopy cover needs to be maintained below a certain level and from this research indications are that level is below 60% (Cooper et al., 2008).

Another management method to mitigate the negative impacts on ground vegetation diversity of high canopy cover is strategic planning for a spatial diversity of structural stages at the plantation scale (French et al., 2008, Humphrey et al., 2003, Smith et al., 2005). In this research the pre-thicket stages of afforestation had a distinctive community not found in the rest of forest cycle i.e. heath and grassland species. There is an awareness of the damage that conifer planting can cause to open-ground and wetland communities such as heath and peatlands (Peterken, 2001, Hill and Jones, 1978, Wallace and Good, 1995). The conservation of early successional species of these open habitats should be encouraged especially in areas where a plantation is unlikely to recruit a well developed woodland vegetation (no seed source in surroundings) and the pre-afforestation habitats were not woodland but perhaps heath or bog (Eycott et al., 2006, French et al., 2008). To balance timber production with the conservation of these early successional species planning for patches of open areas in plantations could be undertaken. Previous work by Smith *et al.* (2007) has suggested that to support well-developed open space habitat in mature spruce plantations, rides and roads should be a minimum of 15m in width and, depending on local conditions, glade areas of 625-900m² should be sufficient to have at least part of the glade well-lit. Planning for a diversity of structural stages should increase representation of the pre-thicket stage at the plantation scale, mitigate the negative impact of closed canopies on ground vegetation diversity, retain areas that may act as sources for (re)colonisation of (woodland) vegetation and lessen the negative visual landscape impacts of even aged, abruptly edged plantations (French et al., 2008, Peterken, 2001, Williams et al., 1998).

The importance of CWD volume to bryophyte species richness highlights the importance of strategic planning to enhance ground vegetation diversity in plantations i.e. an adequate

continuity of deadwood as a habitat resource is required so that there is no local loss of species dependent on deadwood (Humphrey et al., 2002c, Riffell et al., 2011). Current Irish forestry guidelines (Forest Service, 2000b) advise that some deadwood should be left *in situ* after thinning and harvesting, with minimum volumes given for CWD. According to Booth *et al.* (2007) deadwood is usually left on site after felling but occasionally some of the CWD may be removed for domestic use; however, thinning residues are rarely left on site and instead are removed for sale. As Sweeney *et al.* (2010b) report, there is a lack of large diameter logs and snags in Irish plantations so there is a potential for management to increase the availability of this resource by leaving as much deadwood on site as possible, after both felling and thinning. However, it should be noted that if there is infection by fungal pathogens e.g. *Heterobasidion annosum*, at a clearfell site, and if control methods (Pratt and Redfern, 2001) are not successful, the removal of deadwood after clearfell may be required in order to protect the health of future forests in that area, as recommended by Eycott *et al.* (2006). The removal of wood residues after clearfell for use as a commercial fuel is common in Sweden and other Scandinavian countries. In Ireland, this practice is gaining support as a contribution to meeting government targets for renewable energy (Hoyne and Thomas, 2001, Whelan, 2010) highlighting the potential for conflict among forestry management policies that focus on different outcomes.

The retention of stands beyond commercial maturity has previously been recommended to conserve and enhance ground vegetation biodiversity in plantations especially in areas that are exhibiting the potential to develop, or indeed have developed, vegetation of conservation interest (Humphrey et al., 2003, Peterken et al., 1992, Humphrey, 2005, Kerr, 1999). Retention beyond maturity can increase light, nutrients, etc. and consequently increase diversity (Williams et al., 1998). This research lends some support to this

recommendation as it was found that typical woodland species richness increased significantly in the later stages of the forest cycle in both rotations.

The apparent loss of species richness between rotations may have been due to the negative impacts of clearfell management. The negative impacts of clearfell management on ground vegetation include a reduction in light at the forest floor during the closed canopy stage of plantation, periodic disturbance during thinning and intensive disturbance during the clearfelling and replanting phases (Eycott et al., 2006). The implementation of continuous cover forestry (CCF), where structural diversity in forests is promoted by staggering the felling of stands (Farmer and Nisbet, 2004, Malcolm et al., 2001, Mason and Kerr, 2001), would mitigate these negative impacts (Moola and Vasseur, 2004, Cooper et al., 2008). However, CCF is at present not widely implemented in countries such as Ireland and Britain possibly due to the relatively high risk of windthrow (Mason and Kerr, 2004, Mason et al., 2005, Ní Dhubháin et al., 2010). Consequently there is a lack of information regarding how CCF might affect ground vegetation in comparison to plantations managed by clearfell (Mason et al., 2005). We support previous recommendations, especially where CCF is not possible or practical, that the negative impacts of clearfell on ground vegetation may also be mitigated by leaving uncut areas where appropriate (shelterwood systems), and prioritizing areas containing species that are sensitive to harvesting and of conservation interest (Hannerz and Hånell, 1997, Eycott et al., 2006, French et al., 2008, Humphrey, 2005, Cooper et al., 2008, Fahy and Gormally, 1998). On sites that already have typical woodland species the continuity of more open-canopy tree crops (such as pine and larch in comparison to Sitka spruce (Lagergren and Lindroth, 2002, Morén et al., 2000) and planting broadleaf trees may be suitable and is called the “crop continuity” model by Cooper et al. (2008). Conversion by ‘gradual replacement’ (Pryor et al., 2002) to

semi-natural woodland, especially of those stands that have vegetation of conservation interest, could also be considered.

2.6 Conclusions

2.6.1 Implications for forestry policy and practice

In general, methods of management for enhancing ground vegetation diversity in afforestation are applicable to reforestation plantations also. Research on the ecological effects of afforestation in an area can be informative in planning its reforestation. Diversity indicators identified for both rotations by modelling were canopy cover, rotational stage, area of old woodland within 1km and soil pH. Also for vascular diversity there was an interaction between canopy cover and area of old woodland and, for bryophytes between canopy cover and coarse woody debris volume. The most suitable management for an area will be influenced by sustainable forest management goals and the environmental conditions. The results presented here suggest that there is scope for the planning and management of plantations so that they support more woodland species: thinning should occur earlier and more regularly preventing canopy closure and deadwood should be retained after thinning and felling. These findings are applicable to plantation forests in other countries with similar clearfell forest management practices.

3 Does the addition of a native conifer or broadleaved species to a non-native conifer plantation enhance ground vegetation diversity?

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Does the addition of a native conifer or broadleaved species to a non-native conifer plantation enhance ground vegetation diversity? Forest Ecology and Management.

3.1 Abstract

Forestry plantations have potential to enhance biodiversity and Sustainable Forest Management (SFM) promotes the enhancement and conservation of this biodiversity. There is a general acceptance that mixed species plantations support more species than monocultures, especially mixes containing native species. In this paper we present results from the first Irish study on ground vegetation diversity in intimate mixed plantations and compare them with monocultures. In sites located throughout the island of Ireland, we investigated ground vegetation diversity in terms of species richness and the community composition of the non-native conifer Norway spruce (*Picea abies*) mixed with a native conifer, Scots pine (*Pinus sylvestris*), and with a native broadleaf, oak (*Quercus petraea*), and compared these with pure Norway spruce stands. Several factors other than tree crop species were found to be important for ground vegetation diversity; canopy openness, planted tree density, distance to edge of plantation, area of semi-natural woods between 200m to 1km of sites and forest type. Not only is there scope for management to improve diversity by manipulating these factors, but they can also be used to both assess the effect of management in relation to SFM and as indicators of diversity. Differences in ground vegetation species richness between mixed and pure forest types were not statistically

significant. There was a general trend that pure Norway spruce and Norway spruce/Scots pine mixes had similar diversity and were both more diverse than the Norway spruce/oak mixes (except for the trend of higher non-vascular SR in the Norway spruce/oak mixes). Both the Norway spruce/Scots pine mix and Norway spruce/oak mix supported subsets of the pure Norway spruce communities. Factors found to be driving the differences in ground vegetation communities were gradients in soil variables, elevation, age, stand structural measurements and landscape variables at the 1km scale. Management implications for mixed plantations from this research include the recommendation to plant species that are ecologically compatible (those with, for example, similar initial growth rates) in an arrangement conducive to the growth of the secondary species and to undertake management to ensure the secondary species thrives (for example, thinning of the main species). We conclude that it may be preferable, from both an ecological and an economic perspective, to plant the secondary species at a larger scale in non-intimate stands adjacent to the main species rather than in an intimate configuration. Ecologically non-intimate mixed stands may increase diversity as well as or even higher than intimate mixed stands and from an economic perspective they may require less intensive management.

3.2 Introduction

With appropriate planning and management, forestry plantations have the potential to add to the landscape quality and local biodiversity of an area, especially in intensively managed regions (Forest Service, 2000b, Humphrey et al., 2001, 2002b, 2003, Humphrey, 2004, Stephens and Wagner, 2007, Bremer and Farley, 2010, Iremonger et al., 2007).

Sustainable Forest Management (SFM) incorporates the social, environmental and financial aspects of forest management in a holistic manner (Farmer and Nisbet, 2004, McAree, 2002, UNEP, 1992) and forms a major goal of forestry policy in many countries

(Forest Service, 2000b, Forestry Commission, 1998, Christensen and Emborg, 1996, MCPFE Liaison Unit Warsaw, 2007). The conservation and enhancement of biodiversity is a core component of SFM. Ground vegetation is an important element of forest biodiversity and it plays a role in ecosystem functioning e.g. by providing food and/or habitat to insects (Humphrey et al., 1999), mammals (Carey and Harrington, 2001) and birds (Sweeney et al., 2010a). Various factors have an influence on ground vegetation diversity and some may be suitable for use as indicators, thus providing a basis for assessing forest conditions and compliance with SFM policy (Lindenmayer et al., 2000).

Natural forests usually consist of two or more tree species (Rackham, 1992) and the planting of more than one tree species in plantations as a means to enhance diversity is therefore not only intuitive but is supported by research (French et al., 2008, Ferris and Simmons, 2000, Kirby, 1988, Saetre et al., 1997, Smith et al., 2005) and also may be encouraged by policy. Under current Irish forestry policy all new plantings are required to contain a minimum of 20% 'diverse conifers' (which in Ireland are conifers other than Sitka spruce (*Picea sitchensis*) and Lodgepole pine (*Pinus contorta*)) and, where site conditions permit, a minimum of 10 % broadleaves (McAree, 2002, Forest Service, 2000c). Broadleaves and less vigorous conifers often perform poorly when planted on marginal soils with competitive conifers such as Sitka spruce (Iremonger et al., 2007). The planting of more lowland agricultural areas in Ireland which, being more fertile, are suitable for a greater range of tree species than upland areas (Teagasc: Irish Agriculture and Food Development authority, 2005) means the planting of mixed plantations is likely to increase. The 'spatial mix' of species within plantations has important consequences for both biodiversity and plantation productivity (Ferris and Simmons, 2000, Smith et al., 2005). There are generally three types of mixed plantations as follows. The 'non-intimate'

has the secondary species planted in patches within, or adjacent to areas of the main species. The ‘intimate’ mix arrangement is where the secondary species is dispersed as single stems throughout the crop. Tree species that are ecologically compatible e.g. those with similar early growth rates are suitable for planting in intimate mixes (Kerr et al., 1992). Alternating rows of secondary and main tree species are also planted (Kirby, 1988, Ferris and Simmons, 2000). The non-intimate mix has been promoted as the configuration for future plantings in Ireland as it has previously been found effective in diversity enhancement (Forest Service, 2000b, Forest Service, 2000a, Smith et al., 2005).

3.2.1 Why plant mixes?

A number of potential benefits for the forestry industry in planting mixes have been identified. Improved plantation productivity due to higher growth performances have been reported in mixed stands (Kerr et al., 1992). Greater pest and disease resistance as a result of diverse species has also been reported (Hartley, 2002) as well as the protection of the main crop species from, for example, frost by some ‘nurse’ mix species (Hartley, 2002). Mixed species plantations also provide a balance of environmental and economic environmental and economic goals by ameliorating some possible negative effects of single species plantations (monocultures) on biodiversity (Forest Service, 2000b, McAree, 2002, Anon., 1996). Mixed species plantations can contribute to the implementation of SFM as follows. Using a mixture of species increases structural complexity, thereby creating a wider range of ecological conditions and available niches for species to colonise (Simmons and Buckley, 1992). Mixed species plantations usually have increased light penetration on the forest floor owing to differences in individual species growth patterns, leaf size and crown densities (Lagergren and Lindroth, 2002, Morén et al., 2000) and seasonal light variation in mixed plantations with a deciduous component may also allow

for an increase in vernal herb species (Simmons and Buckley, 1992). Broadleaf mixes can reduce the litter fall of conifer needles (Smith et al., 2005), which can negatively affect ground vegetation diversity by smothering development and acidifying soil (De Vries, 1995, Eycott et al., 2006, French, 2005) and accelerate nutrient cycling (Polyakova and Billor, 2007). Mixed species plantations, especially those where the secondary species is native (or is similar to a native tree species) may have the potential to develop a vegetation community similar to semi-natural woodlands (Hartley, 2002, Aubin et al., 2008). However, the identity of the tree species planted is not the only factor influencing ground vegetation diversity and research has found that other factors such as tree crop arrangement, land use history, soil type and plantation age, were more important (Cooper et al., 2008, Peterken, 1993, Williams et al., 1998, Bremer and Farley, 2010, French et al., 2008, Smith et al., 2005).

3.2.2 Research in context

There is a general acceptance that mixed species plantations support more species than monocultures, especially mixes containing native species (Bremer and Farley, 2010, Hartley, 2002, Stephens and Wagner, 2007). Research has been carried out on the species combinations or spatial arrangement, which may enhance mixed species plantation biodiversity the most. The effectiveness of non-intimate mixes in enhancing ground vegetation was investigated by Smith *et al.* (2005) in Irish stands of Sitka spruce with ash (*Fraxinus excelsior*). They found increased survival of vascular plant species under the ash component compared to the Sitka spruce component, although the ash did not increase the diversity of the Sitka spruce component. However, they could not rule out that the non-intimate mix may aid re-colonisation of adjacent components if suitable conditions developed e.g. increased light levels in mature plantations. Kirby (1988), studying alternating rows of Spruce/oak (*Quercus* spp), reported increased diversity under the oak

compared to the Spruce. Ferris and Simmons (2000) studied row mixes of oak/Norway spruce compared with pure Norway spruce (*Picea abies*). They reported thinned mixes had greater cover and diversity of vascular plants than unthinned mixes and pure Norway spruce stands and that bryophyte cover and diversity was highest under pure Norway spruce. The biodiversity of intimately mixed plantations has received little attention in the scientific literature. Saetre *et al.* (1997) compared an intimate mix of Norway spruce/birch (*Betula* spp) with neighbouring pure Norway spruce stands and found the community composition differed between the stands and there was higher vascular plant and lower bryophyte species richness beneath the mix compared to that of pure Norway spruce stands. In this paper we present results from the first Irish study on ground vegetation diversity in intimate mixed plantations and compare them with monocultures.

Managing plantations for timber production while also enhancing biodiversity involves tradeoffs and only with an increased understanding of the ecology of plantations can the balance between these products and ecological services be made (Carnus *et al.*, 2006). The establishment of mixed plantations is a significant forest policy in both Ireland and the UK but previous research fails to inform on the impact these stands have on biodiversity. The objective of this paper is to investigate the ecology of mixed plantations and compare them to pure stands, in terms of their ground vegetation diversity, and how these different plantings may have positive or negative outcomes for plant diversity. This will be achieved through the following aims:

1. To compare the species richness and vegetation community composition of Norway spruce mixed with Scots pine or oak and pure Norway spruce stands i.e. a non-native species mixed with a native species

2. To identify factors important in determining the vegetation communities and species richness of these plantation types, particularly of typical woodland species, for potential use as diversity indicators
3. To recommend management practices for enhancing diversity of ground vegetation in plantations with a mixed canopy of native and non-native species.

The stands in this Chapter can be, at least qualitatively, compared with the mature afforestation stands of Chapter 2 (refer to **section 5.2.**).

3.3 Materials and methods

3.3.1 Site selection

Relevant national forest databases were examined, both in the Republic of Ireland and Northern Ireland, to determine what types of mixed plantations existed in the landscape. Norway spruce (*Picea abies*) was chosen as the main plantation tree species due to the relatively high number of available mixed sites with this species. Sites with oak (*Quercus* spp.) and Scots pine (*Pinus sylvestris*) as the secondary species were chosen as they were relatively well represented in mixed Norway spruce sites that were suitable to survey. In the past oak was one of the most widespread native trees in the Irish landscape (Anon, 2005b) and Scots pine is Ireland's only native pine to be commonly included in commercial and conservation plantings in Ireland (Anon, 2005c). To control for possible differences in stand management between mixed and pure forests, structurally similar sites at the commercially mature stage were surveyed (37 to 58 years after planting). To minimise environmental and climatic variation, mixed and pure forests were located in geographic pairs with most within 5-10km of each other; in one instance, due to a lack of

suitable sites the mixed and pure forests were located approximately 50km apart. Five Norway spruce/oak mixes and five Norway spruce/Scots pine mixes and ten nearby stands of pure Norway spruce were selected, resulting in 20 forest stands in total to be surveyed (**Fig. 3.1**). In all mixed sites, the secondary species accounted for between 5 and 40% canopy cover of the planted crop and was in an intimately mixed configuration with Norway spruce i.e. not clumped but distributed throughout the stand. Plantations containing only Norway spruce are henceforth referred to as ‘pures’, Norway spruce/Scots pine mixes are referred to as ‘Scots pine mixes’, Norway spruce/oak mixes are referred to as ‘oak mixes’ and those with both Norway spruce and either oak or Scots pine are referred to as ‘mixed’.



Figure 3.1: Map of Ireland showing survey sites. ○ Norway spruce/Scots pine mixes, □ Norway spruce/oak mixes and ▲ pure Norway spruce sites are indicated by black triangles.

3.3.2 Data collection

At each site, three 10m x 10m plots were positioned at least 50 m from the forest edge and 50 m from each other to reduce edge and pseudo-replication effects respectively. In each plot, percent cover of ground vegetation species was recorded to the nearest 5%. Cover below 5% was recorded either as 3% (indicating cover of 1–5%) or 0.5% (indicating cover <1%). For bryophytes and lichens, only species forming patches more than 10cm² were recorded. Species forming patches under this size but that were frequently occurring were also recorded. Ground vegetation for this study was defined as vascular plants, mosses, liverworts and lichens growing on the forest floor and on microhabitats e.g. deadwood, rocks and tree bases. Vascular plant nomenclature followed Stace (2010), mosses followed Smith (2004), liverworts followed Paton (1999) and lichens followed Coppins (2002). Vegetation structure was recorded in the 100 m² plots as the percentage cover of vegetation (as for species cover) in the following strata: canopy, understory (≥ 2 m tall), shrub (<2m tall, including climbers and prostrate woody species), field layer (broadleaved herbaceous plants and graminoids) and non-vascular layer. Simpsons reciprocal index ($1/D$) was calculated as a measure of structural diversity using covers of vegetation layers. There were two measures calculated as follows. ‘ $1/D$ no oak’ used the covers of understory (excluding oak as it was planted), shrub, field and non-vascular layer covers but not canopy as it was planted. ‘ $1/D$ oak under’ included oak in the understory in the calculation as that was the structural layer it actually formed part of in the stands. Hemispherical photographs were taken at the centre of the 10m x 10m plot using a tripod-mounted Nikon Coolpix 8400 digital camera with a Nikon LC-ER2 fisheye lens. The camera was erected at 1.3m above ground, levelled and oriented towards magnetic north. The images were later analysed using Gap Light Analyzer 2.0 software (Frazer et al., 1999) and percentage canopy openness was calculated. The diameter at breast height (DBH) at 1.3 m of all planted trees ≥ 2 m tall and all unplanted trees of ≥ 5 cm DBH was recorded and the

density (number) and species of these trees were noted. The percentage cover of leaf litter (broadleaved tree and herbaceous litter) and needle litter were also recorded. Thinning status, type and intensity were recorded from field observations. Line thinning, the systematic removal of trees along designated lines, is usually followed by selective thinning which is the removal of dead, suppressed or poorly formed trees (Forest Service, 2000a). The volume of coarse woody debris (CWD) ≥ 10 cm maximum diameter was recorded and categorised as follows: logs and large branches ($>45^\circ$ departure from vertical); snags (standing deadwood; $\leq 45^\circ$ and ≥ 1 m tall); stumps (<1 m tall), and within three states of decay: sound (intact with very little evidence of decay); moderately decayed (crumbling in the hand); advanced decay (moist, rotten and sometimes hollow). Total CWD volume was also calculated. Annual precipitation was estimated using data from Sweeney *et al.* (2003). Five soil samples were collected to an approximate depth of 10 cm from near the corners and the centre of the 10 m x 10 m plot and bulked in the field. Soil samples were air dried prior to analysis for organic matter content (LOI – $550^\circ\text{C} \times 5$ hrs). Information on previous land use, ground preparation for planting and thinning (type and year(s) carried out) was collected from forest managers but due to the variable quality of these data (and of soil type) these variables were not used in formal analysis. Stand age was determined from the management database. Proximity to old woodland between 200 m and 1 km of sites, with old woodland defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the 3rd edition 6" O.S. maps (1900-1913), and the area of old woodland within 1 km were recorded for all but two sites, where a 3rd edition map was unavailable (note: woodland may or may not be existing at time of survey). Area (km²) of the following land use types within 200 m and from 200 m to 1 km of plots was calculated; quarries, built up areas, intensively managed open land and plantations: extensive land use: extensively managed open land, bushes, semi-natural woodland and scrub: mature

forest: both planted and semi-natural: semi-natural wood lands. Distance to the nearest plantation edge was also measured for each plot.

3.3.3 Data analysis

The following biodiversity metrics were calculated for each plot: total, vascular plant (excluding planted tree species) and non-vascular (bryophyte and lichen) species richness (SR). Species recorded were classified according to their affinity for woodlands: low (not usually found in woodlands), moderate (frequently occurring in both woodlands and unwooded habitats) or high (typical woodland species), using information on habitat preferences from Irish and British floras for vascular plants (Hubbard, 1984, Jermy et al., 1982, Preston et al., 2002, Webb et al., 1996, Grime et al., 2007, Hill et al., 2004) and for bryophytes (Hill et al., 2007, Paton, 1999, Purvis et al., 1992, Smith, 2004, Watson, 1981). β sim (Koleff et al., 2003) was calculated as a metric for species turnover with a maximum value of 1, indicating no species in common, and minimum value of 0, indicating all species common. To relate the vegetation communities to environmental conditions, vascular plants were also classified according to their ecological strategy as competitors (C), stress tolerators (S) or ruderals (R), or a combination of these categories, according to Grime *et al.*'s (1988) CSR model. The species richness of plants in the above categories was calculated for each plot. The percentage cover of vascular and non-vascular species was calculated for each plot.

Site level data were calculated from plot level data by combining the variables from the three 10m x 10m plots by averaging. Plot level data are more sensitive to heterogeneity in richness and ecological processes, while site level data provide an overview of relationships between vegetation communities and factors that may impact them (Smith et

al., 2005). Plot level data were used in correlation analysis. Prior to statistical testing data exploration for normality, heterogeneity of variances, outliers and collinearity was carried out using SPSS 16 (SPSS, 2007), Minitab 13 (2000) and R (R Development Core Team, 2010). Where outliers were detected the data were transformed as appropriate. Non-normal distribution and heterogeneity of variance was dealt with by transformation and if data still did not meet assumptions of parametric tests non-parametric statistics were employed. Non-parametric Kruskal-Wallis tests followed by *post hoc* Mann-Whitney U tests (Dytham, 2003) were used to investigate differences in diversity metrics and measured variables among the forest types. Owing to large differences in some of the environmental characters of the sites within many of the geographic pairs of mixed and pure stands data analysis was not carried out with the pairing as a factor.

To examine patterns in ground vegetation communities, a non-metric multidimensional scaling (NMS) ordination of plot data was performed. This technique is based on ranked distances and has thus been found particularly suitable for the analysis of non-normal data from ecological communities (McCune and Grace, 2002). The “slow and thorough” autopilot settings in PC Ord version 5.26 (McCune and Mefford, 2006) were used which include the following parameters: Sorensen distance measure; 500 maximum number of iterations; Random Starting coordinates; 100 runs with real data; Step down in dimensionality (Initial step length = 0.2); 50 runs with randomized data. NMS axes are arbitrary (Legendre and Legendre, 1998), so varimax rotation was used to help interpret the ordination axes as it maximizes the variance of species correlations with the ordination axes, resulting in groups of plots with very high and very low axis correlations (Lichstein et al., 2002). Spearman’s rho (r) non-parametric correlation analysis was undertaken between plot axis scores and environmental variables to aid interpretation of the

ordination. *Post hoc* *p*-value corrections, such as Bonferroni or Dunn-Sidak, were not applied due to criticisms that they are too conservative as they reduce the level for significance below the usual 0.05 and thus significant relationships may be missed (Dytham, 2003).

Indicator species analysis (McCune and Grace, 2002) was carried out to illustrate those species whose presence characterised each forest type. A perfect indicator species with an indicator value of 100% would be one that was unique to one habitat and was observed in all samples from that habitat (Dufrêne and Legendre, 1997). Indicator values (IV) were derived for each species from the average abundance of each species in a given group of sites over the average abundance of that species in all the sites expressed as a percentage. This value was tested for statistical significance using a Monte Carlo test. Only species with an indicator value greater than 25% and with $p \leq 0.05$ were considered as a species with an IV lower than 25% is not considered to be a good indicator (Dufrêne and Legendre, 1997). Information was collated on the indicator species associated with each forest type with regards to the following: affinity for woodlands (as described previously), Ellenberg values (Hill et al., 1999, 2007, 2004) for light (L), soil moisture (F), soil reactivity (R) and soil nitrogen (N; may be used as a proxy for soil fertility) and their ecological strategies using the CSR model of Grime *et al.* (1988, 2007). As there were too many species in the data set (189) species to display effectively on a species plot ordination only the indicator species for the different forest types and common species (in $\geq 25\%$ or more of plots) are displayed.

Multi-response Permutation Procedures (MRPP) with Sørensen distance measures were used to test for differences in vegetation communities among the forest types at the site level. The distance matrices were rank transformed in order to correct for loss of sensitivity

as community heterogeneity increases and to make the MRPP results more analogous in theory to NMS (Brandtberg *et al.*, 2000). MRPP reports a test statistic T with p-value, (more negative values of T represent stronger separation between groups). However, the p-value is not independent of sample size, so the derived test statistic A is used to describe separation between groups. The statistic approaches 1 when distances within groups are smaller than distances between groups, and is 0 when distances between and within groups are equal. Values of A for ecological communities are commonly below 0.1 while those above 0.3 are considered high (McCune and Mefford, 2006). NMS ordinations, indicator species analysis and MRPP were conducted using PC-Ord version 5.26 (McCune and Mefford, 2006).

Using Generalised Linear Mixed Models (GLMMs) with a Poisson distribution, species richness and typical woodland species richness of vascular plants and non-vascular species were modelled separately at the site level. Site was included in the models as a random factor. Following data exploration variables were transformed when necessary to decrease the influence of outliers and explanatory variables were standardized to prevent convergence. Variables that were deemed ecologically meaningful were included in global models, provided that they were not highly correlated (investigated with Spearman's ρ (r) non-parametric correlation analysis) with more meaningful variables. Correlation analysis showed canopy openness was strongly positively correlated with canopy cover ($r_s = 0.822$, $p < 0.01$) but weakly with structural diversity ($r_s = 0.395$, $p < 0.01$), brash piles ($r_s = 0.382$, $p < 0.01$) and seedling- sapling density ($r_s = 0.356$, $p < 0.01$). Canopy cover was also moderately negatively correlated with basal area ($r_s = -0.449$, $p < 0.01$) and age ($r_s = -0.511$, $p < 0.01$). Planted tree density was strongly negatively correlated with DBH ($r_s = -0.730$, $p < 0.01$), moderately positively correlated with canopy cover ($r_s = 0.464$, $p < 0.01$) and negatively with height ($r_s = -0.400$, $p < 0.01$). Structural diversity was positively

correlated with all vegetation structure covers ($p < 0.01$). CWD volume was correlated with CWD cover ($r_s = 0.335$, $p < 0.01$) but only with some types and decay classes of deadwood. Area of old woodland within 1km was strongly positively correlated with distance to old woodland ($r_s = 0.914$, $p < 0.01$). Each land use was positively correlated with its corresponding one at other scale and at the 200m scale the intensive land uses were correlated with the area of forest ($p < 0.01$) while the extensive land uses were correlated with semi-natural woods at both scales. Elevation and annual precipitation were moderately positively correlated ($r_s = 0.540$, $p < 0.01$). Variance inflation Factor (VIF values < 3) was used to confirm there was no collinearity in final set of variables for modelling (Zuur et al., 2007). The global models for vascular plant SR and typical woodland vascular plant SR included; forest type, canopy openness, planted tree number, LOI, (weighted) Ellenberg N, distance to old woodland, area of semi-natural woodlands within 1km, distance to edge, and, for vascular plant SR, the area of forest within 200 m to 1 km. The non-vascular SR and typical woodland non-vascular SR global models included: forest type, canopy openness, annual precipitation, area of forest at 200 m and CWD volume. No overdispersion was detected as residual deviance / degrees of freedom < 1 (Zuur et al., 2009). Both global models were validated and manual backward model selections were performed using AIC (Akaike Information Criteria) following the methods outlined in Zuur *et al.* (2009). Non-significant variables were retained if they improved the overall model fit by lowering the AIC. Analyses were undertaken using R version 2.11.0 (R Development Core Team, 2010) and the nlme (Pinheiro *et al.*, 2009) and lme4 (Bates and Sarkar, 2006) packages for GLMMS.

3.4 Results

3.4.1 Species richness

A total of 189 species were recorded in the 10m x 10m plots, comprising 153 vascular plant, 31 bryophyte and 2 lichen species. Due to the low occurrence of lichens in this study, non-vascular richness and cover are essentially equivalent to bryophyte richness and cover. There were no species recorded from the vascular plant red data list (Curtis and McGough, 1988) or from the Flora Protection Order (Anon, 1999) and no non-vascular species that are listed as rare in Holyoak (2003). However, one ‘notable’ species (defined as a rare species typically found in woodland, or a species indicative of long-established woodland) of the 30 listed by Perrin et al. (2008), *Prunus padus*, was found in a Norway Spruce/Scots pine plantation established in an area that was previously old woodland. There were six pure sites and four mixed sites on or adjacent to old woodland. Thirty-two percent of vascular plant and 31% of non-vascular species were recorded only once, as were the only two lichen species, *Cladonia coniocraea* and *Lepraria incana*. The vast majority of non-vascular species were recorded as having less than 1% cover, with only 6 species recorded with cover greater than 5%. Almost half (48%) of non-vascular species recorded in this survey were growing on deadwood.

There were no significant differences in species richness metrics between the three forest types (**Table 3.1**). However, a trend was evident with Scots pine mixes and pure sites having almost equal species richness, while the oak mixes had the lowest species richness (except for non-vascular species richness where they had the highest). For all forest types the majority of vascular species were competitors and stress tolerant, with ruderal numbers the lowest, and there were no significant differences in the ecological strategies of vascular plants among the forest types.

Table 3.1. Median values and the interquartile for diversity metrics (SR = species richness) and ecological strategies of vascular plants. Vascular plants were classified using the CSR model of Grime *et al.* (1988, 2007) were plants are classified as competitors, stress-tolerators, ruderals or intermediates between any two or all three of these categories (model not applicable to bryophytes). No significant differences ($p \leq 0.05$) were found between forest types using the Kruskal-Wallis non-parametric test.

	Norway spruce/ Scots pine (n=15)	Norway spruce/ oak (n=15)	Pure Norway spruce (n=30)
Diversity metrics			
Total SR	24.0, 8.50	22.0, 4.0	24.50, 16.0
Vascular SR	15.0, 10.50	13.0, 3.0	13.0, 18.25
Non-vascular SR	9.0, 2.0	10.0, 3.5	10.0, 3.75
Typical woodland SR	14.0, 6.50	12.0, 2.0	13.50, 8.75
Typical woodland vascular SR	8.0, 6.50	7.0, 3.50	8.0, 6.75
Typical woodland non- vascular SR	5.0, 1.0	5.0, 1.50	6.0, 3.0
Species turnover	0.33, 0.12	0.26, 0.18	0.26, 0.13
Competitor SR	14.0, 9.50	12.0, 3.50	12.5, 16.50
Stress tolerant SR	14.0, 9.50	11.0, 4.50	12.0, 15.50
Ruderal SR	5.0, 7.5	6.0, 3.0	6.0, 11.75

3.4.2 Structural and environmental variables

Canopy openness, vascular and non-vascular cover and CWD volume were significantly greater in the Scots pine mixes than other two forest types (**Table 3.2**). Total canopy cover did not differ significantly among Scots pine mixes, oak mixes or pure sites. Canopy cover was separated into that of Norway spruce and of the secondary species (Scots pine or oak) and the canopy cover of Norway spruce was significantly greater in the Scots pine mix than in the oak mix. Canopy openness was lowest in the oak mixes as was the cover of Norway spruce. In oak mixes, the secondary species cover was significantly higher, and DBH significantly lower than in the Scots pine mixes. Oak in the mixed stands undoubtedly added to structural diversity as it was present as understory but, as it was

planted, it was not supposed to be included in the calculations for structural diversity (1/D no oak, **Table 3.2**). However, as it was still understory, additional analysis including oak in the understory (1/D oak under, **Table 3.2**) showed that the structural diversity of the oak mixes was significantly higher than that of pure sites. As the oak was structurally understory, while the Scots pine was part of the canopy, a direct comparison of the mixed forest types was difficult. In both mixed plantations the DBH of the secondary species were significantly lower than the Norway spruce component ($p < 0.05$ for Scots pine mixes and $p < 0.001$ for oak mixes). The DBH of Norway spruce was significantly lower in the Scots pine mixes than in the oak mixes. Not surprisingly needle litter cover was highest in pure sites (non-significantly) and leaf litter cover was significantly highest in oak mixed stands. LOI was significantly higher in both Scots pine mixes and pure sites compared with oak mixes. There were no significant differences among the forest types for geographic variables but trends included; oak mixes being farthest from old woodland; Scots pine mixes had the largest area of semi-natural woods in a 1 km radius, with oak mixes having the largest area within 200 m; pure sites being closest to the plantations edge with oak mixes the most interior. From field observations it was noted that more recent thinning had been carried out in the Scots pine mixes and pure sites than in the oak mixes.

Table 3.2. Median, interquartile of structural, compositional, geographic and functional variables for the three forest types from the 100 m² plots. Significance tested with non-parametric Kruskal-Wallis test followed by Mann Whitney (U) post hoc test. Values for variable are significantly different ($p \leq 0.05$) between the forest types if indicated by a different letter.

Variable (unit)	Norway spruce/ Scots pine (n=15)	Norway spruce/oak (n=15)	Pure Norway spruce (n=30)
<u>Structural</u>			
Canopy openness (%)	6.90, 3.10 ^A	4.57, 2.76 ^B	4.92, 2.62 ^B
Canopy cover main species (%)	60.0, 20.0 ^A	60.0, 27.50 ^B	80.0, 15.0 ^B
Canopy cover mix species (%)	10.0, 7.50 ^A	20.0, 20.0 ^B	n/a
DBH all planted (cm)	26.83, 10.02	26.44, 6.66	26.21, 9.60
DBH main species (cm)	28.30, 11.24 ^A	36.97, 4.33 ^B	26.21, 9.60 ^C
DBH mix species (cm)	21.52, 6.43 ^A	14.80, 3.33 ^B	n/a
Planted tree density (no./100m ²)	8.0, 8.50	7.0, 2.0	8.0, 5.74
Basal area (m ² /100m ²)	0.52, 0.20	0.48, 0.17	0.59, 0.24
Structural diversity (1/D no oak)	2.60, 1.47	1.46, 0.62	1.60, 1.02
Structural diversity (1/D oak under)	2.60, 1.47 ^{AB}	1.82, 0.70 ^B	1.95, 1.01 ^A
<u>Compositional</u>			
Vascular cover (%)	63.0, 83.25 ^{AB}	13.50, 47.0 ^A	17.50, 39.38 ^{BC}
Non-vascular cover (%)	70.0, 32.50 ^A	50.0, 37.50 ^B	50.0, 42.50 ^B
<u>Geographic</u>			
Distance to old woodland (m)	490.0, 606.50	997.0, 858.50	208.0, 447.0
Area of semi-natural woodlands within 1km (km ²)	0.07, 0.18	0.02, 0.02	0.08, 0.11
Area of forest within 200m to 1 km (km ²)	0.65, 0.41	0.66, 0.58	0.68, 0.55
Area of forest within 200m (km ²)	0.09, 0.03	0.10, 0.03	0.09, 0.04
Distance to edge (m)	85.78, 52.96	95.06, 45.29	63.53, 70.05
<u>Functional</u>			
LOI (%)	18.0, 10.0 ^A	14.0, 7.0 ^B	21.50, 30.0 ^A
Ellenberg N	4.90, 0.54	4.53, 0.60	4.67, 0.60
CWD volume (m ³ /100m ²)	0.32, 0.21 ^A	0.20, 0.14 ^B	0.15, 0.18 ^B
Needle litter cover (%)	30.0, 27.50	40.0, 27.50	45.0, 48.75
Leaf litter cover (%)	3.0, 2.50 ^A	15.0, 15.0 ^B	3.0, 2.50 ^A
Annual precipitation (mm)	1118.96, 61.40	997.70, 305.56	1107.83, 181.30

3.4.3 Community composition

The varimax rotated NMS ordination (**Figs. 3.2a, b and c**) was based on the species composition of the ground vegetation plots and a 3D solution was suggested. Cumulative variation in the data explained by the ordination is 80.0 % with Axis 1 accounting for 39.0 %, Axis 2 for 21.4 % and Axis 3 for 19.6 %. Final instability = 0.00000 and the Monte Carlo test showed the stress was significantly different to that expected by chance: final stress = 14.55 ($p = 0.004$). There was a slightly closer grouping of the mix forest types in ordination space, particularly along axes 1 and 2, compared with the wider spread of pure plots indicating that the pure plots supported a greater variety of communities. Heterogeneity in vegetation composition within sites and within forest types was evident in the widely spaced plots from some of the same sites and in the extensive overlap among forest type plots in ordination space respectively.

Figure 3.2 a)

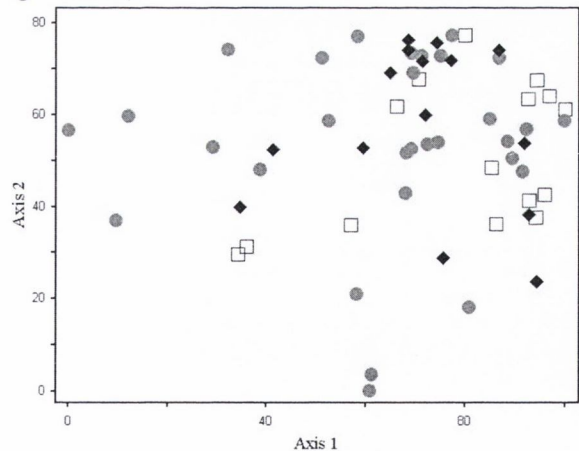


Figure 3.2 b)

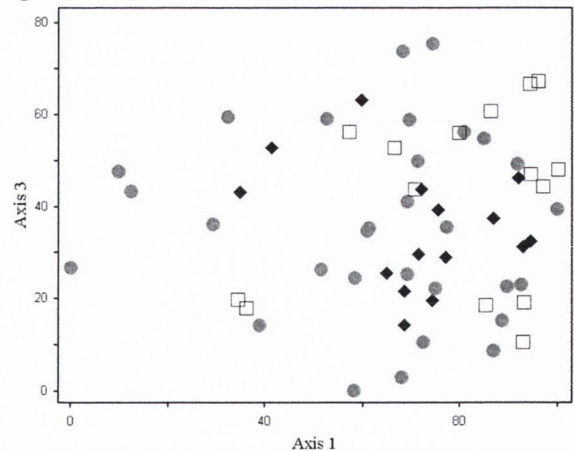


Figure 3.2 c)

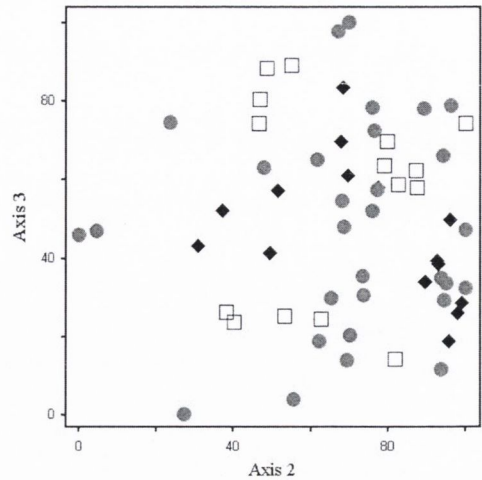


Figure 3.2. a) Axes 1 and 2 b) axes 1 and 3 and c) axes 2 and 3 of the varimax rotated NMS ordination of ground vegetation species composition for Norway Spruce/oak mixes $\blacklozenge$, Norway Spruce/ Scots pine mixes $\square$ and pure Norway spruce $\bullet$. Cumulative variation in the data explained by the ordination is 80.0 % with Axis 1 accounting for 39.0 %, Axis 2 for 21.4 % and Axis 3for 19.6 %. Final stress = 14.55 ($p=0.004$), Final instability = 0.00000.

Table 4.3. Statistically significant Spearman rank correlation coefficients between variables and NMS axis scores. “*” indicates $p<0.05$ and “**” indicates $p<0.01$.

Variable (unit)	Axis 1	Axis 2	Axis 3
Structural			
Canopy openness (%)	.302*	-.324*	
Canopy cover (%)	-.430**		
DBH main species (cm)	.378**		
DBH mix species (cm)	.326*		
Planted tree density (no./100m ²)	-.509**		
Basal area (m2/100m2)		.283*	
Structural diversity (1/D oak under)	.906**		
Compositional			
Understory cover (%)	.392**		
Shrub cover (%)	.743**	-.465**	.283*
Field layer cover (%)	.647**		
Non-vascular cover (%)	.799**		
Geographic			
Distance to old woodland (m)	-.287*	.450**	
Area of semi-natural woodlands within 1km (km ²)	.454**	.559**	.309*
Functional			
Ellenberg N	.337**	-.427**	.672**
CWD volume (m ³ /100m ²)	.272*		
Needle litter cover (%)	-.843**		
FWD cover (%)	-.583**		

Axis 1 from left to right represented strong gradient of decreasing needle litter and moderate gradients in decreasing canopy cover, planted tree density, FWD cover and area of semi-natural woods within 200m to 1 km. Axis 1 also represented a strong gradient of increasing structural diversity underpinned by strong gradients in shrub, field and non-vascular covers and a weak gradient of increasing Ellenberg N. The three sites that scored lowest on axis 1 where three pure Norway spruce sites dominated by the mosses *Pseudotaxiphyllum elegans*, *Mnium hornum* and the liverwort *Calypogeia fissa* all shade plants according to their Ellenberg L values (3-4). These sites were notable for their low diversity and canopy openness and high needle litter cover. Axis 2 from bottom to top represented moderate gradients of increasing area of forest within 200m to 1 km, distance to old woodland and weaker decreasing gradients of Ellenberg N, woody shrub cover and canopy openness. Axis 3 represented a strong gradient from bottom to top of increasing Ellenberg N. On examining the axis scores of the plots within a particular forest type some general trends were seen. Both mixed forest types generally had higher axis 1 scores than the pure sites. This suggests a broad difference in ground vegetation habitat structure and soil conditions between the mixed species and pure forest types. Generally Scots pine mixes had higher axis 3 scores than oak mixes suggesting higher soil fertility. Indicator species analysis results are in **Table 3.3**. MRPP analysis using forest type as the defining factor showed no significant difference, on average, among forest types ($T = -2.22$, $A = 0.01$, $p = 0.37$).

Table 3.3 Percentage indicator values (IV) for significant ($p \leq 0.05$) indicator species with an indicator value (IV) of 25% or above in each forest type (lower IV's than 25% are not considered good indicators (Dufrêne and Legendre, 1997)). Only one indicator species was found for pure Norway spruce forest type but it did not have an $IV \geq 25\%$. Also shown are the attributes of the indicator species. AW is affinity for woodlands (1 low, 2 moderate, 3 high) designated during this project. Ecological strategies are classed as competitors (C), stress-tolerators (S), ruderals (R) or intermediates between any two or all three of these categories (1 - yes, 0 - no) according to Grime *et al.* (1988, 2007). Ellenberg values are for light (L), soil moisture (F), soil reactivity (R) and soil nitrogen (N) according to Hill *et al.* (2007, 2004). L; 1, deep shade – 9, full light. F; 1, extreme dryness – 12, submerged. R; 1, extreme acidity - 9, basic. N; 1,extremely infertile - 9, extremely rich. Refer to **Section 3.3.** for more detail on attribute classification. The mean $\pm$ s.d. of all attribute values are also shown.

	IV	AW	C	S	R	L	F	R	N
Norway spruce/Scots pine									
<i>Fraxinus excelsior</i>	57.2	3	1	1	0	5	6	7	6
<i>Kindbergia praelonga</i>	55.2	3	na	na	na	5	6	5	5
<i>Lonicera periclymenum</i>	48.8	3	1	1	0	5	6	5	5
<i>Corylus avellana</i>	45.8	3	1	1	0	4	5	6	6
<i>Dryopteris filix-mas</i>	32.7	3	1	1	0	5	6	5	5
<i>Metzgeria temperata</i>	28.2	3	na	na	na	5	5	5	3
Mean $\pm$ s.d.	na	3 $\pm$ 0	1 $\pm$ 0	1 $\pm$ 0	0 $\pm$ 0	4.8 $\pm$ 0.37	5.7 $\pm$ 0.47	5.5 $\pm$ 0.76	5 $\pm$ 1
Norway spruce/Oak									
<i>Isoethecium myosuroides</i>	78.3	2	na	na	na	4	6	4	3

Figure 3.3 b)

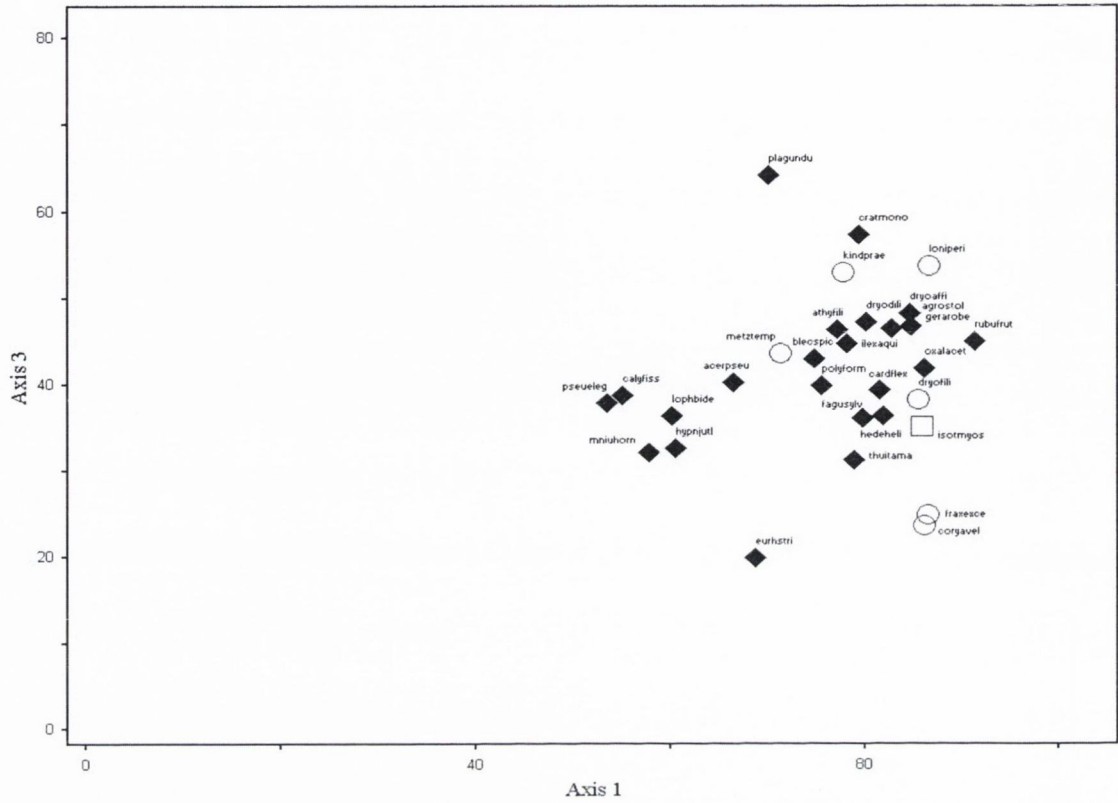


Figure 3.3 c)

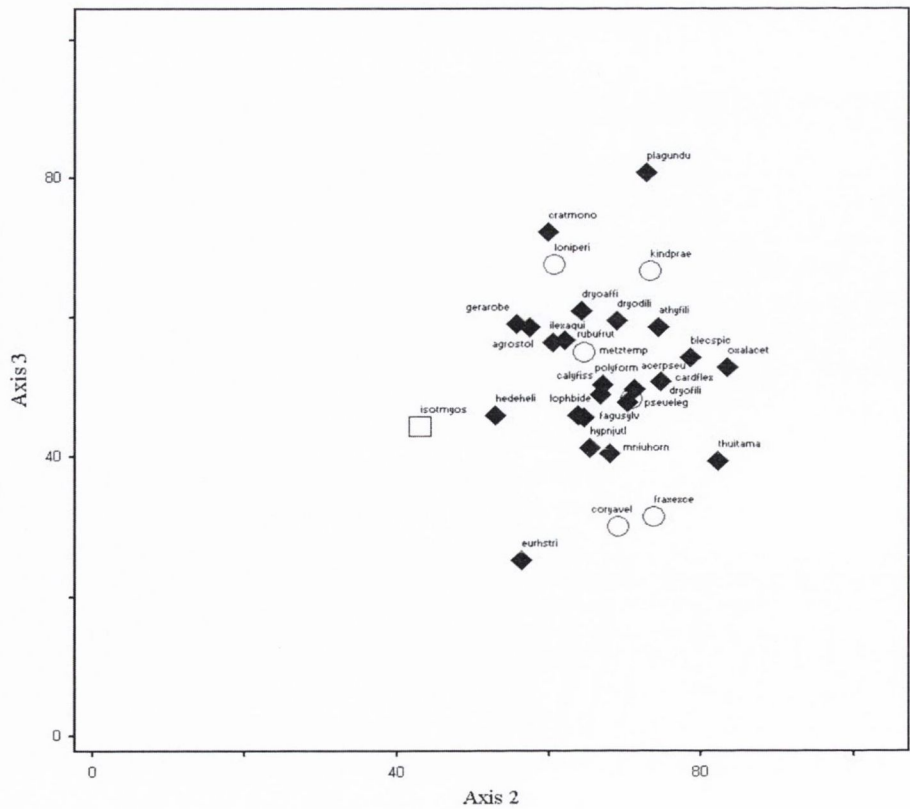


Figure 3.3. (previous 2 pages) **a)** Axes 1 and 2 **b)** axes 1 and 3 and **c)** axes 2 and 3 of the varimax rotated NMS ordination of ground vegetation showing indicator species for ○ Norway Spruce/ Scots pine mixes, □ Norway Spruce/oak mixes and ◆ common species in $\geq 25\%$ of plots. Cumulative variation in the data explained by the ordination is 80.0 % with Axis 1 accounting for 39.0 %, Axis 2 for 21.4 % and Axis 3 for 19.6 %. Final stress = 14.55 ($p=0.004$), Final instability = 0.00000 Species codes are first 4 letters of genus and first 4 letters of species name (refer to **Appendix 1** for details).

3.4.4 Drivers of diversity

Given the variables measured that were non-collinear and ecologically relevant, the modelling results showed a variety of factors were significant in driving differences in the four species richness metrics (**Table 3.3**). Canopy openness and forest type, included in all global models, were only significant in the final models for vascular plant and typical woodland vascular plant SR respectively. For both final vascular models, planted tree density was highly significant. The only geographic variable to be significant was distance to edge in the final vascular plant SR model and area of semi-natural woodland within 200m for the final non-vascular SR model. Area of forest within 200m was the only variable included in the final typical woodland non-vascular model and was only approaching significance. The estimates for vascular SR predicted lower SR with higher planted tree density, distance to edge, greater area of semi-natural woodland between 200 m and 1km and greater distance to old woodland. Higher SR was predicted at higher canopy openness. For non-vascular SR there was a predicted decrease in SR with greater areas of semi-natural woods within 200m and for typical woodland non-vascular SR there was a predicted decrease in SR with greater are of forest within 200m.

Table 3.3. Global model terms and coefficients for model terms in final GLMM models: a) vascular plant SR
b) non-vascular plant SR c) typical woodland vascular SR and d) typical woodland non-vascular SR.

Vascular plant SR					
Global	~ forest type + canopy openness + LOI + Ellenberg N+ planted tree density + distance to old woodland				
model terms	+ area of semi-natural woodlands within 1km + area of forest btwn 200m & 1km +distance to edge				
	Final model terms	Estimate	s.e.	p-value	
	Intercept	2.49	0.08	< 2e-16	***
	Planted tree density (no./100m ²)	-0.45	0.12	0.00006	***
	Canopy openness (%)	0.25	0.07	0.00008	***
	Distance to edge (m)	-0.15	0.08	0.048	*
	Area of semi-natural woodlands				
	btwn 200m & 1km (m ²)	0.14	0.08	0.073	ns
	Distance to old woodland (m)	-0.13	0.08	0.121	ns
Non-vascular SR					
Global model terms	~ forest type + canopy openness + rain fall + area of forest within 200m + CWD volume				
	Final model terms	Estimate	s.e.	p-value	
	Intercept	2.32	0.07	<2e-16	***
	Area of semi-natural woodlands within 200m (m ²)	-0.16	0.07	0.0265	*
Typical woodland vascular plant SR					
Global	~ forest type + canopy openness + LOI + Ellenberg N+ planted tree density + distance to old woodland				
model terms	+ area of semi-natural woods btwn 200m & 1km + distance to edge				
	Final model terms	Estimate	s.e.	p-value	
	Intercept	2.22	0.15	< 2e-16	***
	Planted tree density (no./100m ²)	-0.50	0.11	0.000007	***
	Forest type oak mix	-0.55	0.23	0.016	*
	Forest type pure Norway spruce	-0.23	0.19	0.208	ns
Typical woodland non-vascular SR					
Global model terms	~ forest type + canopy openness + rain fall + area of forest at 200m + CWD volume				
	Final model terms	Estimate	s.e.	p-value	
	Intercept	1.79	0.10	<2e-16	***
	Area of forest within 200m (m ²)	-0.16	0.10	0.085	ns

Significance: *** p ≤ 0.0001; * p = ≤ 0.01

3.5 Discussion

3.5.1 The effect of mixed species stands on ground vegetation species richness

It is expected that addition of a second tree species to a plantation, regardless of the spatial configuration of its planting will enhance the ground vegetation diversity of plantation forests owing to changes in resource availability of, for example, light, soil nutrients and substrate (Barbier et al., 2008, Bremer and Farley, 2010, Ferris and Humphrey, 1999, Hartley, 2002, Stephens and Wagner, 2007). However, this research found that the presence of a second tree species in plantations is not always a useful predictor of ground vegetation diversity, as the addition of Scots pine or oak to Norway spruce plantations did not result in any significant differences in species metrics compared to pure Norway spruce plantations. However, there was a general trend that pure Norway spruce and Scots pine mixes had similar diversity and both were more diverse than the oak mixes, except for the trend of higher non-vascular SR in the oak mixes. There was no significant difference in species turnover among the forest types i.e. the ‘pool’ of species that formed communities in each forest type where of a similar size.

There are several possible explanations we propose for the lack of differences in SR among the forest types. As mentioned, locating suitable mix plantations was a challenge and resulted in a small sample size. Bremer and Farley (2010) also reported inconclusive results regarding the question of mix species plantations supporting more diversity than pure plantations. Challenges with site selection in this research meant there were differences in site history between mixed and pure stands. This may have been a confounding factor contributing to the lack of differences in SR as site history variables such as proximity to old woodland can be an important influence on ground vegetation diversity of plantations, especially in terms of typical woodland species (Peterken and

Game, 1984, Peterken, 2001, Brunet and von Oheimb, 1998, Ferris and Simmons, 2000, French et al., 2008, Bossuyt et al., 1999). It is accepted that mixes should be composed of species that are ecologically compatible for example, with similar early growth rates (Kerr, 1999). According to Grime *et al.*'s (2007) CSR classification, all the planted species in this survey are both competitive and stress tolerant and this may suggest ecological compatibility. However, the choice of oak as a mix species with Norway spruce, seems to have been inappropriate, as oak is slow to establish (Anon, 2005a) and was seen in the oak mixes where there was a significantly lower DBH of the oak compared to the Norway spruce and oak structurally formed, not part of the canopy but the understory. A British study of Norway spruce/oak mixes by Mason and Baldwin (1995) found that the conifer grew much faster than the oak after the initial establishment phase. They concluded that there are few situations where planting conifers intimately to act as a nurse species for broadleaves is appropriate, since the faster growth of the conifer would suppress the broadleaf unless the stand was specifically managed to favour the broadleaved trees (perhaps at the expense of the conifers). Scots pine DBH in the mixed stands was also significantly lower than that of Norway spruce, but the difference was not as pronounced as in the oak mixes. Current Irish forestry policy recommends Scots pine and European larch (*Larix decidua*) as the only conifer species compatible with oak due to their open canopies relative to most commercial conifer species in Ireland but even then they are recommended for planting in non-intimate mixtures (Forest Service, 2000a; Anon, 2005a). In the sites studied for this research, the Norway spruce may have been originally planted as a nurse species for the oak (Griffin, 1999, Kerr et al., 1992); however, it may be that if the oak was severely suppressed by the nurse species, the thinning out of the nurse species that was planned may never have happened. Regardless of whether Norway spruce was planted as a nurse species in these sites, the results agree with previous work on conifer/broadleaved mixes in that, without management to favour the broadleaves, the

mixes will tend to be dominated by conifers over time (Ferris and Simmons, 2000, Mason and Baldwin, 1995). Current forestry policy in Ireland advises that Norway spruce and Scots pine are compatible in mixture and indeed, in the sites studied here, the Scots pine formed a part of the canopy. That needle litter cover in oak mixes, despite its broadleaf component, is higher than that of Scots pine mixes may be due to the oak mixes having significantly lower vascular cover, which left the needle litter highly visible. However, despite the significantly higher canopy openness in Scots pine mixes, that there was no significant difference in SR, suggesting that even mixes with more ecologically compatible species need intensive management to open up the canopy and allow light to reach levels that may impact positively on ground vegetation diversity (Ferris and Simmons, 2000). If mixes are ecologically incompatible, or managed inappropriately, the secondary species may be reduced over the forest cycle to such a low representation in the stand that its presence has no impact on the ground vegetation diversity. Indications of what species may be suitable for planting with Norway spruce come from naturally occurring Norway spruce mixes. In its native habitat of continental Europe it grows with *Fagus sylvatica* (beech) and *Abies alba* (European silver fir) and in Scandinavia, with *Betula spp.* (birch) and Scots pine, with the last two being native species in Ireland.

3.5.2 The effect of mixed species stands on ground vegetation composition

Although the addition of a second species to Norway spruce plantations did not increase species richness, indicator species analysis indicated that that species of the secondary tree impacted ground vegetation composition. The relatively high number of indicator species in the Scots pine mixed forest type suggested a specialised, well defined vegetation community with a lot of similarity in species among plots. The high woodland affinity of all the Scots pine mix indicator species supports this idea of a well defined, specialised community. Two of the six Scots pine mixes indicator species were native tree species, ash

(*Fraxinus excelsior*) and hazel (*Corylus avellana*) and highlighted the potential for this type of mix to develop semi-natural native vegetation. Conversely the other forest types having one (oak mixes) to no (pure Norway spruce) indicator species suggested more generalist communities. Examination of indicator species of the different forest types and their attributes highlighted several interesting relationships between indicator species and site conditions. It was not surprising that the indicator species of oak mixes, *Isotheicum myosuroides*, was adapted to a lower light level than those of Scots pine mixes as the oak mixes had significantly higher canopy cover and lower canopy openness than the Scots pine mixes. The indicator species also highlighted soil condition differences between the forest types in that those of Scots pine preferred acidic soils of intermediate fertility while *Isotheicum myosuroides* of oak mixes preferred moderately acidic infertile soils. These suggested differences in soil characteristics between these two forest types could have influenced the growth performance of the secondary species seen in the significantly lower DBH of oak compared to Scots pine and that oak was structurally an understory component compared to Scots pine in the canopy.

In their study of non-intimate conifer/broadleaf (Sitka spruce/ash) mixtures Iremonger *et al.* (2007) found no effect of the secondary species on the ground vegetation diversity at the site level. However, they found different species assemblages were supported by the ash and Sitka spruce stands and concluded that diversity at the plantation scale was increased by planting a mixture. In this research the intimate non-native conifer/ native conifer mix favoured a typical woodland community. Saetre *et al.* (1997) reported a change in species composition of mixes occurred along a gradient of increasing litter pH, and concluded that the presence of deciduous leaf litter was the most important factor driving differences in vegetation composition. In the present study the both types of mixed stands were clustered in ordination space compared with the pure stands, and changes in

species composition occurred not along gradients in litter pH but along gradients in soil variables, elevation, age, stand structural measurements and landscape variables at the 1km scale.

For each forest type the majority of species followed a competitive and/or stress tolerant strategy while few were ruderals. The similar tolerances and adaptations to environmental conditions of the vascular plant communities suggest similar environmental conditions among the different forest types. As reported in Grime *et al.* (1988) this dominance of competitors and stress-tolerators is typical of habitats such as these commercially mature plantations, where disturbance is rare. Conversely ruderals are often found in habitats where disturbance is common and are often weeds with high demands for nutrients and/or an intolerance of competition.

It is accepted that the extent of a forest canopy strongly influences microclimatic conditions on the forest floor, which in turn impacts ground vegetation diversity and community composition (Raabe et al., 2010, Márialigeti et al., 2009, Carnus et al., 2006, Eycott et al., 2006, Smith et al., 2005). The significantly higher canopy openness in Scots pine mixes compared to pure and oak mix stands suggests increased light availability on the forest floor may have contributed to the higher cover of non-vascular species. Previous studies have found that even shade-tolerant non-vascular species will not thrive in closed canopy conditions (Felton et al., 2010b, French, 2005, Watt, 1931) and that there is an optimum level of light, above and below which non-vascular richness is negatively affected (Coote, 2007). If the canopy is too open, and results in high temperatures and light levels on the forest floor during sunny, hot weather (Raabe et al., 2010), this may cause non-vascular species, which are generally accepted to be drought intolerant (Proctor et al.,

2007), to suffer desiccation and competition from vascular plants (Vanderpoorten and Goffinet, 2009). Conversely, at low light levels, non-vascular species may have a competitive advantage over vascular plants as they are mostly shade tolerant and favour high soil moisture and humidity (Humphrey et al., 2002a, Coote, 2007, Simmons and Buckley, 1992, Vanderpoorten and Goffinet, 2009). However, if the light levels drop below a certain threshold (individual to each species), non-vascular cover and diversity will be negatively affected (Vanderpoorten and Goffinet, 2009). Our results agreed with this optimum of light availability hypothesis in that the sites with lower canopy openness, pure and oak mixes, also had significantly lower non-vascular cover than the Scot pine mixes.

3.5.3 The effect of the secondary species on forest structure

Structurally similar sites were selected to attempt to control for possible differences in management between forest types. Discerning whether the significant differences in certain structural variables among the forest types were due to differences in the typical growth patterns of the planted tree species (Anon, 2005a, Anon, 2005c, Anon, 2005b) or were due to differences in management (such as increased thinning in mix plantations to ensure the secondary species thrives (Mason and Baldwin, 1995, Ferris and Simmons, 2000)) was difficult as management information was not comprehensive for many sites. Structural variables that may help interpret the management history of a site include planted tree density, DBH, basal area and canopy openness (Bremer and Farley, 2010, Hartley, 2002). In this study's sites, as previously mentioned, only canopy openness differed significantly, therefore comparisons among forest types were thought not to be confounded by possible differences in management history. In oak mixes, canopy openness was not only significantly lower than that of Scots pine but, perhaps surprisingly, was significantly lower than the pure sites. Surveys were undertaken during the summer so the

hemiphotographs measured canopy conditions when the oak understory was at its highest cover. Openings visible to the side of, as well as above, the stand are captured by hemiphotographic measurements of canopy openness and the high cover of the oak understory may have blocked more openings. Also, as previously mentioned, field observations indicated that more recent thinning operations had occurred in Scots pine mixes and pure sites than at oak mixes. Differences in the physiognomy of the conifer tree species may have resulted in differences in their canopy openness: Scots pine has an open canopy structure due to its lower leaf area index (Lagergren and Lindroth, 2002) and it is a self pruning species (Bardgett, 2005) whereas Norway spruce has a higher needle area closer to the top of the tree (Morén et al., 2000).

The growth of Norway spruce differed depending on the secondary species it was planted with and this was reflected in the significantly higher canopy cover but lower DBH in the Scots pine mix compared to the oak mix. Piotta's (2005) review comparing tree growth in mixed and pure plantations reported that, depending on whether interspecific competition is higher than intraspecific or *vice versa*, mixed plantations can have either a negative or positive effect on the growth of the main tree species. He reported that, while mixed plantations did not have higher height growth rates, they had higher DBH growth rates. An increase in the growth of the main species was found here as Norway spruce had significantly higher DBH in the oak mix than in the other two forest types. This increased growth of the main species has been previously reported for mixed plantations (Riley, 1995, Kimmins, 1990, De Vries et al., 2003).

3.5.4 Drivers of diversity in mixed species stands

Modelling the drivers of species richness found a relationship between stand structure and SR for some of the metrics. With both vascular SR metrics there was a negative association

with planted tree density and for vascular SR with distance to the edge of the plantation and a positive association with canopy openness. These were consistent with previous findings that light availability is a major influence on ground vegetation diversity of plantations (Gilbert, 2007, Simmons and Buckley, 1992, French et al., 2008, Ferris and Simmons, 2000, Bremer and Farley, 2010, Hartley, 2002). More open canopies, either owing to species planted, management practices, e.g. thinning, and/or proximity to edge (effects), allow more light to reach the ground vegetation layer, thereby increasing diversity (Bremer and Farley, 2010). That lower planted tree density and higher canopy openness were positively related to diversity highlights the importance of strategic planning in forestry with regards to planting species, arrangement of trees in stand and forest cycle management such as thinning (Ferris and Simmons, 2000).

Higher typical woodland vascular plant richness was predicted in Scots pine mixes compared to the other two forest types. It appears the higher canopy openness of Scots pine mix stands made them more favourable habitats for typical woodland species that are adapted for the varying light levels in forests, and so tolerate a certain level of canopy closure but cannot survive below a certain canopy extent (Thomas and Packham, 2007). From the general lack of forest type as a significant variable, it appears that the light environment, rather than the tree species planted *per se* may exert a greater influence on the ground vegetation diversity of plantations (Bremer and Farley, 2010).

Area of existing semi-natural woodland surrounding plantations has been reported as influencing ground vegetation diversity by acting as a seed source (Smith et al., 2005, Williams et al., 1998, Brockerhoff et al., 2008, Felton et al., 2010a, Bremer and Farley, 2010, Carnus et al., 2006). Plantations established on previously forested lands, are generally expected to support higher diversity given time to develop structural diversity,

favorable microclimates and litter and humus layers that encourage plant colonization (Bremer and Farley, 2010, Brockerhoff et al., 2008). Our modelling results found area of semi-natural woods between 200m and 1km was positively associated with vascular SR (non-significantly). However, contrary to what was expected, for non-vascular SR the association between area of semi-natural woodlands within 200m was negative. Vascular plant species generally have wider dispersal abilities than non-vascular species (Vanderpoorten and Goffinet, 2009) so perhaps with larger areas of semi-natural woodland in close proximity to sites there was more successful colonization of vascular plants that then out competed non-vascular species. As many typical woodland species have poor dispersal abilities, proximity to old woodland can be an important influence on their diversity at a recent forest site (Dolman and Fuller, 2003, Rackham, 2006, Peterken and Game, 1984). Our modelling results indicate that the distance of a site from an area of old woodland may be more important to vascular plant richness than whether there is a mix component, as distance to old woodland appears in the final model whereas forest type does not. Further evidence of an influence of site history on typical woodland SR is indicated as the plantation in which the ‘notable’ woodland species of Perrin *et al.* (2008a) occurred in this study was established on an area that was previously old woodland. Moreover, of the 7 sites with highest typical woodland species richness, 5 were pure Norway spruce sites on or adjacent to old woodland. However, it should be noted that the migration of any species is only possible if conditions are favourable to the potential colonists at the ‘receiving’ site (Dzwonko and Gawroński, 1994). The conditions at the study sites here may not have been favourable to colonization by species from surrounding areas resulting in the low occurrence of distance to old woodland and area of semi natural woodland in the final models.

LOI provides a basis for comparing the organic/mineral character of soils (Smith et al., 2005), i.e. higher LOI indicates higher organic content that, for example, is often found in peat soils. It has been reported as impacting ground vegetation diversity (Hunter, 1990). Smith et al. (2005) reported that with increasing LOI there was higher SR in the early growth stages of Sitka spruce plantations. However, in the modelling results for this research it was not found to be significant for any of the species metrics.

Investigations into the potential value of conifer plantations for non-vascular diversity, and how they might be managed to improve habitat quality, have focused on the value of deadwood as a substrate for non-vascular species (Humphrey et al., 2003, Smith et al., 2005, Raabe et al., 2010, Márialigeti et al., 2009). That almost 50% of non-vascular species recorded in this survey were growing on deadwood highlights the importance of this habitat; however, modelling results showed no significant relationship between CWD volume and non-vascular species richness metrics. Deadwood volumes were low in the study sites here when compared to those expected in unmanaged forests (Sweeney et al., 2010b, Kirby, 1998) and this may have contributed to the lack of significant relationships with CWD volume in the models for non-vascular SR. Nevertheless, it is recommended that continuity of deadwood supply should be maintained during the forest cycle so that there is no local loss of deadwood specialist forest species.

3.6 Conclusions and recommendations

In an industry traditionally based on monocultures the presence of a second tree crop species in a plantation is expected to play an important role in the structure and functioning of a plantation ecosystem (Ferris and Humphrey, 1999). However, this research found that the presence of a second species in a plantation is not always a useful predictor of ground

vegetation diversity as there were no significant differences in species diversity metrics between the mixed and pure forest types. It is proposed that, rather than a reflection of the secondary species not impacting on ground vegetation diversity *per se*, this result was due to the low representation in the mature canopy of the secondary species. A number of factors were proposed as causing this including site selection issues, incompatible species planted in inappropriate configurations and inadequate management to ensure that the secondary species thrives. Several factors were found to be important for ground vegetation diversity in these three plantation types namely, canopy openness, planted tree density, distance to edge of plantation, area of semi-natural woodland within 1km of sites and forest type. Not only is there scope for management to improve diversity by manipulating these factors, they have potential as indicators of diversity. The addition of the mix species studied here to Norway spruce did not increase species richness at the stand scale. The Scots pine mixes supported a community with a high proportion of typical woodland indicator species suggesting this mixed plantation type has the most potential of the three forest types to develop native woodland ground vegetation. Factors found to be important in driving the differences in forest type communities were gradients in several soil variables, elevation, age, stand structural measurements and landscape variables at the 1km scale. In this research structural diversity was positively correlated with all total and vascular SR metrics and, as previously reported, it can be used as an indicator of diversity (Peterken and Game, 1984, Munro et al., 2009)

Recommendations for forestry practice from this research include that enhancement of ground vegetation diversity in mixed plantations would benefit from the secondary species forming a substantial and ecologically relevant component of the mixed plantation. This may be achieved by planting more ecologically compatible species in an arrangement

conducive to the growth of the secondary species and undertaking adequate management to ensure the secondary species thrives. Suitable planting arrangements vary from planting the secondary species in patches within a matrix of the main species to planting secondary species at a larger scale in non-intimate stands adjacent to the main species. This second option may be preferable from both an ecological and an economic perspective.

Ecologically non-intimate mixed stands may increase diversity as well as or even higher than intimate mixed stands and from an economic perspective they may require less intensive management. The non-intimate mix in comparison with intimate mixed stands can benefit ground vegetation by creating long gradients of suitable habitat on the forest floor of, for example, increased light and reduced needle litter (Simmons and Buckley, 1992, Smith et al., 2005, Wallace et al., 1992). Management to favour the secondary species may conflict with the commercial viability of plantations either through reduced representation of the commercial crop or due to resource expensive management operations. Previous research on ground vegetation diversity in plantations has demonstrated that among the principal drivers of ground vegetation SR are canopy cover (Raabe et al., 2010, Márialigeti et al., 2009, Carnus et al., 2006, Eycott et al., 2006, Smith et al., 2005). This research also found that canopy cover has a major influence on SR. Further research into which and how secondary species can be best incorporated into forest planning to maximise their potential in enhancing biodiversity is recommended.

4 Vegetation succession in conifer clearfell

To be submitted as: Karen Moore, Daniel L. Kelly, Fraser J.G. Mitchell. Vegetation succession in conifer clearfells. Biological Conservation.

4.1 Abstract

The expansion of woodland areas and the conservation and enhancement of biodiversity are core components of the environmental aspect of Sustainable Forest Management (SFM). These are especially relevant in Ireland, which has one of the lowest forest covers in Europe. The majority of Irish forests are plantations of non-native conifers, with semi-natural woodlands occupying approximately 1% of the land cover. With growing recognition of global deforestation and forest degradation along with the increasing implementation of SFM, woodland restoration and creation are progressively prioritised in forestry policy. While there is some guidance on the establishment of native woodlands on clearfelled conifer stands there is a lack of empirical work. This paper investigates how successional trajectories from conifer clearfell may be manipulated to move towards native woodland restoration by comparing vegetation diversity and composition over a 10 year interval. Large herbivores are major drivers of forest change across the globe and this research represents an important contribution to long-term experiments examining the impacts of large herbivores on vegetation succession. In 1999, nineteen pairs of 400 m² permanent plots were established with one plot of each pair fenced to exclude large herbivores. Vegetation was surveyed in 1999 and in 2009. Exclusion of large herbivores had a significant positive influence on typical woodland species richness and overall vegetation composition over time. The differences in tree development between fenced and unfenced plots indicated that, unless grazing pressure is further reduced in unfenced areas,

woodlands are unlikely to develop in these areas. Previous crop species, soil type, soil pH, brash cover, and time since felling were also found to be influential in explaining differences among vegetation communities. Generally, succession was to a heather dominated vegetation type, with or without fencing. It is recommended that intensive management, e.g. planting, should be delayed further than 10 years so that vegetation and tree regeneration potential can be assessed; however, management of grazing levels and the prevention of bracken dominance may be necessary in certain areas to promote succession, especially if the desired trajectory is to native woodland. Woodland restoration is likely to be most successful near (within approximately 250 m of) existing wooded areas, as dispersal of native tree species and woodland understory vegetation may be facilitated. Deadwood retention should be a priority in restoration sites. In certain circumstances allowing succession to proceed to heathland may be a more feasible conservation outcome than woodland restoration. Alternatives to ‘clearfell and replacement’ management for woodland restoration should be investigated, including ‘gradual replacement’ as these may negate the negative impacts of clearfell on diversity and vegetation succession.

4.2 Introduction

Irish forests developed a substantial, though not uniform, cover during the current interglacial period, i.e. over the last 10,000 years (Mitchell and Ryan, 1997, Mitchell, 2009). However, forest cover began to decline drastically following clearance by Neolithic farmers between 5,000 and 6,000 years ago and deforestation continued until only approximately 1% of Ireland was forested by the early 20th century (Neeson, 1991). Since then, forest cover has increased to approximately 10% of total land cover in the Republic (Forest Service, 2007). Only approximately 1.9% of this is semi-natural

woodland as the majority of the increase was due to state afforestation and currently the non-native conifer, Sitka spruce (*Picea sitchensis*), forms 52% of the forest estate, with other conifers making up 23% and broadleaves 25% (Forest Service, 2007).

Following on from the UN Environment and Development Conference in 1992, international commitments to Sustainable Forest Management (SFM) have resulted in a shift away from viewing forestry solely for timber production towards multi-purpose forestry, giving equal regard to the social, environmental and financial aspects of forests (Farmer and Nisbet, 2004, McAree, 2002, UNEP, 1992). The expansion of woodland areas and the conservation and enhancement of biodiversity are core components of the environmental aspect of SFM (Forest Service, 2000b, Forestry Commission, 1998, Christensen and Emborg, 1996, MCPFE Liaison Unit Warsaw, 2007). With growing recognition of global deforestation and forest degradation along with the increasing implementation of SFM, woodland restoration and creation are progressively being undertaken (Newton and Kapos, 2003) and is especially relevant in Ireland, which has one of the lowest forest covers in Europe (Forest Service, 2007, MCPFE Liaison Unit Warsaw, 2007).

Land previously occupied by conifer plantations can be suitable for active management and/or natural regeneration to pre-forestry habitats i.e. restoration or even habitat creation (Pryor et al., 2002, Thompson et al., 2003). After clearfelling plantations may undergo succession to habitats such as heathland (Eycott et al., 2006) or woodland (Truscott et al., 2004) or indeed they may regenerate into another rotation of the previous plantation species (Hill, 1986). In Ireland, attempts to address the poor quality and low cover of native woodland include not only restoration of existing degraded woods under

programmes such as Coillte's LIFE priority woodland work (Anon, 2009b), but the planting of new native woodlands under programmes like the Millennium Forests Project and the Native Woodland Scheme (NWS). The Millennium Forests project has restored existing woodland and created new native Irish woodland on over 600 ha, with most of the sites on areas that were previously native woodland (Anon, 2009a); however, only one of these sites was a conifer plantation prior to replanting (Lawlor J., pers comm.). The NWS grant-aids the conservation of existing native woodlands and the establishment of new native woodlands on public and private land (Forest Service, 2001). To date, nearly 1023 ha have been managed under the establishment element of this scheme and, of that, an indicative figure for the area of conifer plantation conversion to native woodland is 250 hectares (Foley, N., pers comm.).

A recent focus of restoration efforts in Britain is the conversion of conifer plantations established on old woodland, and called Plantations on Ancient Woodland Site's (PAWS), to semi natural woods (Pryor et al., 2002). Many of the practices of PAWS restoration (Thompson et al., 2003) and for the creation of new native woods (Harmer, 1999, Rodwell and Patterson, 1994, Little et al., 2009) can be applied to the restoration of native woods on conifer clearfell. A major management issue in woodland conservation and restoration programmes on all types of sites is the control of wild and feral populations of large herbivores because, although most European forests evolved under the influence of large grazers, many countries have lost the natural predators of these grazers (Vera, 2000). Heavy grazing can reduce diversity, both in terms of species and structure, and inhibit regeneration of trees (Hester et al., 2000, Kelly, 2002, McEvoy, 2006, Mitchell and Kirby, 1990, Putman et al., 1989, Pigott, 1983). Conversely, grazing at too low a level can be problematic as competitive plant species and/ or vegetation types may become dominant

(Hester et al., 2006, Truscott et al., 2004). Furthermore, there are other factors that may be particular to restoration on clearfell. The previous conifer crop along with its management and harvesting methods used can alter subsequent vegetation succession in ways that may affect woodland restoration (Jalonen and Vanha-Majamaa, 2001, Rodwell and Patterson, 1994, Wallace and Good, 1995, Eycott et al., 2006, Cooper et al., 2008, Moola and Vasseur, 2004, Roberts and Zhu, 2002). Brash on site following clearfelling may also impact access of grazers and affect establishment and growth of woody and herbaceous species (Truscott et al., 2004). Although natural regeneration of native woods is most desirable in terms of both ecology and expense, where conifer plantations were located long distances from significant native tree populations planting would probably be necessary to regenerate native tree species (Little et al., 2009, Brunet and von Oheimb, 1998, Pryor et al., 2002). Clearfelled sites, as disturbed areas, are likely to provide opportunities for the invasion of exotic and /or highly competitive, early successional species often to the detriment and/or exclusion of desired species such as late successional typical woodland species (Cooper et al., 2008). With all of these potential influences on restoration, it is apparent that restoration management at some level would always be required. In Britain, Truscott *et al.* (2004) investigated the restoration of native oakwoods on conifer clearfell over a 2 year period and reported that browsing on seedlings was higher in unfenced areas but in fenced areas increased competition from other vegetation was detrimental to the survival of desired species. Also, although brash excluded grazers, it also resulted in lower survival and growth performance of seedlings.

Despite the lack of empirical research there is guidance on the establishment of woodlands on clearfelled conifer stands, mainly from Rodwell and Patterson (1994) for Britain and Little *et al.* (2009) for Ireland. Site preparation was highlighted as an important influence ,

for example, the prevention of site damage from harvesting machinery and minimisation of the ground area covered with dense brash that could impede natural regeneration.

However, they noted that light brash cover may provide shelter for establishment. They also recommended felling during periods of poor conifer seed production to minimise conifer regeneration.

In this study vegetation succession and habitat restoration were surveyed on clearfelled plantations of, mainly, Sitka spruce after a ten year interval. With regards to the areas under survey in this research oak-birch-holly woodland was deemed to be an appropriate community for restoration. Factors taken into account in this decision by Smith (2003) included the ecology of surrounding existing semi-natural woodlands, soil type, climate and historical evidence (Carey, 2009, Mitchell, 1988). The conservation value of these upland acid oakwoods in Ireland is recognized and they are included as “old sessile oak woods with *Ilex* and *Blechnum* in the British Isles” in Annex 1 of the EU Habitats Directive (91A0) (Fossitt, 2000). At the time of the first survey, plots were established with fencing, and planting and weeding were undertaken to compare restoration *via* natural succession with intensive management. In this paper we quantitatively compare results from the first vegetation diversity and composition survey in 1999 carried out by Smith *et al.* (2003) with a second survey undertaken in 2009. The key aims of this paper are as follows:

1. to compare directly the species richness and vegetation composition between the time of treatment establishment and 10 years later

2. to identify factors important in determining the succession of vegetation communities on conifer clearfell, particularly regarding communities of conservation interest
3. to recommend management practices for restoration of native woodland on conifer clearfell

In this chapter the plots were set up as long-term experimental sites so rather than relying solely on the chronosequence approach for this successional study it was possible to resurvey these sites after 10 years. This increases the robustness of the results from a chronosequence approach especially where there may be confounding differences among sites. The plots were set up as part of a chronosequence with time since felling differing between sites and are not in that sense directly comparable to the earlier stages of plots in Chapter 2. However, this chapter and Chapter 2 represent outcomes of different management options for foresters according to whether the clearfell site is replanted with the same crop or restored to native woodland. The results from this research will inform our understanding of how succession maybe influenced by different management techniques and thus how resources can be used efficiently for habitat restoration on conifer clearfell.

4.3 Methods

4.3.1 Site selection and design of permanent plots

In 1999, 13 pairs of 400 m² experimental plots were established in the Wicklow Mountains in the east of Ireland and 6 pairs in the upland areas of Killarney National Park in the southwest by Smith (2003) (**Fig. 4.1**). The sites were located on clearfelled conifer plantations that were not going to be replanted with timber crop species and had been

felled between 1 to 12 years prior to initial survey in 1999. These two areas encompass a broad range of environmental conditions and, in particular, they are at opposite ends of the main climatic gradient in Ireland, increasing the wider geographical applicability of this study. The climate of Killarney is extremely oceanic, with high rainfall and mild temperatures whereas the central Wicklow Mountains are slightly more continental, receiving less rain (Mitchell and Ryan, 1997). From first and second edition OS maps it was found that no sites were likely to have been semi-natural woodland prior to afforestation.

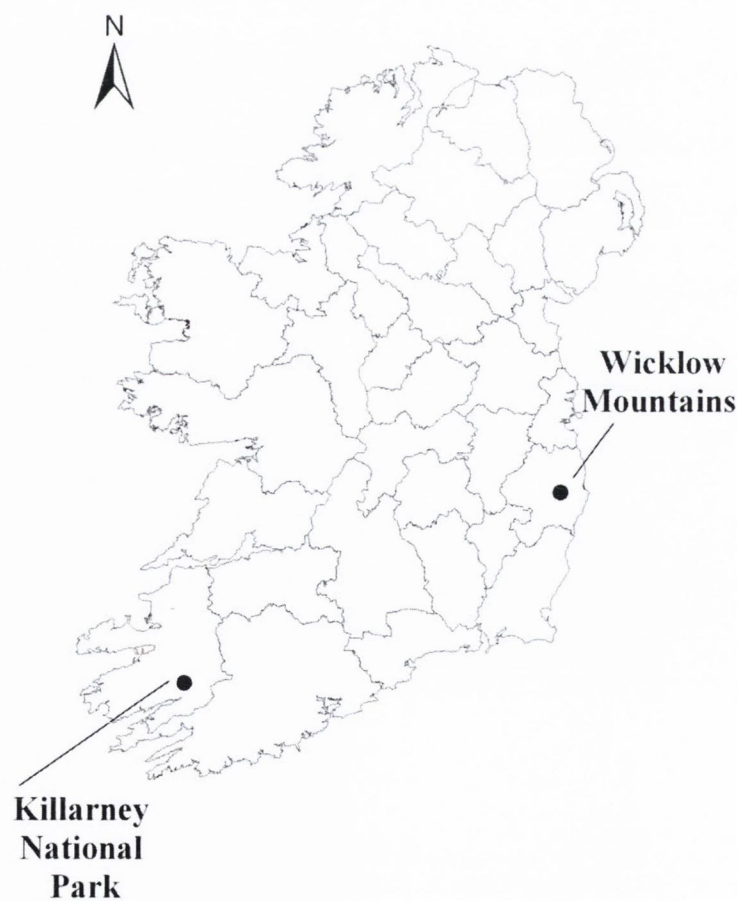


Figure 4.1. Locations of the Killarney National Park and Wicklow Mountains study sites (counties are outlined in map).

Site characters of the plots resurveyed in 2009 are outlined in **Table 4.1**. The majority of plots were located mostly in former plantations of Sitka spruce, however, 3 pairs were on former lodgepole sites, 2 pairs were in former larch sites and another pair was on a former mixed stand of lodgepole and Sitka spruce (hereafter referred to as mixed). Time since felling in 1999 varied from less than 2 years in 9 plots to 5-11 years in the remaining 10 plots. Brown earths and podzolics were the soil type of 5 pairs of plots, peat and podzols were in 3 pairs of plots each with the remaining 8 plots on peaty podzols. Most soils were not gleyed. Distance to native seed source varied greatly among the plots (n= 19, mean 314 m $\pm$ s.e. 48).

Table 4.1. Site characters of the plots resurveyed in 2009 are outlined below. The previous crop species are *Picea sitchensis*, Sitka spruce: *Pinus contorta*, lodgepole pine: *Larix kaempferi*, Japanese larch. Soil type assigned during initial survey in 1999 according to Gardiner and Radford (1980) Gleying; 1 – present, 0 – absent. Distance to native seed sources are averaged values for plots in groups of pairs.

Location	Previous Crop	Fell Year	Soil type	Gleying	Distance to native seed source (m)
Killarney	<i>Picea sitchensis</i>	1994	blanket peat	0	250
	<i>Picea sitchensis</i>	1994	blanket peat	0	250
	<i>Picea sitchensis</i>	1994	blanket peat	0	250
	<i>Picea sitchensis</i>	1988	peaty podzol	1	100
	<i>Picea sitchensis</i>	1988	podzol	1	100
	<i>Picea sitchensis</i>	1988	podzol	1	100
Wicklow	<i>Larix kaempferi</i>	1991	brown earth	0	125
	<i>Larix kaempferi</i>	1991	brown earth	1	125
	<i>Pinus contorta</i> + <i>Picea sitchensis</i> mixed	1993	brown podzolic	0	125
	<i>Picea sitchensis</i>	1998	peaty podzol	0	500
	<i>Picea sitchensis</i>	1998	podzol	0	600
	<i>Pinus contorta</i>	1997	peaty podzol	0	600
	<i>Pinus contorta</i>	1997	peaty podzol	0	600
	<i>Picea sitchensis</i>	1998	peaty podzol	1	600
	<i>Picea sitchensis</i>	1998	brown earth	0	180
	<i>Picea sitchensis</i>	1998	peaty podzol	0	180
	<i>Pinus contorta</i>	1997	peaty podzol	0	600
	<i>Picea sitchensis</i>	1998	brown earth	0	180
	<i>Picea sitchensis</i>	1993	peaty podzol	0	500

A chronosequence approach was employed by investigating stands felled at different times as well as the repeat sampling after 10 years. Chronosequence studies, however, are often subject to confounding site influences that are independent of time and in this study, due to the limited availability of suitable clearfelled areas, balanced sampling was not possible across felling year, previous conifer crop, soil type or site location. Plot position within a given clearfell was determined randomly where possible but avoided unusual areas e.g. extremely wet areas (with high covers of *Sphagnum* spp) and the edges of the previous plantation. The plots were managed under the 'clearfell and replacement' method of restoration. Three experimental treatments were applied at plot establishment outlined below.

1. Pairs of 400 m² large herbivore exclosures with 400 m² unfenced control within 1-3 m. The remaining two treatments were allocated to the four 10 × 10 m quarters of the plot of each fenced and unfenced plot.
2. Planting in each plot of two randomly selected quarters with 18 sessile oaks (*Quercus petraea*) and the other two quarters with an oak-birch mix of 6 oak and 12 downy birch (*Betula pubescens*).
3. Weeding (manually) of planted trees in one randomly chosen quarter of each planting mix (100% oak and the oak-birch mix). All exotic species were removed from each weeded quarter.

4.3.2 Data collection

Individual vascular plant species cover to the nearest 5% were recorded from eleven 1 m² quadrats in each plot in 1999 and in 2009 from 5 quadrats (a randomly chosen subset of the original eleven quadrats and encompassing each treatment type). Vascular plant

nomenclature followed Stace (2010). In both years percent ground covers were also estimated to the nearest 5% of all field layer species combined (herbaceous species and dwarf shrubs e.g. heather (*Calluna vulgaris*)), all woody species (including tree seedlings and large shrubs, brambles (*Rubus* spp) and gorse (*Ulex* spp) but not dwarf shrubs), bryophytes, bare soil, exposed rock, plant litter, brash and deadwood. Brash was defined as woody debris less than 5 cm diameter whereas deadwood was defined as stumps and logs greater than 5 cm diameter. In 1999 data on previous crop, time since felling, landuse prior to plantations (from first and second edition Ordnance Survey maps), soil type and gleying (Gardiner and Radford, 1980) were collated and soil pH was measured (using a glass electrode on field moist soil) **Table 4.1**. In 1999 the distance to nearest significant native seed source of trees was estimated in metres from the plots (significant seed source was a group of > 20 mature trees e.g. native woodland, riparian vegetation) **Table 4.1**. In 2009, as a proxy for canopy development, the stem density of both planted and naturally regenerated trees 100 cm and over in height (number per 400m²) were calculated for both years. Structural variables include stem density and all ground covers.

4.3.3 Data analysis

Vascular plant species richness (SR) was calculated for each quadrat. To assess the restoration efforts species recorded were also classified according to their affinity for woodlands: low (not usually found in woodlands), moderate (frequently occurring in both woodlands and unwooded habitats) or high (typical woodland species), using information on habitat preferences from Irish and British floras for vascular plants (Hubbard, 1984, Jermy et al., 1982, Preston et al., 2002, Webb et al., 1996, Grime et al., 2007, Hill et al., 2004) and for bryophytes (Hill et al., 2007, Paton, 1999, Purvis et al., 1992, Smith, 2004, Watson, 1981). (Refer to **Appendix 1** for details).

Prior to statistical testing data exploration for normality, heterogeneity of variances, outliers and collinearity was carried out using SPSS 16 (SPSS, 2007), Minitab 13 (2000) and R (R Development Core Team, 2010). Where outliers were detected the data were transformed as appropriate (detailed in results). Non-normal distribution and heterogeneity of variance was dealt with by transformation and if data still did not meet assumptions of parametric tests satisfactorily non-parametric statistics were employed.

Non-metric multidimensional scaling (NMS) ordinations were used to illustrate relationships between vegetation of plots and environmental variables as this technique is based on ranked distances and has thus been found particularly suitable for the analysis of non-normal data from ecological communities (McCune and Grace, 2002). The “medium” autopilot settings in PC Ord version 5.26 were used giving a compromise between fast results and a thorough search for the solution of best fit (McCune and Mefford, 2006). The following parameters are used: Sorensen distance measure; 200 maximum number of iterations; Random Starting coordinates; 50 runs with real data; Step down in dimensionality (Initial step length = 0.2); 50 runs with randomized data. NMS axes are arbitrary (Legendre and Legendre, 1998), so varimax rotation was used to help interpret the ordination axes as it maximizes the variance of species correlations with the ordination axes, resulting in groups of sites with very high and very low axis correlations (Lichstein et al., 2002). With NMS a low final stress and instability are sought (McCune and Grace, 2002). Multi-response Permutation Procedure (MRPP) was used to test differences between groups. The T statistic describes separation between groups with more negative values representing a stronger separation. The p-value associated with T is not independent of sample size, so the statistic A , chance-corrected within-group agreement, is used to illustrate homogeneity *within* groups i.e. higher values indicate a stronger separation

between groups. A approaches 1 when distances within groups are smaller than the distances between groups and $A < 0$ when distances within groups are larger than the distances between groups. Community ecology values are commonly below < 0.1 and those above > 0.3 are considered high (McCune and Grace, 2002).

NMS ordination and MRPP analysis were undertaken to investigate whether there was an effect of weeding and planting experimental treatments from 1999 on species composition in 2009. Species occurring in less than five plots were removed from data for this analysis to decrease instability and stress of NMS. There was no treatment effect of weeding or planting by 2009 thus quadrat data were averaged per plot and these average plot values were used in analyses (refer to **section 4.4.1** for detailed results).

Means of diversity metrics (no rare species deleted) and structural variables were calculated per fencing treatment for each year and significant differences were explored both between fenced and unfenced pairs in the same year and in the same plot over the 10 year time period (t-test used for parametric data and, where transformation did not satisfy parametric assumptions the non-parametric test, Mann Whitney was used, or if paired, the Wilcoxon signed rank test).

MRBP (Multi-Response Block Procedure) is a variation of MRPP for paired sample designs. It uses a blocking variable to focus on within block differences thus reducing variation due to other factors and maximizing the ability to detect a treatment effect due to the block (McCune and Grace, 2002). MRBP was carried out on fenced and unfenced plot pairs in each year separately. MRPP was carried out for each year separately to investigate

the influence of the categorical variables soil type, gleying and previous crop on species composition. MRPP for each year between the two survey locations investigated whether locational effect would be strong enough to justify splitting the data into Killarney and Wicklow plots. Spearman's rho (r) non-parametric correlation analysis between variables and NMS axis scores and among variables for each year separately were carried out to aid interpretation of the ordination and investigate possible drivers of species composition differences and correlation respectively. *Post hoc* p -value multiple comparisons corrections, such as Bonferroni or Dunn-Sidak, were not applied due to criticisms that they are too conservative as they reduce the level for significance below the usual 0.05 and thus significant relationships may be missed (Dytham, 2003). Correlations were viewed with caution when they did not appear to be ecologically meaningful.

NMS of data from both years combined was carried out, with species occurring in two or less plots over both years removed to reduce the influence of rare species. The distance that plots moved in ordination space over the 10 year period was calculated using NMS axis scores and

$$d = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2}$$

where d is distance in three dimensional space x_1, y_1 and z_1 are NMS axis scores for axis 1, 2 and 3 respectively at time 1 and x_2, y_2 and z_2 are scores at time 2. To investigate changes in community structure over the 10 year interval Spearman's rank correlations between cover layers and NMS axis scores of both years together were calculated.

Cluster analysis was used to define a minimum number of groups that provide an interpretable summary of the data in terms of vegetation types, but at the same time, to minimise information loss that occurs through amalgamation (McCune and Grace, 2002). Flexible beta clustering with the Sørensen distance measure and β set at -0.25 was used (Lance and Williams, 1967). To choose vegetation clusters different levels of clustering were compared using the sum of significant indicator values (Dufrêne and Legendre, 1997). Maximising the sum of significant indicator values maximises the variation in species distribution explained by a clustering solution. Visual inspection of the dendograms from different levels of clustering highlighted a reasonable separation of plots and the resultant clusters were named for the two species with highest cover.

All data exploration, correlation analysis and tests of significant differences were carried out with SPSS 16 (SPSS, 2007). NMS ordinations, cluster analysis, MRPP and MRBP were conducted using PC-Ord version 5.26 (McCune and Mefford, 2006).

4.4 Results

4.4.1 Impacts of weeding and planting experimental treatments

NMS analysis was undertaken to investigate whether there was an effect of weeding and planting experimental treatments from 1999 on species composition in 2009. However, the structure of data at the quadrat level (a large sample number with a relatively small number of species (<70) and a large proportion of zero's in data) led to highly unstable NMS results (instability > 0.01 with ideal instability being < 0.000001). To accommodate the structure of the data they were split according to location (Killarney and Wicklow) and again into fenced and unfenced, resulting in four subsets of data. NMS ordinations and cluster analysis results were plotted as ordinations and dendograms respectively. Results from the four subsets of data indicated that, in 2009, there was no treatment effect of

weeding or planting. This was confirmed by MRPP pairwise analysis carried out between each treatment type in the four subsets of data, which found no significant differences in species composition among the treatments ($p > 0.05$). As no treatment effect of weeding or planting was found, and to ensure stability and low stress in NMS analyses, quadrat data were averaged per plot and were used in all following analyses.

4.4.2 Species richness and community structure— impacts from fencing treatment and changes over time

In plots resurveyed in 2009 a total of 41 vascular species were recorded in 1999 and a total of 65 vascular species and 52 bryophyte species were recorded in 2009. As bryophyte SR was not recorded in 1999 it was not included in calculations for SR metrics. There were no significant differences between fenced and unfenced plots for either species richness or typical woodland species richness within either year (**Table 4.2** W values). Species richness in fenced plots did not change significantly over the ten year interval, however, there was a significant increase in typical woodland SR in the fenced plots in 2009 compared with 1999. There was no significant difference in species turnover (β_{sim}) between the fenced (0.33 ± 0.03) and unfenced (0.36 ± 0.04) plots over time ($p=0.342$). *Calluna vulgaris*, from here on referred to as *Calluna*, was highlighted as an important species in the succession of the majority of the plots (refer to **Section 4.4.5** and **Fig. 4.4**) and we investigated if there was a relationship between *Calluna* cover and fencing but there were no significant differences in *Calluna* cover between years with same treatment or between treatments in same year. For structural variables between fenced and unfenced pairs there were no significant differences in 1999 while by 2009 there was significantly higher stem density and woody vegetation cover in fenced plots (**Table 4.2** U values). Over time structural variable covers changed significantly in both fenced and unfenced plots except for bryophyte cover and, in unfenced plots, woody vegetation cover. The

changes over the 10 years involved an increase in stem density, woody vegetation and herb cover while all other layer covers decreased. In **Table 4.2** the results from the Mann Whitney in 1999 comparing the different treatments indicated starting conditions between the fenced and unfenced were similar i.e. no significant differences. However, the Wilcoxon signed rank tests between the same treatments in different years indicated there was a significant change in both treatments over time for most variables. The Mann Whitney results from 2009 showed after the ten year interval the conditions between fenced and unfenced pairs were still similar (except for woody vegetation cover and stem density mentioned earlier).

Table 4.2. Median (interquartile) vascular diversity metrics and structural variables per plot in each year (n=19) and treatment (n = 19). Significant differences between years with same treatment were tested using non-parametric Wilcoxon signed rank test (*W*) and between treatments in same year were tested with non-parametric Mann Whitney (*U*). “*” indicates significant difference between treatments (*p* < 0.05). “ns” is non-significant.

		1999	2009	<i>W</i>
Diversity metrics				
Species richness	Fenced	13.0 (6.0)	13.0 (5.0)	
	Unfenced	12.0 (8.0)	13.0 (6.0)	<i>ns</i>
	<i>U</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>
Typical woodland species richness	Fenced	3.0 (2.0)	3.0 (2.0)	*
	Unfenced	3.0 (2.0)	3.0 (4.0)	<i>ns</i>
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Community structure				
Stem density (no.per 400m ²)	Fenced	3.0 (4.0)	116.0 (96.0)	*
	Unfenced	1.0 (3.0)	11.0 (92.0)	*
	<i>U</i>	<i>ns</i>	*	
Woody vegetation cover (%)	Fenced	2.0 (3.0)	35.60 (34.0)	*
	Unfenced	3.0 (5.25)	4.70 (18.60)	<i>ns</i>
	<i>U</i>	<i>ns</i>	*	
Herb cover (%)	Fenced	29.0 (67.0)	69.0 (29.0)	*
	Unfenced	33.0 (58.0)	86.0 (34.0)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Bare soil cover (%)	Fenced	4.0 (6.0)	0.0 (0.0)	*
	Unfenced	5.0 (5.0)	0.0 (0.0)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Litter cover (%)	Fenced	11.0 (24.0)	0.0 (1.0)	*
	Unfenced	12.0 (20.0)	0.0 (1.60)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Brash cover (%)	Fenced	31.0 (39.0)	0.0 (0.60)	*
	Unfenced	21.0 (32.0)	0.0 (0.70)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Deadwood cover (%)	Fenced	10.0 (12.0)	0.0 (1.0)	*
	Unfenced	9.0 (5.0)	0.4 (4.0)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Rock cover (%)	Fenced	1.0 (4.0)	0.0 (0.0)	*
	Unfenced	4.0 (7.0)	0.0 (0.10)	*
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Bryophyte cover (%)	Fenced	20.0 (20.0)	17.0 (26.40)	<i>ns</i>
	Unfenced	17.0 (15.0)	23.0 (22.50)	<i>ns</i>
	<i>U</i>	<i>ns</i>	<i>ns</i>	
Calluna cover (%)	Fenced	4.0 (3.0)	48.33 (47.0)	<i>ns</i>
	Unfenced	4.0 (9.0)	37.0 (57.0)	<i>ns</i>
	<i>U</i>	<i>ns</i>	<i>ns</i>	

4.4.3 Vegetation and environment relationships

MRBP was used to investigate the influence of fencing on species composition and showed that although in 1999 there was no significant effect (p=0.4), by 2009 the effect of

fencing on the species composition between each pair of fenced and unfenced plots was significant ($T = -5.04$, $A = 0.06$, $p=0.001$). MRPP results showed there was an effect of geographical location (Killarney or Wicklow) on species composition in both 1999 ($T = -5.39$, $A = 0.11$, $p=0.0006$) and 2009 ($T = -3.06$, $A = 0.05$, $p=0.02$). However, the low A statistics, especially in 2009, indicated that the vegetation differences between the groups were small relative to the within-sample heterogeneity of each group and so did not justify splitting the data set by geographical location. MRPP comparison of soil type showed that each type had a significantly different vegetation community both in 1999 ($T = -8.05$, $A = 0.22$, $p<0.001$) and in 2009 ($T = -9.50$, $A = 0.22$, $p<0.001$). MRPP found significantly different communities according to previous crop in 1999 ($T = -8.46$, $A = 0.27$, $p<0.001$) except for the mixed and larch plots ($p=0.12$) which had communities that were not significantly different. In 2009 all communities were significantly different according to previous crop type ($T = -8.46$, $A = 0.27$, $p<0.001$) except for the mixed and Sitka spruce plots ($p= 0.21$) whose communities were not significantly different. Although presence or absence of gleying of soil was significant in 1999 ($T = -2.16$, $A = 0.05$, $p=0.04$) the low A statistic for 1999 indicates that the effect was small and it was not significant for 2009 ($p=0.30$).

The varimax rotated NMS results for both years analysed separately gave a 3D solution (ordinations not shown) and the cumulative variation in the data explained by the ordinations were 81.6% for 1999 (final stress =12.23, instability $<10^{-3}$) and 92.3% for 2009 (final stress =10.5, instability $< 10^{-5}$). Monte Carlo test showed that the stress was significantly different to that expected by chance for both ordinations (final stress $p= 0.0196$). Spearman rank correlation coefficients between variables and NMS axis scores (**Table 4.3**) indicated that time since felling had a stronger influence on communities in

1999 than in 2009. In 1999 time since felling was correlated with most structural variables (positively with stem density $r_s = 0.433$, $p < 0.01$, woody vegetation $r_s = 0.439$, $p < 0.01$, herb cover $r_s = 0.841$, $p < 0.01$ and negatively with covers of bare soil $r_s = -0.539$, $p < 0.01$, leaf litter $r_s = -0.662$, $p < 0.01$ brash $r_s = -0.774$, $p < 0.01$ and deadwood $r_s = -0.379$, $p < 0.05$) whereas in 2009 it was only weakly positively correlated with covers of herb ($r_s = 0.332$, $p < 0.05$) and brash ($r_s = 0.326$, $p < 0.05$). Soil pH was weakly correlated with axes; positively with axis 1 and negatively with axis 3 in 1999 and negatively with axis 1 in 2009. Distance to native seed source was positively correlated to axes 2 and 3 in 1999 and with axis 1 in 2009. Stem density was strongly negatively correlated with axis 2 in both years with the correlation strongest in 2009. For both years stem density was, not surprisingly, positively correlated with woody vegetation cover again with the correlation stronger in 2009 (1999 $r_s = 0.441$, $p < 0.01$ and 2009 $r_s = 0.762$, $p < 0.01$). Brash cover was correlated more strongly with all axes in 1999 than 2009 and was positively correlated with deadwood cover (1999 $r_s = 0.616$, $p < 0.01$ and 2009 $r_s = 0.563$, $p < 0.01$). In 1999 herb cover was negatively correlated with all axes and in 2009 bryophyte cover was positively correlated with axes 1 and 3.

Table 4.3. Statistically significant Spearman rank correlation coefficients between variables and NMS axis scores for both years ordinate separately (ordinations not shown). “*” indicates $p<0.05$ and “**” indicates $p<0.01$.

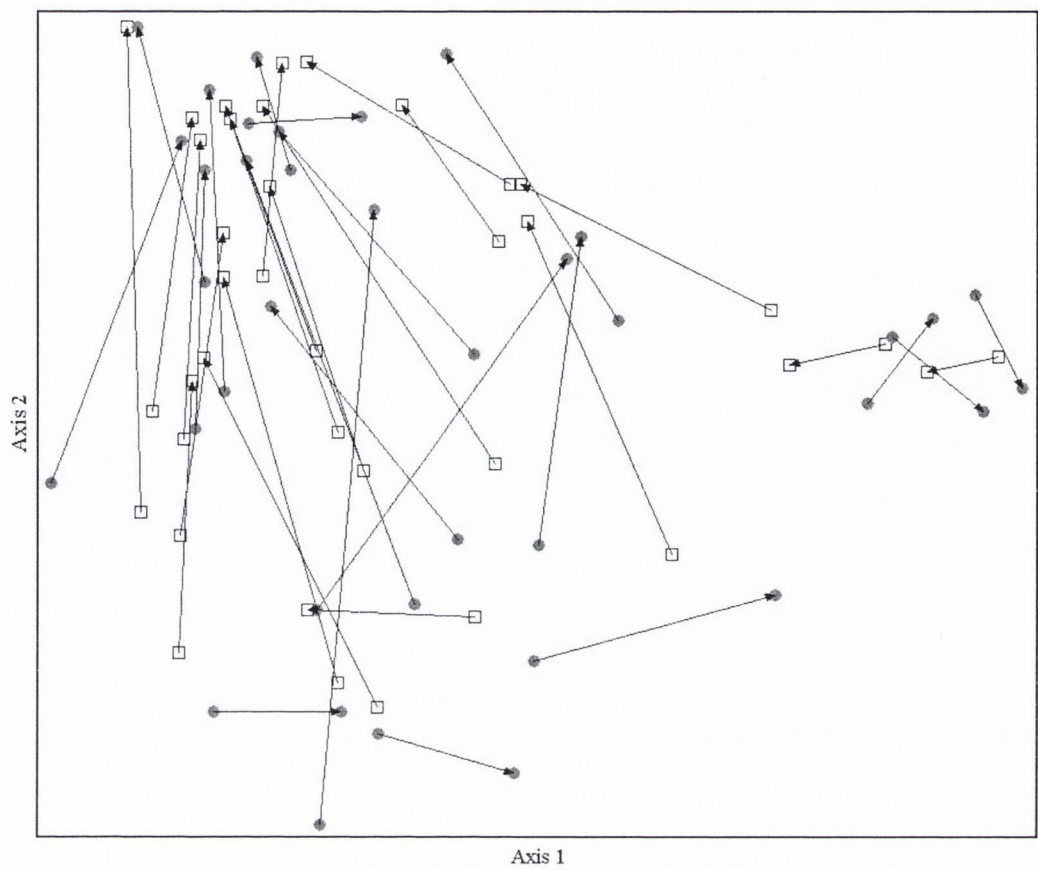
	1999			2009		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Site characters						
Time since felling	-.544**	-.553**	-.423**			
Soil pH	.328*		-.332*	-.363*		
Distance to native seed source		.385*	.589*	.583**		
Structural variables						
Stem density (no. per 400m ²)		-.409*			-.633**	
Woody vegetation cover (%)	-.495**	-.389*			-.475**	
Herb cover (%)	-.613**	-.324*	-.676**			
Bare soil cover (%)						.414**
Leaf litter cover (%)	.548**					-.321*
Brash cover (%)	.481**	.345*	.645**	.426**	.358*	
Deadwood cover (%)			.567**		.358*	
Rock cover (%)					.385*	
Bryophyte cover (%)				.475**		.384*

4.4.4 Vegetation succession

MRBP analysis indicated that vegetation composition changed significantly between the two surveys ($T = -18.26$, $A = 0.19$, $p < 0.001$). To better understand the direction of vegetation change, an NMS ordination was conducted on mean species cover data for plots in both 1999 and 2009 together. The varimax rotated NMS results for both years gave a 3D solution and the cumulative variation in the data explained by the ordination was 84.0% with axis 1 accounting for 30.2%, axis 2 for 29.4% and axis 3 for 24.3% (final stress = 12.65, $p = 0.0196$ and instability = 0.0009 (**Figs. 4.2a, b and c**). Successional trajectories were plotted with the arrows pointing from position in ordination of plot in 1999 towards the plot position in 2009.

The successional trajectories in the NMS ordination showed that some plots had changed vegetation composition substantially, i.e. moved relatively far in ordination space, over the time period, while others had hardly changed at all. **Fig. 4.2a** showed there was a cluster of 5 plots to the far right of axis 1 and mid way on axis 2 that had not, in relative terms, moved far in ordination space along these axes over the time interval. These plots were dominated by *Pteridium aquilinum* (from here referred to as bracken) at both surveys (refer to *pteriaqui* on species plot **Fig. 5.2a**). There is a convergence of plots over time indicated by the successional arrows in **Figs 4.2a-c** converging at the left of axis 1 top of axis 2 (**Fig 4.2a**), left of axis 1 top of axis 3 (**Fig 4.2b**) and to the right of axis 2 and top of axis 3 (**Fig 4.2c**). *Calluna* is a common influential species in the ordination positions of these plots (refer to *callvulg* on species plots **Figs 4.3a-c**). The majority of plots to the left of axis 1, however, had moved a greater distance up axis 2 over time. This variation in the magnitude of change in vegetation composition was reflected in the relatively low *A* statistic of the MRBP (*A*=0.19). The majority of plots, both fenced and unfenced, had moved up along axis 2 over time. Although over time there was a general shift of plots to the left along axis 1, all plots that moved to the right of axis 1 were unfenced. **Fig. 4.2b** showed all plots moved up axis 3 over time. Over the 10 year period fenced plots moved on average more (1.16 NMS axis units $\pm$ 0.81) than unfenced (0.91 NMS axis units $\pm$ 0.10) but this difference was only approaching significance (t-test, *p*=0.056).

a)



b)

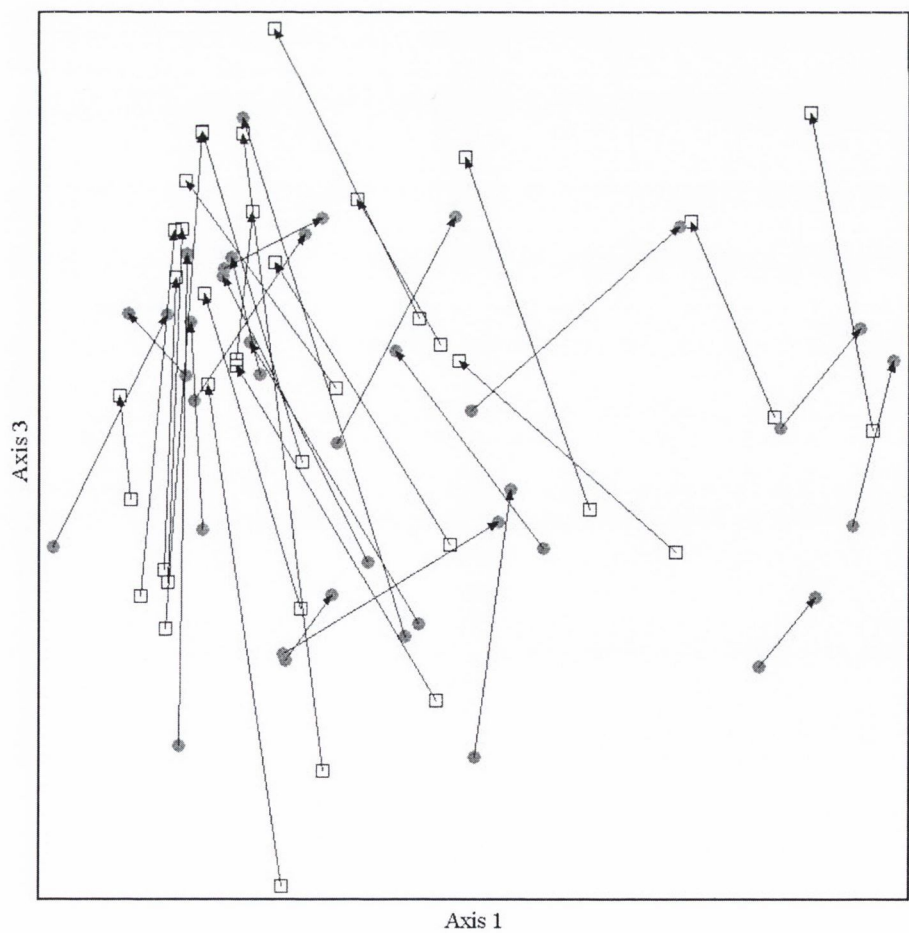


Figure 4.2 c)

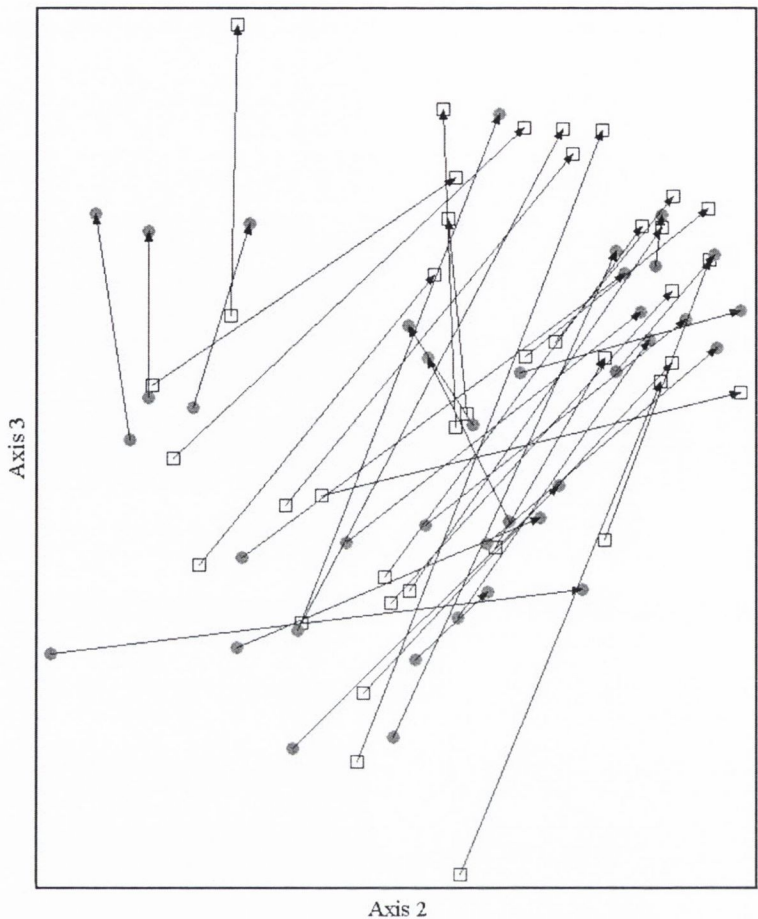


Figure 4.2 (next two pages). **a)** Axes 1 and 2 **b)** axes 1 and 3 and **c)** axes 2 and 3 of the varimax rotated NMS ordination of species composition and cover for fenced (black open squares) unfenced (grey filled circles) plots. Cumulative variation in the data explained was 84.0% - axis 1: 30.2%, axis 2: 29.4% and axis 3: 24.3% (final stress = 12.65, $p = 0.0196$ and instability = 0.0009). Successional trajectories are indicated by lines between the same plots with arrows pointing from 1999 to 2009 positions in ordination space.

The results of Spearman’s rank correlations between structural variables and NMS axis scores of both years together showed correlations were weakest with axis 1, strongest with axis 3 and some strong and some weak with axis 2 (**Table 4.4**). Stem density (highly correlated with woody vegetation cover ($r_s = 0.689$, $p < 0.01$)) and herb cover were highly correlated with axes 2 and 3. The covers of non-vegetation layers (bare soil, rock, leaf litter, brash and deadwood) were negatively correlated with axes 2 and 3. These non-vegetation layers were all also significantly, but weakly, negatively correlated with both stem density and herb cover ($r_s > 0.336$, $p < 0.01$). Axis 1 was weakly correlated negatively with stem density, woody vegetation cover and bryophyte cover and weakly correlated positively with herb cover.

Table 4.4. Spearman rank correlation coefficients between structural variables and NMS axis scores for both years ordinated together. “*” indicates $p < 0.05$ and “***” indicates $p < 0.01$.

	Axis 1	Axis 2	Axis 3
Stem density (no.per 400m ²)	-.304**	.658**	.656**
Woody vegetation cover (%)	-.316**	.251*	.622**
Herb cover (%)	.359**	.550**	.574**
Bare soil cover (%)		-.543**	-.689**
Leaf litter cover (%)		-.528**	-.531**
Brash cover (%)		-.521**	-.795**
Deadwood cover (%)		-.371**	-.745**
Rock cover (%)	.262*	-.348**	-.495**
Bryophyte cover (%)	-.293*		

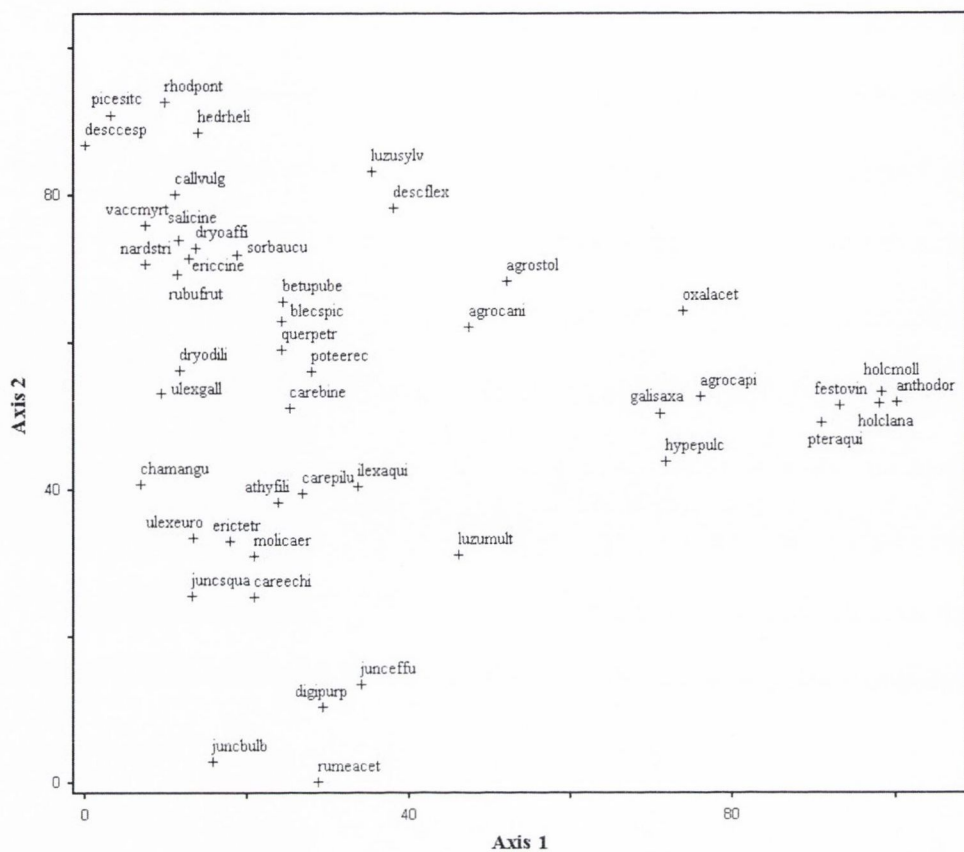


Figure 4.3 a)

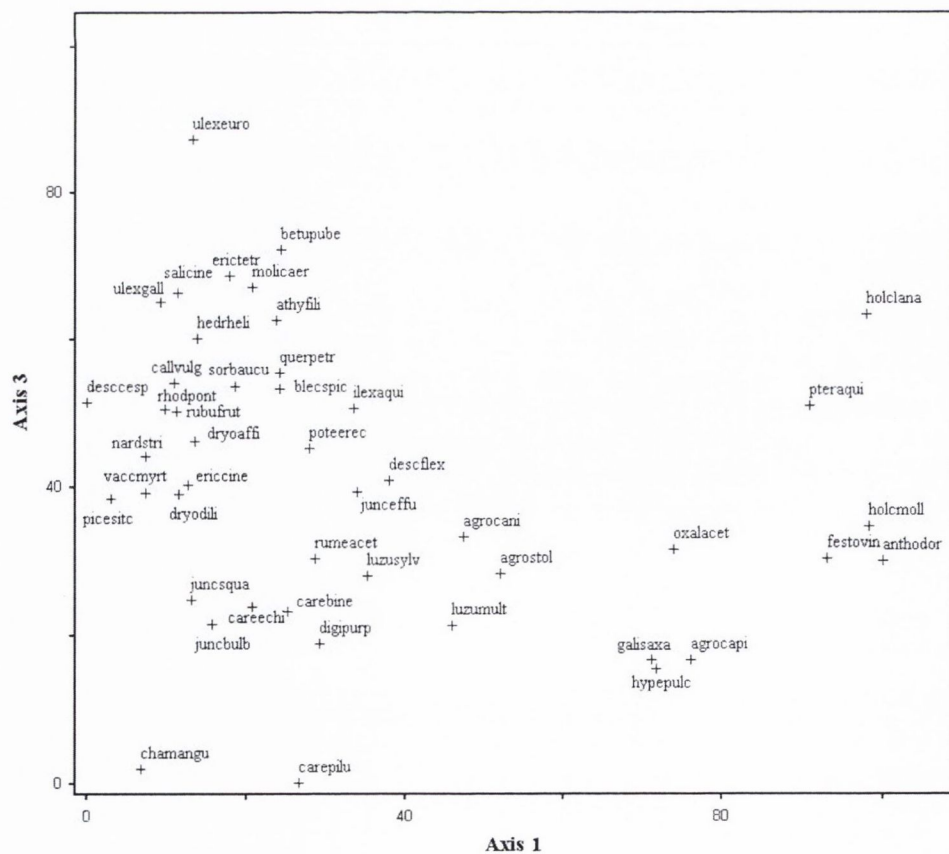


Figure 4.3 b)

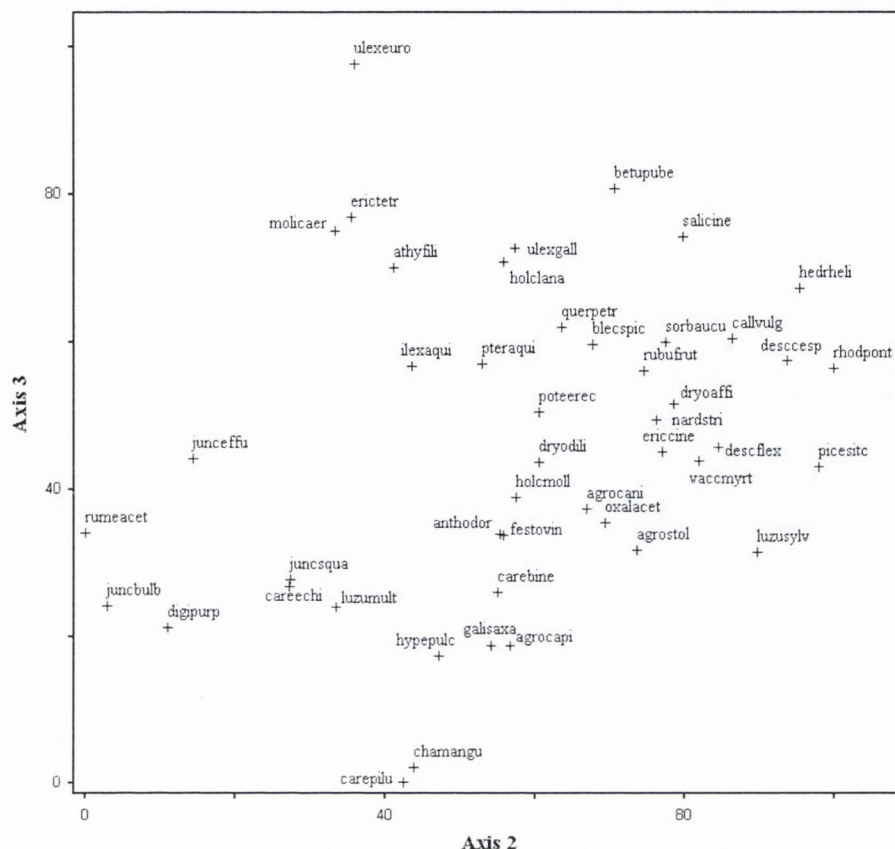


Figure 4.3 c)

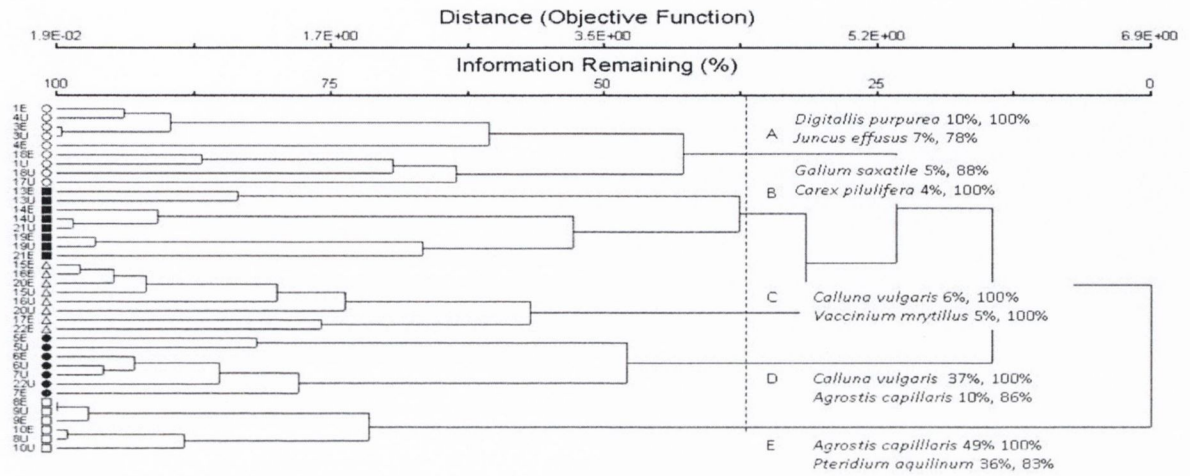
Figure 4.3 (and previous page) a) axes 1 and 2 **b)** axes 1 and 3 and **c)** axes 2 and 3 of species plots for the varimax rotated NMS ordination of species composition and cover. Cumulative variation in the data explained was 84.0% - axis 1: 30.2%, axis 2: 29.4% and axis 3: 24.3% (final stress = 12.65, $p = 0.0196$ and instability = 0.0009). Species codes are first 4 letters of genus and first 4 letters of species name (refer to **Appendix 1** for details).

4.4.5 Changes in vegetation types over the survey period

The five-cluster solution for 1999 (**Fig. 4.4a**) and the six cluster solution for 2009 (**Fig. 4.4b**) were chosen to represent the different vegetation types. Generally very few plots that clustered together in 1999 also clustered together in 2009. However, cluster E in 1999 and F in 2009 had almost total consistency in plot membership over the time period and this appeared to be driven by the cover of bracken. Although in 1999 many of the pairs of fenced and unfenced plots occurred in the same cluster by 2009 the majority of these pairs had split up and occurred in different clusters. There was little evidence in 2009 of clusters

containing a majority of either fenced or unfenced plots. While two of the 1999 clusters had *Calluna* as either primary or secondary dominant in cover, by 2009 this was the case in five of the six clusters.

a)



b)

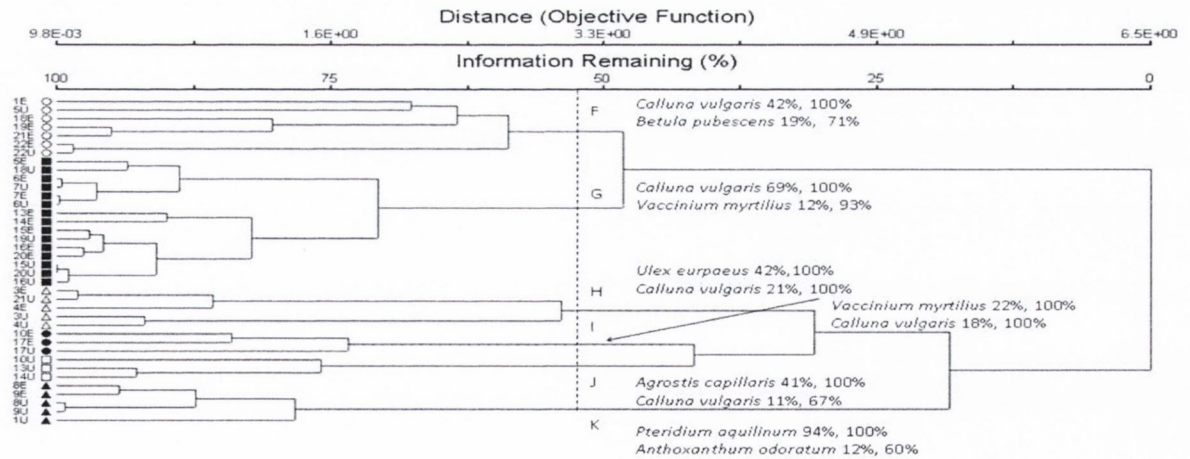


Figure 4.4. Dendrogram of (a) 5 cluster solution (dashed line) A-E for 1999 plots and (b) 6 cluster solution F-K for 2009 plots both formed by flexible beta clustering ($\beta = -0.25$). For each cluster the cover (%) and frequency (%) respectively of the two commonest species are given after the species names. The different symbols highlight which cluster the plot is a member of. The plot codes are “E” for exclosed and “U” for unfenced.

4.4.6 Result summary

There were no significant differences between fenced and unfenced plots for either species richness or typical woodland species richness within either year. The only significant differences between fenced and unfenced plots in the same year were with stem density and woody vegetation cover being greater in fenced plots in 2009. Although species richness did not change over time in fenced plots compared with unfenced, SR of typical woodland plants increased in fenced plots. There was a significant change in the composition of the vegetation developing on clearfells over the 1999-2009 sampling interval. There was more homogeneity among fenced plot communities in 2009 than among unfenced. Weeding and tree planting mixture did not have significant effects on vegetation succession by 2009. Fencing, soil type and previous crop were highlighted as significant drivers of differences in species composition in both years while the effect of plot location was weak. Communities, especially those of fenced plots, separated out over the time period with regards to vegetation structure measured by stem density and herb cover and, on average, fenced plot composition changed more than unfenced although not significantly. Time since felling strongly influenced communities in 1999 but not by 2009 whereas stem density was a stronger influence in 2009 compared with 1999. Cluster analysis found that very few plots that grouped together in 1999 were still in same group in 2009. Although in 1999 many of the pairs of fenced and unfenced plots occurred in the same cluster by 2009 the majority of these pairs had split up and occurred in different clusters.

4.5 Discussion

4.5.1 Impacts of treatments on species richness and composition over time

As there were no significant differences in species composition among the weeding or planting treatments I conclude that there was no significant effect of these treatments on

vegetation succession over the ten year interval. The lack of an impact of fencing on SR after 10 years may be a result of the relatively short time interval between the initial survey and resurvey. Kelly (2000) reported in fenced Irish oak woodlands that an increase in SR followed fence establishment but this increase was transient and by the time of the resurvey (after 26 years) SR levels had decreased below those of the initial survey. This highlights the importance of long-term monitoring as diversity was seen to fluctuate over a longer time scale. Fenced plots accumulated a significantly higher diversity of typical woodland species over the time period whereas unfenced plots did not perhaps reflecting the palatability and/or susceptibility to trampling of these species by grazers if they established outside the fenced plots (Kelly, 2000, Putman et al., 1989). Typical woodland species are, in general, adapted to the differing light levels in forests (Thomas and Packham, 2007, Hardtle et al., 2003) in order to cope with factors such as seasonal changes in canopy cover of deciduous trees and canopy gaps. Thus it is also possible that the higher woody vegetation cover in these fenced plots offered a shaded light environment more suitable for these typical woodland species. In the current investigation, bryophyte cover appeared unchanged during the ten year interval in both fenced and unfenced plots, notwithstanding the possibility mentioned above that a fluctuation in cover during the 10 year interval between surveys may have been missed. It is possible that the identity of the bryophyte species changed over time, however, as bryophyte species were not identified at the initial survey it was not possible to investigate this. Changes over the 10 years in non-vegetation layers was due to the brash and deadwood decaying and the bare soil and exposed rock being covered by increasing vegetation layer cover.

With the removal of grazers, fencing can result in increased plant competition (Hester et al., 2006) that can be detrimental to the growth of certain species. High levels of grazing

can also retard the growth and survival of some species and vegetation types (Truscott et al., 2004). There are critical thresholds in relation to grazing intensity above and below which negative impacts on SR have been reported (Kirby et al., 1994, Hester et al., 2000). In fact the exclusion of grazers via fencing is increasingly considered unsuitable in the long term, except in extremely heavily grazed or deforested areas such as clearfell (Hester et al., 2000, Perrin et al., 2006). The preferred solution is to reduce animal numbers or introduce temporal fluctuations in density so levels of trampling and grazing are sufficient to accommodate species establishment while also light enough to promote survival of the desired vegetation types (Truscott et al., 2004, Mitchell et al., 1996, Hobbs, 2006, Hester et al., 2006). In this research, the fact that there was significantly more woody vegetation cover in fenced plots in comparison to unfenced suggests that, in the absence of other grazing controls, fencing can be important in woodland succession, specifically for the initial (<10 years) establishment and survival of trees. It is important to note that there is uncertainty as to whether the main driver of change by large herbivores is via trampling or grazing, however, most studies on the impact of large herbivores have focused on grazing effects rather than those of trampling (Hester et al., 2006, Hester and Baillie, 1998).

It is not surprising that there were no significant differences in community structure between fenced and unfenced pairs in 1999 as this was the time of fence establishment and these adjacent plots would be expected to have had similar environmental characters and vegetation. Over the 10 years however, the impact of fencing was evident as the exclusion of large herbivores resulted in significantly higher stem density and woody vegetation cover in fenced plots in 2009. This may have been from a combination of increased regeneration and survival rates of planted trees compared to unfenced plots (Perrin et al., 2006, Kelly, 2000, Putman et al., 1989). The differences in stem density between fenced

and unfenced plots in this study indicate that unless grazing pressure is further reduced woodlands are unlikely to develop in these unfenced areas. An estimate of herbivore numbers may place the results of this study in context. The ranges of the three established deer species in Ireland, sika (*Cervus nippon*), red (*Cervus elaphus*) and red-sika hybrids, have increased significantly in the past 30 years, and this has been taken to suggest that population sizes have also increased (Carden et al., 2010). In Killarney, the large herbivores were sika and red deer whereas in Wicklow, deer populations were red-sika hybrids (Cabot, 1999) and sheep had also exerted strong grazing pressure. Goats are primarily browsers, but switch to grazing if the quality of the forage is high (Mitchell and Kirby, 1990). Trespass by sheep occurred in the past in both Wicklow and Killarney, however, since the time of the first survey in 1999, this pressure has substantially reduced owing to changes in farming practices following the EU Common Agricultural Policy reforms from 1992 onwards (Connolly, 2000). Over the ten year interval of the survey it appears, in general, that while grazing pressure from deer has increased, from sheep it has decreased, resulting in an overall decrease in grazing pressure. Starting conditions between the fenced and unfenced plots were similar and again after the ten year interval they were still similar as the only significant differences in either SR or layer covers were for stem density and woody vegetation cover (**Table 4.2**). However, the same treatment significantly changed over time for most variables. This indicated that time was a stronger driver of species richness change than whether the plot was fenced or not. This may have been contributed to by lower than expected grazing levels impacting the unfenced plots.

Although impacts of fencing on species richness were non-significant, fencing not only impacted on stem density and by 2009 it had a significant impact on community composition, and therefore succession. The joint NMS for both years (**Fig 4.2**) showed that

herb cover increased more in fenced plots relative to unfenced, and in fenced plots the covers of non-vegetation layers decreased more relative to unfenced as wood decayed or bare areas were covered by developing vegetation. Many unfenced plots moved in ordination space along axes that were correlated with increased herb cover and decreased stem density and bryophyte cover. In general, bryophytes are shade adapted as they compromise between absorbing sufficient light to photosynthesise and not suffering exposure to excess light that may cause dessication and at extremes cellular damage (Marschall and Proctor, 2004, Vanderpoorten and Goffinet, 2009). These adaptations may confer a competitive advantage to bryophytes in shady conditions (French et al., 2008, Humphrey et al., 2002a, Ferris et al., 2000, Hill, 1986). The unfenced plots perhaps lost bryophyte cover over time due to a lack of canopy development (low stem density) compared with fenced plots, which may have left unfenced plots exposed to high light levels and/or trampling not conducive to the development of a vigorous bryophyte layer.

On average, the majority of the fenced plots moved in one direction in ordination space (uni-directional successional trajectories) while the unfenced moved in various directions. It remains to be seen at the next resurvey whether the fenced plots continue to move, in successional terms, at a faster rate than unfenced plots and whether they converge.

4.5.2 Environmental and site history drivers of succession

Generally there were significantly different communities supported depending on what previous crop had been planted. There was a larger impact (higher *A* statistic) of previous crop type in 1999 compared to 2009 which was not surprising, as the first survey was when the influence of former site conditions would be expected to be stronger. NMS showed that the plots on former lodgepole stands were in the same clusters in 1999 and 2009 (both

Calluna and *Vaccinium myrtillus* dominated) and, although they occupied slightly different locations in ordination space in 1999, they had converged by 2009. Previous crop species can greatly impact the initial conditions for succession after clearfelling (Bremer and Farley, 2010, Eycott et al., 2006). Sitka spruce plantations can cast dense shade, which has a negative impact on vascular plant richness and communities (Eycott et al., 2006, Hill, 1986, Schoonmaker and McKee, 1988, Smith et al., 2005, Carnus et al., 2006, French et al., 2008). Lighter-shading species, such as the lodgepole pine and larch in this study, can conversely support substantial vascular plant populations (Forest Service, 2000b, Hill, 1979, Horgan et al., 2004). However, succession following clearfelling depends more precisely on the condition of the previous crop (e.g. thinned or not) by influencing what species can establish (Hill, 1986). If the stand was of high cover with no or extremely depauperate ground vegetation at maturity, e.g. Sitka spruce, removal of the canopy would constitute a high level disturbance as the light environment changes dramatically. In this case, early succession may be dominated by species from the seed bank or those that survived vegetatively during the clearfell process or in nearby habitats (Hill, 1986, Brunet and von Oheimb, 1998, Eycott et al., 2006, Ferris and Simmons, 2000, Humphrey et al., 2003, Williams et al., 1998). Where the previous crop was a lighter-shading species the light environment will not change as drastically following clearfelling and remnant understory species may be more important in subsequent vegetation succession, compared to the colonisation of new species. Thus vegetation change may be smaller after clearfell of lighter shading tree crops in comparison with that of areas that were previously under densely shading crops. From field observations of existing larch stands surrounding the bracken-dominated former larch plots of clusters E and K it appears that the bracken in the clearfelled plots is a remnant understory species that has increased cover following an increase in light conditions after clearfell (Hill, 1986). These plots changed little in terms of NMS successional trajectories. Other species that have short-lived seeds and cannot

form long term seed banks must rely on dispersal shortly prior to or after felling and must do so before all the potential colonisation sites are occupied (Hill, 1986, Brunet and von Oheimb, 1998, Eycott et al., 2006, Ferris and Simmons, 2000, Humphrey et al., 2003, Williams et al., 1998, Dolman and Fuller, 2003). There was no significant difference by 2009 between vegetation that had developed on plots previously planted with a mix and those with Sitka spruce. Most likely the lodgepole pine was grown with Sitka spruce as a nurse species and so the spruce formed a pure crop at maturity (Forest Service, 2000a). This resulted in the plots that were planted as mixed stands clustering with the pure Sitka spruce plots in 2009. Due to the small number of plots established on former non-Sitka spruce areas, the successional trajectories seen in these plots here should be used with caution to predict succession on clearfells of species other than Sitka spruce.

Soil type was another factor responsible for differences in vegetation communities as previously found by Hill (1986) and French *et al.* (2008). Robust interpretation of soil type effects may be hindered, as there was an imbalance in number of plots on more mineral-rich brown earths and brown podzolics compared with poorer, more organic-rich soils such as podzols and peat. No influence of gleying on vegetation communities may also have been confounded by a lack of balance in sites as 14 out of the 19 plots had no evidence of gleying. Further confounding the influence of soil type may be the importance of soil type in crop species selection for forestry (Forest Service, 2000a, Horgan et al., 2004, Forestry Commission, 2004). Sitka spruce is the most widely planted and highest wood producing conifer over a range of sites in Ireland growing best on heavy gleyed soils whereas growth is limited on infertile peats. In this study it was planted on blanket peat, podzols, peaty podzols and brown earth. Lodgepole pine grows well on a wide range of sites and has been commonly planted on peat and podzol soils and in mixtures with Sitka

spruce. At sites in this study it was planted on peaty podzols and in a mix with spruce on brown podzolics. Japanese larch suits fertile soils and in this study it was planted on mineral rich brown earth. Thus, whether it was the soil type or the previous crop type that exerted a greater proximate influence on succession is difficult to discern as forestry planning relates one to the other.

Soil pH has previously been reported as impacting on ground vegetation composition (Smith et al., 2005, Ferris et al., 2000, Wilson et al., 2001, French et al., 2008, Roche et al., 2009). According to the NMS from 1999 and also from 2009 soil pH was influential in driving differences in community composition among plots. Soil pH may impact on vegetation composition by influencing the nutrient uptake of vegetation e.g. nitrogen (Ferris et al., 2000, Hardtle et al., 2003, Wilson et al., 2001) with certain species adapted to an optimum range of pH (Grime et al., 2007, Ellenberg, 1974, Hill et al., 2007, Hill et al., 2004).

In new forests such as plantations or restoration sites, distance to existing semi-natural woodland has been reported as influencing ground vegetation diversity by acting as a seed source (Smith et al., 2005, Williams et al., 1998, Brockerhoff et al., 2008, Felton et al., 2010a, Bremer and Farley, 2010, Carnus et al., 2006). Typical woodland species are recognised as generally having inefficient dispersal mechanisms so the closer a new forest is to an existing semi-natural woodland the greater the chance that recruitment of typical woodland species will occur (Cooper et al., 2008, Hill, 1979, Peterken and Game, 1984, Verheyen and Hermy, 2001). Distance to native seed source varied widely among the plots and, in agreement with the above, was highlighted by correlation analysis as an influential driver of community composition differences in both 1999 and 2009 (**Table 4.3**).

Time since felling had more of an effect on vegetation composition in 1999 than 2009 for the same reason that previous crop was more influential in 1999 than in 2009 – both factors lessen I their impact over time. In 1999 as time since felling increased there was higher stem density, woody vegetation development and herb cover and consequently, there was a decrease in all other structural layers as wood decayed and/or bare areas were ‘covered up’ by vegetation. However, by 2009 time since felling was only weakly positively related to herb cover perhaps as colonisation sites had filled up for woody species (Dolman and Fuller, 2003) and so only the herb cover continued to fluctuate.

Brash cover was more influential on vegetation composition in 1999 than 2009 as over time it decays. Brash and deadwood (hereafter referred to as woody debris) left on site after felling can release nutrients to the soil as it decays (Hodge and Peterken, 1998). Woody debris may also exert a physical effect on regeneration by deterring grazers or conversely retarding vegetation development by covering potential establishment sites (Truscott et al., 2004). Woody debris can also provide habitat for saproxylic (deadwood dependent) species including bryophytes (Humphrey and Peace, 2003, Smith et al., 2005). Although there was no correlation between woody debris and bryophyte cover in either year there may have been a relationship with bryophyte species richness (Hodge and Peterken, 1998, Humphrey et al., 2002a, Ferris et al., 2000, French et al., 2008) as there was significantly more brash on site in 1999, unfortunately bryophyte SR was not recorded during the first survey in 1999. Hodge and Peterken (1998) suggested that for restored (or new) native woodlands deadwood retention and maintaining deadwood supply should be priorities, especially on sites close to existing native woodlands, as it would offer opportunities for colonization of saproxylic species.

4.5.3 Successional change over 10 years

The dominance, based on cover and frequency, of *Calluna* in the vegetation types found in 2009 was notable. *Calluna* is a light demanding species with an Ellenberg value for light of 8 (on scale of deep shade tolerant = 1 to high light demanding = 9) and so it is not tolerant of deeply shady conditions such as those of a typical Sitka spruce plantation (Hill et al., 2004). Where forestry is felled, light increases and often *Calluna* from the seed bank and/or surrounding areas regenerates. The exclusion of grazers further favours the development of *Calluna* dominated vegetation (Hill, 1986). From the cover and frequency of *Calluna* in the 2009 it can be seen that, over this 10 year time interval, with or without fencing, the vegetation is succeeding to *Calluna* domination. In Europe *Calluna*-dominated heaths and moorlands are considered of high conservation importance (Thompson et al., 1995)

The complexity of factors interacting on vegetation succession is illustrated in clusters E in 1999 and K in 2009 which had almost total consistency in plot membership over the time period but the plots of which moved in various successional directions according to NMS. In the K cluster of 2009 three of these plots were near to each other in Glendalough, previously planted with non-Sitka spruce crops on mineral rich soils and were all felled in the same year. Two of these plots were dominated by bracken at both surveys and in 2009 they clustered with a bracken-dominated plot from Killarney which on the NMS can be seen over time to move in ordination space closer to them. The other plot members from cluster E in 1999 split into 2 clusters in 2009 according to whether they were fenced or not, with the fenced plot following a successional trajectory away from grass domination to *Calluna*-dominated vegetation (Cluster I). The unfenced plot, however, remained grass dominated. If dominant in an area, bracken, can impact the establishment of other species, and thus the rate and direction of vegetation succession, by shading and competition in the

summer and smothering with decaying foliage in the winter (Palmer et al., 2001, Truscott et al., 2004, Royo and Carson, 2006). The alteration of the rate of succession by dense bracken swards was seen here as the plots that were bracken-dominated in 1999 moved little in ordination space. Management for the prevention of bracken dominance would thus be necessary to promote succession, especially if the desired trajectory is to native woodland.

Cluster analysis confirmed that differential successional change is occurring, as plots that clustered together in 1999 were clustered separately in 2009. Although the NMS of both years together showed a general movement of fenced plots in one direction (with many unfenced plots moving in another) the cluster analysis confirmed that the fenced plots were not all developing into one, or even a few, vegetation types, as there was no dominance of any clusters by fenced (or conversely unfenced) plots. This indicates that other factors were also impacting succession such as soil type and time since felling.

4.6 Conclusions and recommendations

The intensive management strategies of weeding and tree planting did not have significant effects on vegetation succession over the 10 years. Although soil type, pH and previous crop were important in influencing succession in clearfells the results from this study showed there was also scope for manipulating succession by fencing. Moreover, the more successful establishment of both planted and naturally regenerating trees in fenced plots compared with unfenced plots highlights not only that grazing levels are still high in these areas but the importance of this intensive fencing management regime for woodland restoration in certain areas as these. In areas where bracken is of high cover, management

for the prevention of bracken dominance would be necessary to promote succession, especially if the desired trajectory is to native woodland. For restoration of native woodlands deadwood retention and maintaining deadwood supply should be a priority. We concur with previous recommendations that each large herbivore species is required to be managed to, and maintained at, levels that minimize negative impacts on land-use objectives, such as woodland restoration, (Hester et al., 2006, Hobbs, 2006) while also taking the potentially conflicting requirements of various interested parties, such as commercial forestry and recreational hunters into account (Carden et al., 2010). This is a very complex issue that, in Ireland certainly, is a long way from being resolved as there is no national large herbivore management policy or responsible organisation (Purser et al., 2010). This study highlights the challenge of isolating the main drivers of succession (Hester et al., 2006) and the various potential influences that have rarely been considered holistically (Barbier et al., 2008). For example, in this investigation, varying management such as grazing levels and site attributes, such as soil type, combined with the effects of previous crop species make it challenging to discern proximate influences on vegetation succession in clearfell. Care should be taken when scaling up successional trajectories at the small scale of this study to predict large-scale dynamics (Hester et al., 2006), nonetheless, this research represents an important contribution to long-term experiments following the impacts of large herbivores on vegetation succession. The successional trajectories of these plots should be used with caution to predict succession on clearfells of species other than Sitka spruce. It is recognised that a long time may be required for the establishment of typical woodland species with inefficient dispersal mechanisms (Cooper et al., 2008, Hill, 1979, Peterken and Game, 1984, Verheyen and Hermy, 2001) and this emphasises the importance of maintaining habitat continuity in the plots where they are already found. The negative impacts of clearfell management on ground vegetation (outlined by Eycott *et al.* (2006)) highlight the importance of alternative restoration

methods to 'clearfell and replacement'. Pryor *et al.* (2002) have developed a 'gradual replacement' model for restoring conifer plantations to native woodland. Another alternative, called the 'crop continuity' model by Cooper *et al.* (2008), is to maintain the continuity of an open canopy by selecting suitable tree crops or planting broadleaves on sites that already have typical woodland species. These models are important to consider for future research on the restoration of sites to native woodland. In certain circumstances allowing succession to proceed to heathland may be a more feasible conservation outcome than woodland restoration. When considering active management of restoration it is interesting that in this study time, being a ten year interval, was a stronger driver of successional change than grazing or in other words whether the plot was fenced or not.

5 General Discussion

The main objective of this thesis is to contribute to an improved understanding of how vegetation succession of forestry plantations can be manipulated so that the subsequent successional trajectories contribute to the enhancement of biodiversity as part of Sustainable Forest Management. This was achieved by surveying the ground vegetation and natural tree regeneration in a range of forest types in Ireland chosen to represent the impacts of different management options on succession of vegetation communities, with particular regard to typical woodland species. Firstly, I compared quantitatively the ground vegetation communities of afforestation with second rotation reforestation to identify factors important in determining vegetation succession over these rotations. Management practices were recommended for promoting typical woodland ground vegetation establishment over successive rotations (Chapter 2). Secondly, I quantitatively compared the ground vegetation communities of mature stands of a non-native conifer with mature stands of the same non-native conifer intimately mixed with two different native species to identify factors important in determining the vegetation of these plantation types. Management recommendations were made for enhancing diversity of ground vegetation, particularly of typical woodland species, in these plantations (Chapter 3). Thirdly, I quantitatively compared the ground vegetation communities developed on conifer clearfell over a ten year interval and to identify factors important in determining vegetation succession. The conservation value of the vegetation communities after 10 years was assessed and management recommendations for the restoration of native woodland on conifer clearfell were made (Chapter 4). In this final chapter I summarise the results of these investigations, synthesise the main results from all chapters, explore the implications of this thesis and make some suggestions for future research.

5.1 Summaries

5.1.1 Summary chapter 2

In Chapter 2 factors influencing the ground vegetation diversity of reforestation in Sitka spruce stands were investigated using a chronosequence approach and these results were quantitatively compared with those from a previous chronosequence survey in afforestation (Iremonger et al., 2007). Diversity was high during early pre-thicket stages, was at a minimum during the dense mid-rotation stages of closed-maturing and re-opening, but increased again after thinning during the mature stage. This trend in species richness for reforestation agreed with previous work investigating the dynamics of ground vegetation diversity in plantations (Franklin, 1988, Hill, 1979, Hill, 1986, Humphrey et al., 2003, Williams et al., 1998, Kirby, 1988, Smith et al., 2005, Eycott et al., 2006, Fahy and Gormally, 1998, French et al., 2008). Some authors have predicted that ground vegetation diversity should continue to increase through successive rotations (Peterken, 2001, Hill, 1979, Williams et al., 1998). This investigation, however, demonstrated there was no such increase. Both species richness and turnover results suggested that the development of ground vegetation diversity through the afforestation cycle was maintained in the reforestation cycle but was not substantially enhanced. Also in Chapter 2 the impact on succession by the planting of the same crop species after clearfell was investigated with particular reference to the development of a typical woodland community. There was a significant increase in typical woodland species richness over each forest cycle in agreement with conceptual models of ground vegetation succession in successive plantation rotations (Peterken, 2001, Hill, 1979). However, there was no increase in typical woodland diversity over the two successive rotations, contrary to the conceptual model predictions. Chapter 2 showed that typical woodland vascular SR of plantations was positively related with area of old woodland, agreeing with Smith *et al.* (2005). Despite

each rotation having very different starting points, there was floristic convergence over the two rotations driven by canopy cover, area of old woodland, soil pH and CWD volume. Diversity indicators identified for both afforestation and reforestation were structural diversity, canopy cover, rotation, area of old woodland and soil pH. For vascular diversity the interaction of canopy cover with area of old woodland and for bryophyte species richness CWD volume were also identified as indicators.

5.1.2 Summary chapter 3

In Chapter 3 pure Norway spruce stands were compared quantitatively with intimately mixed stands of Norway spruce and oak or Scots pine. This was to determine the effectiveness of intimate mixes in enhancing ground vegetation diversity and to investigate if different communities develop in an intimately mixed stand compared to a pure stand. From the literature there was a general acceptance that mixed species plantations support more species than pure stands (Bremer and Farley, 2010, Hartley, 2002, Stephens and Wagner, 2007, Ferris and Humphrey, 1999, Barbier et al., 2008). However, this research showed that the presence of a secondary species in plantations is not always a useful predictor of ground vegetation diversity. There was a lack of significant differences in diversity metrics between mixed and pure forest types. It was proposed that this resulted not from the mixed planting not impacting ground vegetation diversity *per se*, but rather from the low representation in the mature canopy of the secondary species. A number of factors were proposed as causing this including challenges of site selection, incompatible species planted in inappropriate configurations and inadequate management to ensure the secondary species thrives. Factors were found to be important for ground vegetation diversity in these three plantation types were canopy openness, planted tree density, distance to edge of plantation, area of semi-natural woods within 1km of sites and forest

type. There is scope for management to improve diversity by manipulating these factors and they have potential as diversity indicators. Although the addition of a secondary species to Norway spruce did not increase species richness at the stand scale the Scots pine mixed stands supported a community with a high proportion of typical woodland indicator species. This suggests that Norway spruce/Scots pine mixes have the potential to develop native woodland vegetation. Important factors in driving the differences among the three forest type communities were gradients in soil variables, elevation, age, stand structural measurements and landscape variables at the 1km scale.

5.1.3 Summary chapter 4

Chapter 4 investigated how successional trajectories from conifer clearfell may be manipulated to move towards oak native wood restoration by comparing vegetation diversity and composition over a 10 year interval. There was no significant effect of weeding or planting treatments on species composition, however, fencing and its exclusion of large herbivores had a significant positive influence on typical woodland species richness and overall vegetation composition over time. Over the 10 year interval the majority of fenced plots changed position in ordination space along a similar successional trajectory while the unfenced plots changed along various trajectories; however, fenced plots were not all developing into one, or even a few, vegetation types. In this study time, being a ten year interval, was a stronger driver of successional change than grazing or, in other words, whether the plot was fenced or not. The species of the previous tree crop can greatly impact the initial conditions for succession after clearfelling (Bremer and Farley, 2010, Eycott et al., 2006) and Chapter 4 showed that generally there were significantly different communities depending on the species of the previous tree crop. However, succession following clearfelling can depend more precisely on the condition of the

previous crop, which can influence what species are recruited and what species successfully establish (Hill, 1986). Soil type was another factor found to be influential in differences among the vegetation communities in Chapter 4. However, robust interpretation of soil type effects may have been hindered as there was an imbalance in soil types represented in the plots surveyed. Moreover there was probably confounding of the influence of soil type with previous tree crop species as soil type is so important in tree crop species selection for forestry. Soil pH was found to be influential in driving differences in community composition among plots as also reported by previous authors (Smith et al., 2005, Ferris et al., 2000, Wilson et al., 2001, French et al., 2008). As time since felling increased there was a higher stem density, woody vegetation development and herb cover. However, by 2009 time since felling was only weakly positively related to herb cover, perhaps as colonisation sites had filled up for woody species. Brash cover was, not surprisingly, more influential on vegetation composition in 1999 than 2009 as over the time interval it decayed. The dominance, based on cover and frequency, of heather in the vegetation types found in 2009 is notable and, after 10 years, with or without fencing, succession was to heather-dominated vegetation. The differences in stem density between fenced and unfenced plots indicated that unless grazing pressure is further reduced in these unfenced areas native woodlands are unlikely to develop.

5.2 Synthesis

Canopy cover (Chapter 2), canopy openness (Chapter 3) and stem density (Chapters 2 and 3) were found to be important drivers of diversity and community differences in this thesis. Thus light availability was a major influence on ground vegetation diversity and succession of these forest types in agreement with previous research in plantations (Gilbert, 2007, Simmons and Buckley, 1992, French et al., 2008, Ferris and Simmons, 2000, Bremer and

Farley, 2010, Hartley, 2002) and in woodland restoration (Little et al., 2009, Rodwell and Patterson, 1994).

In Chapters 2-4 the possible influences of old woodland and existing woodland, in terms of their area around and distance to the study sites were investigated. Plantations established on or near previously forested lands (referred to as old woodland in this thesis) are generally expected to support higher diversity due to the possibility of establishment of species in the seed bank and/or remnant vegetation in these new forests (Bremer and Farley, 2010, Bockerhoff et al., 2008). Chapter 2 reported typical woodland vascular SR of plantations was positively related with area of old woodland agreeing with this hypothesis and with previous research in plantations by Smith *et al.* (2005). Typical woodland species are recognised as generally having inefficient dispersal mechanisms thus proximity to seed sources of this type of vegetation is expected to be influential on the development of a woodland vegetation in new forests (Cooper et al., 2008, Hill, 1979, Peterken and Game, 1984, Verheyen and Hermy, 2001). There was evidence in Chapter 3 that proximity to old woodland may also be important to total vascular and typical woodland vascular species richness in agreement with the above hypothesis and with previous work (Dolman and Fuller, 2003, Rackham, 2006, Peterken and Game, 1984). Area of existing semi-natural woodland surrounding plantations has been reported as influencing ground vegetation diversity by acting as a seed source (Smith et al., 2005, Williams et al., 1998, Bockerhoff et al., 2008, Felton et al., 2010a, Bremer and Farley, 2010, Carnus et al., 2006). In Chapter 3 the area of semi-natural woods in surroundings was positively linked to vascular SR but negatively associated with non-vascular SR and these different relationships may be indicative of the generally wider dispersal capabilities of vascular plant species compared with non-vascular species. Conditions such as high

canopy cover at study sites in Chapter 3 may not have been favourable to colonization by species from surrounding areas and may have contributed to the lower than expected importance of proximity to old woodland and the differing influence of area of semi-natural woods as drivers of vascular and bryophyte SR. In Chapter 4 distance to native seed source was highlighted as an influential driver of community composition differences in both years, in agreement with previous research (Dolman and Fuller, 2003, Rackham, 2006, Peterken and Game, 1984).

Deadwood is accepted as being of importance to non-vascular species richness (Márialigeti et al., 2009, Smith et al., 2005, Humphrey et al., 2002c, Raabe et al., 2010). In chapter 2 CWD volume was found to be of relatively higher importance to typical woodland bryophyte SR compared with overall bryophyte SR and we proposed that typical woodland bryophytes are perhaps more likely to be adapted to exploiting deadwood. Although in Chapter 3 there was no significant relationship between CWD volume and non-vascular diversity almost 50% of non-vascular species were recorded as growing on deadwood. Brash cover in Chapter 4 was reported as influential on vegetation composition, more so in 1999 as by 2009 it had mostly decayed; however, there was no correlation between cover of woody debris and bryophyte cover in either year.

Previous research in plantations has reported varying relationships between soil pH and species richness and impacts of soil pH on community composition (Eycott et al., 2006, Ferris et al., 2000, Kirby, 1988, Smith et al., 2005, French et al., 2008, Wilson et al., 2001). In Chapter 2 soil pH was found to be a relatively important negative influence on bryophyte SR and, to a lesser extent, on vascular plant SR (a positive association at low pH (<5.0) and, above a threshold of about pH 5.0, a negative association). In Chapter 4 soil pH

and soil type were influential in driving differences in community composition between the plots at both surveys.

All stands surveyed in Chapter 3 were mature (and afforestation) so some results can be, at least qualitatively, compared with the mature afforestation stands in Chapter 2. As only 2 lichen species were recorded in Chapter 3 non-vascular and bryophyte SR was treated as the same metric for this informal comparison and referred to as bryophyte SR. The trend was that mature Sitka spruce had higher total, vascular and bryophyte SR than both mixes and the pure Norway spruce. For typical woodland SR the trend was the Scots pine mix had higher total and vascular typical woodland SR than the Sitka spruce while the oak mix and Norway spruce pure had similar values to Sitka spruce. Among all forest types typical woodland bryophyte SR was similar. In conclusion, there was a trend for higher total ground vegetation diversity metrics in Sitka spruce stands than in either the Norway spruce pure or mixed, however, in terms of typical woodland diversity it was the Scots pine mixed that supported the highest diversity.

In conclusion, the forest types studied in this thesis have the potential to make an important contribution to the enhancement of biodiversity. In their review Lockwood and Pimm (2001) report that ecosystems can be enhanced or restored with a broad array of species, such that the ecosystems functions at a particular site can be largely independent of the specific species composition. For example, the light regime required by typical woodland species can be provided by many types of trees, even, as this research has shown, by non-native conifers in a country where the majority of native forest would be deciduous.

5.3 Relevance of the research

5.3.1 Methodological considerations

The choice for researchers is often a stark one. An option is to obtaining funding for a chronosequence study that may result in confounding site factors distorting the research findings due to a violation of chronosequence assumptions. The second option may be to obtain short-term funding for a long-term study.

The decision to study a chronosequence in Chapters 2 and 4 was influenced by the need to obtain results with a specified budget and within a time limit. The data reported in Chapters 2 and 3 were derived from the BIOFOREST project which was funded from 2001-2005 and the FORESTBIO project which was funded from 2007-2010 while in Chapter 4 the restoration plots PhD project received funding from 1999-2002. A drawback of chronosequences encountered during this research was in Chapter 2; the retention, or indeed loss, of species between rotations could not be quantitatively verified on a site by site basis because, due to the chronosequence experimental design as different afforestation and reforestation sites were surveyed. Again certain factors expected to be influential according to literature could not be investigated as they differed among the plots due to a less than ideal chronosequence. Unfortunately due to constraints on availability of sites for selection the plots in Chapter 2 varied with regards to some variables (site characters and site histories) both within each rotation and between the two rotations. Many of these differing site variables were found to be influential factors on diversity and community composition. Thus it is possible that if the chronosequence had consisted of an ideal, each site having the same history and differing only in age, that different factors may have been found influential. Despite these considerations this research has delivered valuable results to facilitate in the development of policies to promote the enhancement of biodiversity in

forestry plantations. Long-term monitoring of permanent plots is vital to evaluate the success of particular manipulations in ecological restoration (Prach and Walker, 2011). Even where spontaneous regeneration is being relied on for restoration the process will require long-term monitoring so that decisions can be made on an ongoing basis on whether active restoration management is needed at some stage. In Chapter 4 the plots were set up as long-term experimental sites so rather than relying solely on the chronosequence approach for this successional study it was possible to resurvey these sites after 10 years. This increased the reliability of the results compared with a chronosequence approach especially in this research where there are confounding differences among plots. Nonetheless, chronosequences, even those with confounding factors, can have a very important role in ecological research, not only when resources are finite but when results are urgently needed to inform critical conservation programmes.

In Chapter 3 canopy openness was measured objectively and quantitatively by hemiphotography and canopy cover was measured subjectively and qualitatively by the same observers at all sites, namely myself and another field researcher. An informal comparison of the two methods showed a difference in tests of significant differences of the two variables among the forest types. Hemiphotography measures include light entering from the side of the stand and include understory above 1.3 m in its measurement. As suggested in Chapter 3 this may have led to an under estimation of canopy openness in the oak mixes as the oak understory was in full leaf and thus at its highest cover at time of survey (summer). Canopy cover measurements involved subjectively estimating the canopy foliage cover only in the 10m x 10m plots and did not include light entering from sides of the stand. This method is generally open to recorder error, however, as the two recorders in this research were the same at all sites there is consistency in subjective

recording. In conclusion, it is important to be aware of what exactly these two methods are measuring.

5.3.2 Implications and practical applications of the research

5.3.2.1 Context of research in plantations of Chapters 2 and 3

The PLANFORBIO research programme, running from 2007 to 2012, comprised several individual research projects, with over-arching objectives aimed at improving our understanding of flora and fauna diversity in Ireland's forest estate. It was intended to address forest diversity and management and focus on forest types that were being encouraged through State policies and financial incentives. One of the PLANFORBIO research projects FORESTBIO was concerned with informing management decisions for biodiversity conservation and sustainable management of a range of contemporary Irish forest types. It was under this project that chapters 2 and 3 of this thesis were undertaken. Target taxa for this research were, as well as ground vegetation, birds, ground dwelling and canopy dwelling invertebrates, Lepidoptera and epiphytes. To date papers that have been published from FORESTBIO research include one on ground vegetation diversity in reforestation compared with afforestation (data set incomplete compared to the one presented in this thesis. Refer to **Appendix 2**) with myself as lead author (Moore, 2007), deadwood in forests, (Sweeney et al., 2010b), several on birds (Sweeney et al., 2010a, Sweeney et al., 2010d, Sweeney et al., 2010c), ground dwelling invertebrates (Oxbrough et al., 2012, Oxbrough et al., 2010) and canopy dwelling invertebrates (Martin, 2009).

5.3.2.2 Forest planning and management

Soil pH was found important to diversity and composition in Chapters 2 and 4 and soil type was found influential on composition in Chapter 4. As soil properties are almost

impossible to manipulate by forest management this research supports the assessment of soil type and properties as part of strategic forest planning (Forest Service, 2000a, Horgan et al., 2004, Forestry Commission, 2004).

There is scope for manipulating some factors found influential in these studies, such as forest structure and deadwood, to enhance diversity over successive rotations.

Manipulating forest structure by thinning was supported by the findings of Chapters 2 and 3 as a practical management tool to enhance ground vegetation diversity. The negative impact of a closed canopy on ground vegetation diversity seen in Chapters 2 and 3 highlighted the importance of preventing the canopy closing, however, present recommendations suggest thinning after the canopy is expected to close (Booth et al., 2007). Management policy for earlier thinning to prevent canopy closure should be implemented where appropriate (with caution applied in areas susceptible to windthrow). Canopy closure can also be prevented by planting with more open canopy trees (Cooper et al., 2008) and by the strategic planning for spatial diversity of structural stages at the plantation scale (French et al., 2008, Humphrey et al., 2003, Smith et al., 2005). Planning for a diversity of structural stages will not only mitigate the negative impact of closed canopies on ground vegetation diversity, but increase representation of the distinctive pre-thicket stage, retain areas that may act as sources for (re)colonisation of woodland vegetation and lessen the negative visual landscape impacts of even aged, abruptly edged plantations (French et al., 2008, Peterken, 2001, Williams et al., 1998).

In this thesis deadwood in general was found to be of importance to non-vascular species richness, as a habitat and as an influence on community composition agreeing with previous findings (Márialigeti et al., 2009, Smith et al., 2005, Humphrey et al., 2002c,

Raabe et al., 2010). The manipulation of deadwood amount and type were both management options supported in this research for enhancing non-vascular diversity. Current Irish forestry guidelines (Forest Service, 2000b) advise that some deadwood should be left *in situ* after thinning and harvesting, with minimum volumes given for CWD. However, as Sweeney et al. (2010b) reported, there is a lack of CWD logs and snags in Irish plantations so there is potential for management to increase the availability of this resource by leaving as much deadwood on site as possible, after both felling and thinning (caution needs to be applied in areas infected with fungal pathogens). The potential for conflict among forestry management policies that focus on different outcomes, such as one on timber yield and another on the enhancement of biodiversity, was highlighted as the removal of deadwood after clearfell for use as a renewable energy is gaining support in Ireland (Hoyne and Thomas, 2001, Whelan, 2010).

The research on mixed plantations indicated that the enhancement of ground vegetation diversity in mixed plantations could benefit from the secondary species forming a substantial and ecologically relevant component of the mix plantation. This may be achieved by planting more ecologically compatible species in an arrangement conducive to the growth of the secondary species and undertaking appropriate management to ensure secondary species thrives. Suitable planting arrangements vary from planting species in patches within a matrix of the main species or, it may be preferable from both ecological and economic perspectives, to plant species at a larger scale in non-intimate stands adjacent to the main species. Ecologically non-intimate mixed stands may increase diversity as well as or even higher than intimate mixed stands and from an economic perspective they may require less intensive management. Management to encourage the secondary species, such as intensified thinning around native trees (especially broadleaves)

to increase their competitiveness, may also enhance the habitat for typical woodland species. However, the enhancement of the secondary species may conflict with the commercial viability of plantations in some areas either through reduced representation of commercial crop or due to resource expensive management operations.

There were some similar methods of management recommended for enhancing ground vegetation diversity in the four plantation types studied in this thesis; Sitka spruce afforestation and reforestation and pure and mixed Norway spruce. These were stand structure manipulation, alternatives to clearfell and deadwood retention. That these ongoing management practices were recommended in all Chapters for all forest types emphasises that non-intervention is not an option when enhancement of biodiversity is an expected outcome of a plantation rotation. This is especially so when woodland restoration is desired following clearfell and in areas where large herbivores are numerous.

5.3.2.3 Conservation

An over mature stand retained beyond commercial maturity can increase light, nutrients, etc. and consequently increase diversity and has previously been recommended to conserve and enhance ground vegetation biodiversity in plantations especially in areas that exhibit the potential to develop, or indeed have developed, vegetation of conservation interest (Humphrey et al., 2003, Peterken et al., 1992, Humphrey, 2005, Kerr, 1999). We have demonstrated (in agreement with previous research) that proximity of old woodland is important to ground vegetation diversity and, as outlined above, an over mature stand can also enhance biodiversity. So if a section of mature stand is left standing at clearfell it will become over mature and has the potential to be a source of biodiversity for the developing reforestation crop if it itself is diverse. In Chapter 2 results where typical woodland species

richness increased significantly in the later stages of the forest cycle in both rotations further supports this recommendation of retaining over mature stands or sections of stands at clearfell.

Although not research here alternative management options, especially for stands that have vegetation of conservation interest, were given some support by results presented here including, continuous cover forestry (CCF), shelterwood systems, ‘crop continuity’ and conversion by ‘gradual replacement’ to semi-natural woodland. Caution was noted with regard to some of the alternative management practices that may leave stands exposed to windthrow such as CCF and shelterwood.

It is recognised that a long time may be required for the establishment of typical woodland species with inefficient dispersal mechanisms (Cooper et al., 2008, Hill, 1979, Peterken and Game, 1984, Verheyen and Hermy, 2001) emphasising the importance of maintaining habitat continuity in the plots where they are already found. The negative impacts of clearfell management on ground vegetation (outlined by Eycott *et al.* (2006) and proposed as a factor in the loss of species richness between rotations in Chapter 2), mean alternative harvesting methods to clearfell and to ‘clearfell and replacement’ restoration methods are important. Especially on sites that already had typical woodland species, their continuity may be enhanced by planting more open-canopy tree crops, termed the “‘crop continuity’” model by Cooper et al. (2008) or the conversion by ‘gradual replacement’ (Pryor et al., 2002) to semi-natural woodland could also be considered. These management alternatives to clearfell may maintain the diversity gains of the afforestation cycle through the reforestation cycle and may support vegetation succession and restoration of sites to native woodland.

Diversity indicators for plantations were identified in this research. Positive correlations between structural diversity and SR metrics agree with previous findings of Peterken and Game (1984) and Munro (2009) in suggesting that structural diversity can be used in the field as an indicator for diversity in the four plantation types studied in this thesis; Sitka spruce afforestation and reforestation and pure and mixed Norway spruce. Diversity indicators identified for both afforestation and reforestation were canopy cover, rotation, area of old woodland, soil pH. For vascular diversity the interaction of canopy cover with area of old woodland and for bryophyte SR CWD volume were also identified as indicators. Contrary to expectations, the presence of a mixed species canopy was found to be not necessarily an indicator of diversity. For mixes potential diversity indicators identified were canopy openness, planted tree density, distance to edge of plantation, area of semi-natural woods within 1km of sites and forest type.

There was a trend for higher total ground vegetation diversity metrics in Sitka spruce stands than in either the Norway spruce pure or mixed, however, in terms of typical woodland diversity it was the Scots pine mixed that supported the highest diversity.

5.3.2.4 Vegetation succession and restoration ecology

To encourage vegetation succession in conifer plantations towards that of typical woodland ground vegetation communities management interventions are required such as thinning. The results in Chapter 4 showed time was a stronger driver of successional change than whether the plot was fenced or not. The results presented in Chapters 2 showing distinctive heath and grassland communities in pre-thicket suggests that the conservation of these early successional communities should be encouraged especially in areas where a plantation is unlikely to establish woodland ground vegetation and perhaps where the pre-

afforestation habitats were heath or peatland. This can be achieved by planning for forest gaps and rides and planting mosaics of stands of different ages. Chapter 4 found succession to heather dominated vegetation and supports the management option that, especially where there is a lack of local seed sources to support natural regeneration of woodland, allowing succession to proceed to heathland may be a more feasible conservation outcome than woodland restoration. If dominant in an area bracken can upon the impact rate and direction of vegetation succession so management for the prevention of bracken dominance is necessary to promote succession, especially if the desired trajectory is to native woodland or *Calluna*. This research supports previous recommendations that large herbivore species should be managed and maintained at levels that minimize negative impacts on land-use objectives, such as woodland restoration (Hester et al., 2006, Hobbs, 2006). In Ireland this is a very complex issue that is a long way from being resolved as there is no national large herbivore management policy or responsible organisation (Purser et al., 2010). Chapter 4 highlighted the challenge of isolating the main drivers of succession and processes as outlined by Hester et al. (2006). Moreover, care should be taken when scaling up successional trajectories at the small scale of the study in Chapter 4 to predict large-scale dynamics as outlined by Hester *et al.* (2006). Furthermore, due to the small number of plots established on former non-Sitka spruce areas the successional trajectories seen in these plots here should be interpreted with caution in predicting succession on clearfells of species other than Sitka spruce. Nonetheless, this research represents an important contribution to long-term experiments following the impacts of large herbivores on vegetation succession.

5.4 Further research

The findings of this research allow for further research opportunities, some of which are outlined below.

- Continuous cover forestry, shelterwood systems and conversion by ‘gradual replacement’ are not widely practised in Ireland, and there is consequently a lack of information regarding their effect on biodiversity and how they compare to plantations managed for clearfell harvest that were investigated in this thesis. It is recommended that these alternative management options should be further investigated especially with regards to stands that have vegetation of conservation interest.
- Retention of over-mature trees may be a more practical option in many situations than large-scale conversion of clearfell to CCF systems and further research topics include the effect of size, shape and location in landscape of retained patches, the diversity they support and their impacts on surrounding forest (as potential seed sources).
- Further research into how mixes can best be incorporated into forest planning for timber production and in enhancing biodiversity is recommended, for example, what species are ecologically compatible for a mixed plantation, what is the suitable planting arrangement for the species and what management is appropriate. This research investigated mature mixed species stands and so the effects of mixed planting on the earlier stages of the cycle should be investigated, in order to identify whether a secondary species exerts a stronger influence on diversity before canopy closure. That the enhancement of the secondary species in mixed plantations may conflict with commercial viability in some areas either through reduced

representation of commercial crop or due to resource expensive management operations needs further research.

- The continued long-term monitoring of the restoration sites is necessary to understand woodland development and to assess the impacts of the methods employed at the time the plots were set up. There is an opportunity to set up new experimental plots in close proximity to the existing ones and to conduct additional experiments, for example, different methods of introducing understory vegetation, 'gradual replacement'. Further research in terms of the restoration study, include investigating tree establishment after planting from seed and a study of the succession of other taxa in clearfells. It remains to be seen at the next resurvey whether the fenced plots continue to move, in successional terms, at a faster rate than unfenced plots and whether they continue to converge. Moreover, will the vegetation types be as dominated by *C. vulgaris* or will a more typical woodland community have developed in some plots.
- Research on the effects of different grazing regimes on diversity of plantations and in woodland restoration is needed in order better predict the effects that grazing management may have.

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APPENDIX 1 Species list

The ground vegetation species recorded during the studies in Chapter 1 afforestation and reforestation Sitka spruce plantations; in Chapter 2, pure Norway spruce, Norway spruce/oak mixed (NS/Oak mixed) and Norway spruce/Scots pine mixed (NS/Scots pine mixed) plantations and in Chapter 3, native oak restoration on conifer clearfell sites (restoration sites). Vascular plant nomenclature followed Stace (2010), mosses followed Smith (2004), liverworts followed Paton (1999) and lichens followed Coppins (2002). The species habitat preferences are also indicated with regards to their woodland affinity. For details of species classification refer to Section 2.3.3.

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Abies alba</i>	abicalba		x				High
<i>Acer platanoides</i>	acerplat			x			High
<i>Acer pseudoplatanus</i>	acerpseu	x	x	x	x		High
<i>Agrostis canina s.l.</i>	acerpseu	x	x	x		x	Moderate
<i>Agrostis capillaris</i>	agrocapi	x	x	x	x	x	Moderate
<i>Agrostis gigantea</i>	agrogiga	x					Low
<i>Agrostis species</i>	agrosp				x		na
<i>Agrostis stolonifera</i>	agrostol	x	x	x	x	x	Moderate
<i>Ajuga reptans</i>	ajugrept	x	x	x	x		High
<i>Allium ursinum</i>	alliursine	x					High
<i>Alopecurus pratensis</i>	alopprat	x					Low
<i>Angelica sylvestris</i>	angeslyv	x					Moderate
<i>Anthoxanthum odoratum</i>	anthodor	x	x			x	Moderate
<i>Arrhenatherum elatius</i>	arrhelat	x					Low
<i>Arum maculatum</i>	arumacu		x				High
<i>Athyrium filix-femina</i>	athyfili	x	x	x	x	x	High
<i>Atrichum undulatum</i>	atriundu	x	x	x	x		High
<i>Betula pendula</i>	betupend	x	x		x		Moderate
<i>Betula pubescens</i> (planted)	betupenp					x	na
<i>Betula pubescens</i>	betupube	x	x		x	x	Moderate
<i>Blechnum spicant</i>	blecspic	x	x	x	x	x	High
<i>Brachythecium rutabulum</i>	bracruta	x	x	x			Moderate
<i>Brachypodium sylvaticum</i>	blecspic	x	x		x		High
<i>Breutelia chrysocoma</i>	breuchry	x					Low
<i>Bryoerythrophyllum recurvirostrum</i>	bryorecu	x					Moderate
<i>Bryum pseudotriquetrum</i>	bryupseu	x					Low
<i>Calliargon cordifolium</i>	callcord	x					Moderate

Species name	Species code	Chapter 1	Chapter 2	Chapter 2	Chapter 2	Chapter 4	Woodland Affinity
		Sitka spruce	Pure Norway spruce	NS/Oak mixed	NS/Scots pine mixed	Restoration sites	
<i>Calliergonella cuspidata</i>	callcusp	x					Moderate
<i>Calluna vulgaris</i>	callvulg	x	x			x	Moderate
<i>Calypogeia fissa</i>	calyfiss	x	x	x	x		Moderate
<i>Calypogeia muelleriana</i>	calymuel	x	x	x	x		Moderate
<i>Campylopus flexuosus</i>	campflex	x	x				Moderate
<i>Campylopus introflexus</i>	campintr	x					Low
<i>Campylopus pyriformis</i>	camppyri	x					Moderate
<i>Cardamine flexuosa</i>	cardflex	x	x	x	x		Moderate
<i>Cardamine hirsuta</i>	cardhirs	x	x				Low
<i>Cardamine pratensis</i>	cardprat	x		x			Moderate
<i>Carex binervis</i>	carebine	x					Low
<i>Carex diandra</i>	caredian	x					Low
<i>Carex disticha</i>	caredist	x					Low
<i>Carex echinata</i>	careechi	x					Moderate
<i>Carex elata</i>	careelat	x					Moderate
<i>Carex flacca</i>	careflac	x	x	x			Low
<i>Carex hirta</i>	carehirt	x					Low
<i>Carex nigra</i>	carenigr	x					Low
<i>Carex ovalis</i>	careoval	x		x			Low
<i>Carex paniculata</i>	carepani	x					Low
<i>Carex pendula</i>	carepend				x		High
<i>Carex pilulifera</i>	carepilu	x					Low
<i>Carex remota</i>	careremo	x	x	x	x		High
<i>Carex species</i>	caresp		x	x			na
<i>Carex strigosa</i>	carestri				x		High
<i>Carex sylvatica</i>	caresylv	x	x		x		High
<i>Carex viridula</i>	careviri	x					Low
<i>Centaurea nigra</i>	centnigr	x					Low
<i>Centaurea scabiosa</i>	centscab	x					Low
<i>Cephalozia bicuspidata</i>	cephbicu	x	x				Moderate
<i>Cephaloziella divaricata</i>	cephdiva	x					Low
<i>Cephaloziella hampeana</i>	cephhamp	x					Low
<i>Cerastium fontanum</i>	cerafont	x	x				Low
<i>Ceratodon purpureus</i>	cerapurp	x					Low
<i>Chamerion angustifolium</i>	chamangu	x	x	x	x		Moderate
<i>Chrysosplenium oppositifolium</i>	chryoppo	x	x	x	x		High

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Circaea lutetiana</i>	circlute		x	x	x		High
<i>Cirsium arvense</i>	cirsarve	x					Low
<i>Cirsium dissectum</i>	cirsdiss	x					Low
<i>Cirsium palustre</i>	cirspalu	x	x		x		Moderate
<i>Cirsium vulgare</i>	cirsvulg	x					Low
<i>Cladonia coniocraea</i>	cladconi			x			High
<i>Climacium dendroides</i>	climdend				x		Moderate
<i>Corylus avellana</i>	coryavel		x		x		High
<i>Cotoneaster species</i>	cotosp				x		na
<i>Cotoneaster x watereri</i>	cotowate				x		Low
<i>Crataegus monogyna</i>	cratmono	x	x	x	x		Moderate
<i>Cynosurus cristatus</i>	cynocris	x					Low
<i>Dactylis glomerata</i>	cynocris	x	x				Moderate
<i>Dactylorhiza maculata</i>	dactmacu	x					Moderate
<i>Daltonia splachnoides</i>	daltspla	x					Moderate
<i>Deschampsia cespitosa</i>	desccesp	x		x	x		Moderate
<i>Deschampsia flexuosa</i>	descflex	x					Moderate
<i>Dicranella heteromalla</i>	dicrhete	x	x	x			Moderate
<i>Dicranum majus</i>	dicrmaju	x					High
<i>Dicranum scoparium</i>	dierscop	x	x				Moderate
<i>Digitalis purpurea</i>	digipurp	x	x	x			Moderate
<i>Diplophyllum albicans</i>	diplalbi	x					Moderate
<i>Dryopteris aemula</i>	dryoaemu	x	x	x			High
<i>Dryopteris affinis</i>	dryoaffi	x	x	x	x		High
<i>Dryopteris carthusiana</i>	dryocart	x					High
<i>Dryopteris x complexa</i>	dryocomp		x				High
<i>Dryopteris dilitata</i>	dryocart	x	x	x	x		High
<i>Dryopteris filix-mas</i>	dryocart	x	x	x	x		High
<i>Dryopteris species</i>	dryocart				x		na
<i>Elytrigia repens</i>	elytrepe	x					Low
<i>Epilobium brunnescens</i>	epilbrun	x	x				Low
<i>Epilobium montanum</i>	epilmont	x	x	x	x		Moderate
<i>Epilobium obscurum</i>	epilobsc	x	x				Low
<i>Epilobium palustre</i>	epilpalu	x					Low
<i>Epilobium species</i>	epilsp		x		x		na

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Epipactis helleborine</i>	epiphell		x	x			High
<i>Equisetum arvense</i>	equiarve	x					Low
<i>Equisetum species</i>	equisp			x			na
<i>Equisetum sylvaticum</i>	equisylv				x		Moderate
<i>Erica cinerea</i>	ericcine	x					Low
<i>Erica tetralix</i>	erictetr	x					Low
<i>Eriophorum vaginatum</i>	eriovagi	x					Low
<i>Euonymus europaeus</i>	euoneuro				x		Moderate
<i>Eurhynchium striatum</i>	eurhstri	x	x	x	x		High
<i>Fagus sylvatica</i>	fagusylv	x	x	x	x		High
<i>Festuca ovina</i>	festovin	x					Low
<i>Festuca rubra</i>	festrubr	x					Low
<i>Festuca tenuifolia</i>	festtenu	x					Low
<i>Filipendula ulmaria</i>	filiulma	x					Moderate
<i>Fissidens adianthoides</i>	fissadia				x		Low
<i>Fissidens bryoides</i>	fissbryo	x		x			Moderate
<i>Fissidens taxifolius</i>	fisstaxi	x	x		x		Moderate
<i>Fragaria vesca</i>	fragvesc		x		x		High
<i>Fraxinus excelsior</i>	fraxexce	x	x	x	x		High
<i>Frullania dilatata</i>	fruldila	x					Moderate
<i>Frullania tamarisci</i>	frultama	x	x				Moderate
<i>Fuchsia magellanica</i>	fuchmage	x	x				Low
<i>Galeopsis tetrahit</i>	galetetr	x					Low
<i>Galium aparine</i>	galiapar	x	x	x			Moderate
<i>Galium palustre</i>	galipalu	x	x		x		Moderate
<i>Galium saxatile</i>	galisaxa	x					Low
<i>Galium uliginosum</i>	galiulig			x			Low
<i>Geranium dissectum</i>	geradiss	x					Low
<i>Geranium robertianum</i>	gerarobe	x	x	x	x		Moderate
<i>Geum urbanum</i>	geumurba		x				High
<i>Glyceria fluitans</i>	glycflui		x				Low
<i>Hedera helix</i>	hedeheli	x	x	x	x		High
<i>Heterocladium heteropterum</i>	hetehete		x				High
<i>Holcus lanatus</i>	holclana	x	x		x		Low
<i>Hookeria lucens</i>	hookluce	x	x	x	x		Moderate
<i>Hyacinthoides non-scripta</i>	hyacnons	x	x		x		High
<i>Hylocomium splendens</i>	hylosple	x					Moderate

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Hypericum androsaemum</i>	hypeandr	x	x				High
<i>Hypericum humifusum</i>	hypehumi	x					Low
<i>Hypericum perforatum</i>	hypeperf	x					Low
<i>Hypericum pulchrum</i>	hypepulc	x	x		x		Low
<i>Hypnum andoi</i>	hypnando	x	x	x	x		High
<i>Hypnum cupressiforme</i>	hypncupr	x					Low
<i>Hypnum jutlandicum</i>	hypnjutl	x	x	x	x		Moderate
<i>Hypnum resupinatum</i>	hypnresu	x	x	x	x		Moderate
<i>Hypochaeris radicata</i>	hyporadi	x					Low
<i>Ilex aquifolium</i>	ilexaqui	x	x	x	x		High
<i>Isoetecium alopecuroides</i>	isotalop		x				High
<i>Isoetecium myosuroides</i>	isotmyos	x	x	x	x		High
<i>Juncus acutiflorus</i>	juncacut	x					Moderate
<i>Juncus articulatus</i>	juncarti	x					Low
<i>Juncus bufonius</i>	juncbufo	x					Low
<i>Juncus bulbosus</i>	juncbulb	x					Low
<i>Juncus comglomeratus</i>	junccong	x					Low
<i>Juncus effusus</i>	junceffu	x	x	x	x		Low
<i>Juncus squarrosus</i>	juncsqua	x					Low
<i>Juncus subnodulosus</i>	juncsubn	x					Low
<i>Juncus tenuis</i>	junctenu	x					Moderate
<i>Kindbergia praelonga</i>	kindprae	x	x	x	x		High
<i>Kurzia pauciflora</i>	kurzpauc	x					Low
<i>Lathyrus linifolius</i>	lathlini	x	x				Moderate
<i>Lathyrus pratensis</i>	lathprat	x					Low
<i>Lejeunea lamacerina</i>	lejelama	x	x	x	x		Moderate
<i>Leontodon autumnalis</i>	leonautu		x				Low
<i>Lepidozia reptans</i>	lepirept	x					High
<i>Lepraria incana</i>	leprinca		x				Moderate
<i>Leucanthemum vulgare</i>	leucvulg	x					Low
<i>Listera cordata</i>	listcord			x			Moderate
<i>Listera ovata</i>	listovat	x					Moderate
<i>Loeskeobryum brevirostre</i>	loesbrev		x				High
<i>Lolium perenne</i>	lolipere		x				Low

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Lonicera periclymenum</i>	loniperi	x	x	x	x		High
<i>Lophocolea bidentata</i>	lophbide	x	x	x	x		Moderate
<i>Lophocolea heterophylla</i>	lophhete	x	x	x	x		High
<i>Lophozia incisa</i>	lophinci	x					Moderate
<i>Lophozia ventricosa</i>	lophvent	x					Moderate
<i>Lotus corniculatus</i>	lotucorn	x					Low
<i>Lotus pedunculatus</i>	lotupedu	x					Low
<i>Luzula multiflora</i>	luzumult	x	x		x		Moderate
<i>Luzula pilosa</i>	luzupilo	x					High
<i>Luzula species</i>	luzusp		x		x		na
<i>Luzula sylvatica</i>	luzusylv	x		x			High
<i>Lysimachia nemorum</i>	lysinemo	x	x		x		High
<i>Lathyrus sativus</i>	lythsati	x					Low
<i>Mentha aquatica</i>	mentaqua	x					Moderate
<i>Metzgeria furcata</i>	metzfurc	x	x	x	x		High
<i>Metzgeria temperata</i>	metztemp	x	x	x	x		High
<i>Microlejeunea ulicina</i>	micruclic	x			x		High
<i>Mnium hornum</i>	mniuhorn	x	x	x	x		High
<i>Molinia caerulea</i>	molicaer	x		x			Moderate
<i>Neckera complanata</i>	neckcomp		x	x	x		High
<i>Neckera crispa</i>	neckcris	x			x		Low
<i>Neckera pumila</i>	neckpumi	x	x				Moderate
<i>Nowellia curvifolia</i>	nowecurv				x		Moderate
<i>Oxalis acetosella</i>	oxalacet	x	x	x	x		High
<i>Oxyrrhynchium hians</i>	oxyrhian	x					Moderate
<i>Pellia endivifolia</i>	pellendi	x	x				High
<i>Pellia epiphylla</i>	pellepip	x					Moderate
<i>Pellia neesiana</i>	pellnees	x					Moderate
<i>Phleum pratense</i>	phleprat	x					Low
<i>Phyllitis scolopendrium</i>	phylscol	x	x		x		High
<i>Picea abies</i> (unplanted)	piceabieu		x	x	x		High
<i>Picea sitchensis</i> (unplanted)	picesitcu	x					High
<i>Picea sitchensis</i> (planted)	picesitcp	x					na
<i>Pinus contorta</i> (unplanted)	pinucontu	x					High
<i>Pinus sylvestris</i> (planted)	pinusylvp				x		na
<i>Plagiochila asplenioides</i>	plagaspl	x	x		x		High

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Plagiomnium rostratum</i>	plagrost	x	x		x		Moderate
<i>Plagiomnium undulatum</i>	plagundu	x	x	x	x		High
<i>Plagiothecium undulatum</i>	platundu	x	x	x	x		Moderate
<i>Plantago lanceolata</i>	planlanc	x					Low
<i>Plagiothecium denticulatum</i>	platdent	x					High
<i>Plagiothecium laetum</i>	platlaet	x					High
<i>Pleurozium schreberi</i>	pleuschr	x					Moderate
<i>Poa pratensis</i>	poaprat	x					Low
<i>Poa trivialis</i>	poatriv	x					Moderate
<i>Polystichum aculeatum</i>	polycamb	x	x		x		Moderate
<i>Polytrichum commune</i>	polyvulg	x	x		x		Moderate
<i>Polytrichastrum formosum</i>	polyform	x	x	x	x		High
<i>Polytrichum juniperinum</i>	polyvulg	x					Low
<i>Polygala serpyllifolia</i>	polyserp	x					Low
<i>Polystichum setiferum</i>	polycamb	x	x	x			High
<i>Polypodium vulgare</i> s.l.	polycamb	x	x	x	x		na
<i>Potentilla anglica</i>	poteangl	x	x				Low
<i>Potentilla erecta</i>	poteerec	x	x	x			Moderate
<i>Potentilla palustris</i>	potepalu	x					Low
<i>Potentilla reptans</i>	poterept				x		Low
<i>Potentilla sterilis</i>	potester	x	x				High
<i>Primula vulgaris</i>	primvulg	x	x		x		High
<i>Prunus avium</i>	prunaviu			x			High
<i>Prunus padus</i>	prunpadu				x		High
<i>Prunus spinosa</i>	prunspin				x		Moderate
<i>Prunella vulgaris</i>	primvulg	x					Low
<i>Pseudotaxiphyllum elegans</i>	pseueleg	x	x	x	x		High
<i>Pseudoscleropodium purum</i>	prunvulg	x	x	x	x		Moderate
<i>Pteridium aquilinum</i>	pteraqui	x					Moderate
<i>Quercus petraea</i> (planted)	querpetr			x		x	na
<i>Quercus petraea</i> (unplanted)	querpetr	x					High
<i>Quercus robur</i> (planted)	querrobu			x			na
<i>Quercus robur</i> (unplanted)	querrobu	x	x	x	x		High

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Quercus species</i> (unplanted)	querrobu		x		x		High
<i>Racomitrium heterostichum</i>	racohete	x					Low
<i>Racomitrium lanuginosum</i>	racolanu	x					Low
<i>Radula complanata</i>	raducomp		x		x		High
<i>Ranunculus auricormis</i>	ranuauri	x					High
<i>Ranunculus flammula</i>	ranuflam	x	x				Low
<i>Ranunculus repens</i>	ranurepe	x	x		x		Moderate
<i>Rhizomnium punctatum</i>	rhizpunc	x					Moderate
<i>Rhododendron ponticum</i>	rhodpont	x					High
<i>Rhynchoetium confertum</i>	rhynconf		x				Moderate
<i>Rhytidadelphus loreus</i>	rhytlora	x		x	x		Moderate
<i>Rhytidadelphus squarrosus</i>	rhytsqua	x					Moderate
<i>Rhytidadelphus triquetris</i>	rhyttriq	x	x		x		Moderate
<i>Riccardia chamedryfolia</i>	ricccham	x					Moderate
<i>Rorippa species</i>	rorisp		x				na
<i>Rosa species</i>	rosasp	x	x				Moderate
<i>Rubus caesius</i>	rubucaes	x					Low
<i>Rubus fruticosus</i> agg.	rubufrut	x	x	x	x		Moderate
<i>Rubus idaeus</i>	rubuidae	x	x	x	x		Moderate
<i>Rubus spectabilis</i>	rubuspec			x			High
<i>Rumex acetosella</i>	rumeacel	x					Low
<i>Rumex acetosa</i>	rumeacet	x					Low
<i>Rumex conglomeratus</i>	rumecong	x					Low
<i>Rumex obtusifolius</i>	rumeobtu	x					Low
<i>Salix aurita</i>	saliauri	x					Low
<i>Salix caprea</i>	salicapr				x		Moderate
<i>Salix cinerea</i>	salicine	x	x		x		Moderate
<i>Salix x multinervis</i>	salimult	x					Moderate
<i>Salix x pontederiana</i>	salipont	x					Moderate
<i>Salix x reichardtii</i>	salireich	x					Moderate
<i>Salix repens</i>	salirepe	x					Low
<i>Salix species</i>	salicine				x		na
<i>Sambucus nigra</i>	sambnigr	x	x	x	x		Moderate
<i>Sanicula europaea</i>	sanieuro		x		x		High
<i>Scapania gracilis</i>	scapgrac	x					Moderate
<i>Schoenus nigricans</i>	schonigr	x					Low

Species name	Species code	Chapter 1 Sitka spruce	Chapter 2 Pure Norway spruce	Chapter 2 NS/Oak mixed	Chapter 2 NS/Scots pine mixed	Chapter 4 Restoration sites	Woodland Affinity
<i>Scrophularia nodosa</i>	scronodo		x				Moderate
<i>Senecio aquaticus</i>	seneaqua		x				Low
<i>Senecio jacobaea</i>	senejaco	x	x				Low
<i>Solanum nigrum</i>	solanigr	x					Low
<i>Sonchus asper</i>	soncaspe		x				Low
<i>Sorbus aucuparia</i>	sorbaucu	x	x	x	x		Moderate
<i>Sphagnum capillifolium</i>	sphacapi	x					Moderate
<i>Sphagnum cuspidatum</i>	sphacusp	x					Low
<i>Sphagnum denticulatum</i>	sphadent	x					Moderate
<i>Sphagnum girgensohnii</i>	sphagirg	x					Low
<i>Sphagnum inundatum</i>	sphainun	x					Moderate
<i>Sphagnum palustre</i>	sphapalu	x					Moderate
<i>Sphagnum papillosum</i>	sphapapi	x					Low
<i>Sphagnum recurvum</i> agg.	sphareag	x					Moderate
<i>Sphagnum squarrosum</i>	sphasqua	x					Low
<i>Sphagnum subnitens</i>	sphasubn	x	x				Low
<i>Stachys sylvatica</i>	stacsylv	x					High
<i>Stellaria graminea</i>	stelgram		x				Low
<i>Stellaria uliginosa</i>	stelulig			x			Low
<i>Succisa pratensis</i>	succprat	x					Low
<i>Symphoricarpos albus</i>	sympalba		x				Moderate
<i>Taraxacum species</i>	taraspp.	x	x				Low
<i>Taxus baccata</i>	taxubacc		x				High
<i>Teucrium scorodonia</i>	teuscor	x					Moderate
<i>Thamnobryum alopecurum</i>	thamalop		x	x	x		High
<i>Thuidium tamariscinum</i>	thuitama	x	x	x	x		High
<i>Thuja occidentalis</i>	thujocci				x		High
<i>Trichophorum cespitosum</i>	triccesp	x					Low
<i>Trifolium pratense</i>	trifprat	x					Low
<i>Ulex europaeus</i>	ulexeuro	x	x				Low
<i>Ulex gallii</i>	ulexgall	x					Low
<i>Ulota crispa</i> s.l.	ulotcris	x	x	x	x		High
<i>Urtica dioica</i>	urtidioi	x	x	x			Moderate
<i>Vaccinium myrtillus</i>	vaccmyrt	x	x	x			Moderate
<i>Veronica chamaedrys</i>	verocham	x	x		x		Moderate

Species name	Species code	Chapter 1	Chapter 2	Chapter 2	Chapter 2	Chapter 4	Woodland Affinity
		Sitka spruce	Pure Norway spruce	NS/Oak mixed	NS/Scots pine mixed	Restoration sites	
<i>Veronica montana</i>	veromont	x	x		x		High
<i>Veronica officinalis</i>	verooffi	x		x			Low
<i>Veronica serpyllifolia</i>	veroserp	x			x		Low
<i>Veronica species</i>	verosp			x			na
<i>Vicia sepium</i>	vicisepi		x		x		Low
<i>Viola palustris</i>	violpalu	x					Moderate
<i>Viola reichenbachiana</i>	violreic	x					High
<i>Viola riviniana</i>	violrivi	x	x	x			Moderate
<i>Viola species</i>	violsp		x	x	x		na

APPENDIX 2

Moore et al. (2008) Ground flora diversity of Sitka spruce reforestation plantations *(in press)*

Ground flora diversity of Sitka spruce reforestation plantations.

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Ireland is committed to the principles of Sustainable Forestry Management (SFM), and inherent to these are the conservation and enhancement of biodiversity in plantation forests. The BIOFOREST project, completed in 2006, investigated the ground flora diversity of Sitka spruce afforestation (first rotation) plantations. This present study is the first investigating the ground flora diversity of reforestation (second rotation) plantations of Sitka spruce in Ireland and is carried out within the framework of the FORESTBIO project, a multidisciplinary study of Ireland's plantations and native woodlands.

The objective of this present study is to compare ground flora diversity in afforestation and reforestation plantations. Twenty forests around Ireland were selected to form a chronosequence, enabling a comparative study of the ground flora in contrasting geographical regions, and at a varied range of elevations and soil types. To account for

differences in ground flora diversity, structure and composition, a range of forest management and environmental information was collected.

The preliminary results reported here show clear differences in ground flora diversity, structure and composition among sample plots in Sitka spruce stands and between the structural stages of the forest cycle, as also found in afforestation research. Stand structural stage was not found to be a good predictor of ground flora diversity as stands are sensitive to disturbances such as gaps in the canopy. The hypothesis that deadwood would be an important diversity indicator (as found for afforestation) was not validated. Several structural and functional ground flora diversity indicators were highlighted i.e. brash piles, canopy openness, moderately decayed logs, non vascular plant cover and vascular plant species richness. No single diversity indicator or index should be used for assessment, rather several should be investigated. Diversity indicators can be manipulated by appropriate integrated management programmes e.g. thinning regime to prevent canopy closure to enhance ground flora diversity at the stand scale thus furthering the implementation of SFM.

INTRODUCTION

1.1 Afforestation and reforestation

There has long been concerns expressed about the impact of afforestation on the natural environment (World Commission for Environment and Development, 1987: Cabot, 1999: Bengtsson et al. 2000: Food and Agricultural Organisation of the UN, 2000: Peterken, 2001) however these concerns are only recently informing research and policy relating to forestry (United Nations, 1992: Forestry Commission, 2002: Iremonger et al. 2007).

Moreover, it is becoming evident from recent research that, with appropriate management, there is a significant potential for forestry plantations to add to the landscape quality and local biodiversity of an area (Cantrell, 1998: Forest Service, 2000: Iremonger et al. 2007). Reforestation will play an increasingly important role in Ireland's commercial forestry owing to increasing areas of the forest estate 'coming of age' for the second and even third rotations of tree crop. Thus, the impacts on biodiversity of reforestation are being investigated to discern the effects of re-planting tree crops in multiple rotation on the same land.

1.2 Sustainable Forest Management

Ireland is committed to the practice of Sustainable Forest Management (SFM), which, under the Helsinki Process (Coillte, 2007) is defined as the "use of forests and forested areas in a way and at a pace which allows the preservation of their biological diversity, productivity, regeneration ability, vitality, as well as their capability of fulfilling relevant ecological, economic, and social functions at local, national, and global levels now and in the future, in a way which does not damage other eco-systems." Plantation forests are undisturbed for long periods during their rotation and have the capacity to support important levels of biodiversity (Humphrey et al. 1999; 2000; 2002; 2003; Peterken, 2001). In Ireland the promotion of SFM and the need for biodiversity policies in forestry management to be scientifically supported has initiated several research and development programmes. From 2001 to 2006, the BIOFOREST project (Iremonger et al. 2007) provided much-needed basic information on biodiversity in Ireland's conifer plantations and attempted to relate vegetation community composition and diversity to stand characteristics and site types across a geographical range. BIOFOREST found that forestry plantations can make a significant positive contribution to biodiversity in the landscape if

appropriately planned and managed, and conversely, can have a negative effect if not (Ironmonger et al. 2007). Moreover BIOFOREST indicated that afforestation biodiversity increases with stand age in agreement with Franklin's diversity model (1982: as cited in Smith et al. 2007) where diversity peaks before canopy closure, is at a minimum during the dense, closed canopy stage, (especially with Sitka spruce dominated stands) peaks before canopy closure and increases again with canopy thinning (opening).

1.3 Reforestation

The FORESTBIO project was developed in response to BIOFOREST project recommendations for future research. FORESTBIO running from 2007 to 2010 (<http://www.ucc.ie/en/planforbio>) is undertaking, among other research, the first investigation in Ireland of the impacts on ground flora diversity of reforestation with Sitka spruce. There are several factors that affect reforestation biodiversity that are not relevant to afforestation sites such as amount of deadwood on site and pre-planting treatment e.g. burning. Moreover initial conditions are likely to be more comparable between reforestation sites than between afforestation sites as pre-plantation afforestation habitats can vary from, for example, blanket peat to productive grassland. It is acknowledged there is a need for information on the biodiversity of second rotation forests as a function of site type, previous crop composition and management, felling and harvesting patterns (extent of blocks felled: nearness to existing forest), treatment of residues and deadwood and site preparation.

Research on reforestation in other countries focuses mostly on the restoration of native forests for habitat rehabilitation rather than silviculture (commercial forestry). In Britain, Pryor et al. (2002) researched the restoration of native forest on land previously planted with conifers on ancient woodland sites. There is a body of research on the effects of clear-

felling and reforestation with Sitka spruce on edaphic and hydrological chemistry (Robertson, Hornung & Kennedy, 2000) but little on the biodiversity of reforestation. Hill (1979) suggested that with each rotation, the diversity of woodland species increases, and that of open habitat species decreases and there would be an overall increase in diversity with subsequent rotations, especially where silviculture is based in clear-felling, as in Ireland.

In this study, we investigate ground flora diversity across the forest cycle in Sitka spruce reforestation. Our research is the first to compare ground flora diversity in reforestation with afforestation (mainly with regard to the results of the BIOFOREST project). The preliminary results presented in this paper are the initial findings of the FORESTBIO project. We focus particularly on using data collected in the field to explore the relevant drivers of ground flora diversity in the investigated environments. We aim to make recommendations on identity of biodiversity indicators that may be used to assess the effect of site management practices on biodiversity and identify sites that, potentially, are of high biodiversity value.

2 METHODS

2.1 Study sites

This study was conducted as part of a larger, multidisciplinary investigation of forestry and biodiversity in Ireland (Ironmonger et al. 2007) and, as for BIOFOREST, a chronosequencing approach was employed to compare biodiversity across the reforestation cycle i.e. representative stands are surveyed at different stages of the forest management cycle. This “substituting space for time” (French, 2005) allows vegetation successions to

be studied without the need for monitoring over long periods. It is important, with chronosequencing, that site selection ensures that the sites are comparable with, for example, similar soils, climate, altitude, site history etc. and have the same site history and rotational age. Stand structural types across the forest cycle were delineated according to age and forest structure following French (2005).

Table 1. Stand structural types. Information from French (2005).

Stand structure	Age (years)	Forest structure
Pre-thicket	0 – 10	Open canopy
Thicket	8 – 15	Closed canopy
Mid - rotation	20 - 30	Thinning results in reopening conifer OR if no thinning closed mature canopy
Commercially mature	35- 50	Conifers >50 yrs over mature

To maximise the geographical spread of sites across Ireland while also controlling for confounding variation among age classes due solely to site environmental factors a ‘geographical cluster’ experimental design was employed. The four stand structural types were represented in each of the five clusters i.e. 20 sites in total (Figure 1) and within each cluster sites were matched for soil type, elevation and geographical location.

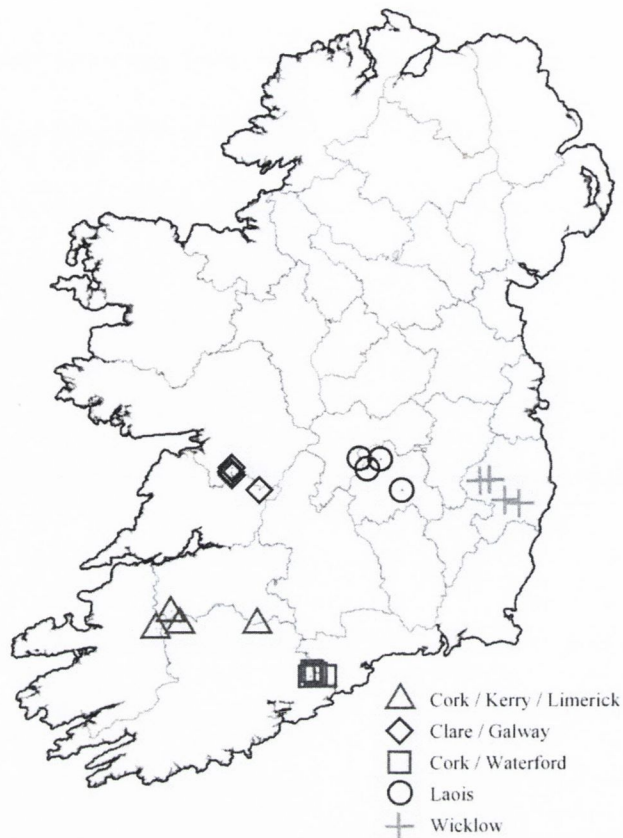


Figure 1. Location of Sitka spruce reforestation study sites with geographical clustering highlighted.

2.2 Vegetation sampling

From May to July 2007 at each site three replicates of 100 m² plots were surveyed in representative areas of the stand. Each plot is identified by a unique alphanumeric code. The first 5 letters are the site code. Following this a number identifies the 10 × 10 m plot, e.g. BALLY2. At each site three 10 x 10 m² plots were positioned at least 50m from the forest edge and 50m from each other to reduce edge and pseudo-replication effects respectively.

Ground flora for this study is defined as vascular plants, mosses, liverworts and lichens growing on the forest floor and on microhabitats such as deadwood and stumps.

Henceforth in this study bryophytes and lichens will both be referred to as non vascular flora (unless specific reference to either taxon is required). In each plot, percent cover of terrestrial vascular plant, bryophyte and lichen species was recorded to the nearest 5%.

Cover below 5% was recorded either as 3% (indicating cover of 1–5%) or 0.5% (indicating cover <1%). For bryophytes and lichens, only species forming patches more than 5 cm² were recorded. Vascular plant nomenclature followed Stace (1997), mosses followed Smith (2004) and liverworts followed Paton (1999).

2.3 Environmental and structural data sampling

Vegetation structure data were collected at 100 m² scale and included average height and percentage cover of vegetation in different strata (Table. 2). For mid-rotation and mature plantations, where it was felt that stand structure was not adequately captured in the 10 x 10m plot owing to trees being larger and more widely spaced, a 20 x 20m plot was used.

Table 2. Details of vegetation strata recorded.

Strata	Description
Canopy layer	Uppermost tree stratum defined by relative rather than absolute height; planted trees included regardless of structural stage.
Large shrub / understory layer	Woody vegetation below the upper tree stratum and $\geq 2\text{m}$ tall.
Dwarf shrub layer	Woody vegetation $< 2\text{m}$ tall including tree seedlings and saplings, small shrubs, vegetation with a bramble growth habit and climbers.
Field layer	Vascular herbs, including graminoids (grasses, rushes and sedges) and ferns but excluding climbers and woody species.
Ground layer	Mosses, liverworts and lichens.

The light environment of each plot was characterized by hemispherical photography as detailed in Smith et al. (2007). (Rich, 1990: as cited in French, 2005). Non-conifer leaf litter and conifer needle litter cover were visually estimated separately for each 100 m^2 plot. Thinning status of the stand, intensity of mammal grazing, silvicultural and recreational disturbances were ranked on semi-quantitative scales. For further details on methodology for recording deadwood volume and type, soil type and pH see French et al. (2008).

2.4 Data analysis

Species richness, Simpson's reciprocal and Whittaker's beta diversity index (Whittaker, 1972) were employed as diversity indices using the vegetation data of naturally regenerated flora only, from the 100 m² plots. To avoid pseudo-replication, biodiversity metrics, plant abundances and environmental data in smaller sample units were averaged or otherwise combined for analyses focusing on larger scales. While, perhaps, less sensitive to heterogeneity at the 100m² scale this larger analytical scale facilitates examination of between-site ground flora variation by removing within-site variation.

Here we focus on species richness i.e. the number of species in a unit of study as our primary measure of biodiversity, as this is a widely accepted and intuitive biodiversity measure method (Magurran, 2004) and has previously been found suitable for use in plantations (French et al. 2008). However, it should be noted that total species richness does not indicate whether the species involved are of conservation significance and will also underestimate the conservation value of important but naturally species-poor habitats.

Prior to statistical testing, variables were inspected for conformity to the assumptions of parametric statistics, i.e. normal distribution and non-parametric statistics were used as required. As expected for community data the distribution was non-normal. Correlation analyses were performed to explore the relationships among environmental and structural variables and between them and diversity indices. Data Desk 6.0 was used to compute Spearman's rank correlation coefficient (r) was used (Sokal & Rohlf, 1995). The significance of the correlations was tested using a t-test [$t = r_s * \sqrt{((n-2)/(1-r_s^2))}$] where n is the number of sample units (Kent and Coker, 1992).

The two-factor nested design ANOVA (with sites as the nested factor within the main factor of stand structural stage) was used to identify differences in diversity indices among, and within, the structural stage. Cochran's test for equality of group variances was used and found to be not significant ($C = 0.2161$) so the raw data were analysed. A SNK post-hoc multiple comparison test was used to compare species richness within structural stages and to identify significant differences. ANOVA analyses were conducted using GMAV (1997).

Non-metric multidimensional scaling (NMS) was carried out using PC-ORD for Windows Version 5.0 (McCune & Mefford, 2006) to explore the relationships between variables. The NMS autopilot mode was used (rather than manually adjusting the parameter settings and option selections in PC-ORD) to assist in making multiple runs and as it chooses the best solution at each dimensionality and tests for significance. Table 3 shows the autopilot parameters for a "slow and thorough" analysis used in this research. In autopilot mode all options are set automatically except for the distance measure, and, as recommended for community data, the Sørensen (Bray-Curtis) distance was selected (McCune & Mefford, 2006).

Table 3. Autopilot (slow and thorough) parameter set up for NMS used in analysis.

Parameter	Result
Number of axes	6
Number of runs with real data	250
Stability criterion	0.000000
Iterations to evaluate stability	89
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	250

Percent of variance was calculated as an after-the-fact evaluation of the quality of the data reduction, along with an assessment of how the variance explained is distributed among the primary axes.

3 RESULTS

The results of the analyses outlined in section 2 will be shown below, but as the results themselves are only preliminary this precludes a complete and final presentation of the analysis here.

3.1 Ground flora community

A total of 182 plant species were recorded in the 100m² quadrats including 97 vascular plant and 65 non vascular species. The most floristically rich sites in both vascular and non vascular species were a pre-thicket (59 species recorded) and a mature (52 species recorded). The most species impoverished site inventoried was a mid rotation with 11 species. The sites that were found to have less than average species richness of 32 ($n = 20$, $se = 3.4$) were two thicket, all the mid rotation and two mature sites. There was a large variation in species richness recorded among the stands (SR range 11-59).

3.2 Ground flora dynamics over the forest cycle

Through the Sitka spruce structural cycle, mean total ground flora species richness peaks during pre-thicket stage, decreases during the thicket stage, is at a minimum during mid rotation, and increases again during the mature stage (Fig. 2). This also describes the relationship between afforestation stand structural stage and ground flora diversity (French et al. 2008). ANOVA analysis highlighted that these differences in species richness among stages were significant. On average the pre-thicket stands support the highest number of ground flora species with an average of 29 ($n = 15$, $se = 1.7$) species per 100 m² quadrat. For non vascular flora richness the pre-thicket and mature stands have the same species richness (mean SR = 10, $n = 15$, $se = 1.1$ for the former and 0.7 for the latter stage) and the thicket stage has just one less species on average.

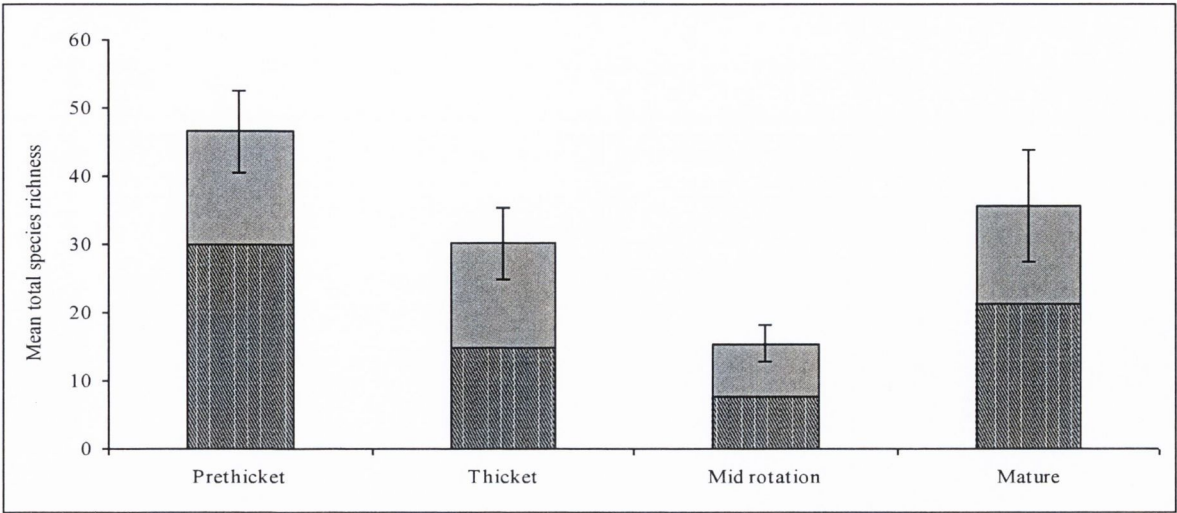


Figure 2. Relationship between reforestation ground flora diversity measured as species richness over the forest cycle. Species richness is represented as grey for vascular and white for non vascular species. Error bars indicate total SR standard error.

3.3 NMS ordination

The NMS ordination joint plot shown in Figure 3 is based on the composition of the total ground flora and allows differences and similarities in ground flora composition among structural stages to be visually assessed. The ‘slow and thorough’ NMS autopilot run recommended a 3-D solution (final stress = 8.61). The ordination clearly highlights the difference in vegetation composition between the early forest stages and the established stands e.g. pre-thicket and mature stages are well separated along axis 2. The blue lines of the joint plot indicate the correlations between the variables and the ordination axes with longer lines indicating a stronger correlation. Their orientation also indicates the axes with which they show correlation e.g. canopy openness is correlated with axis 2.

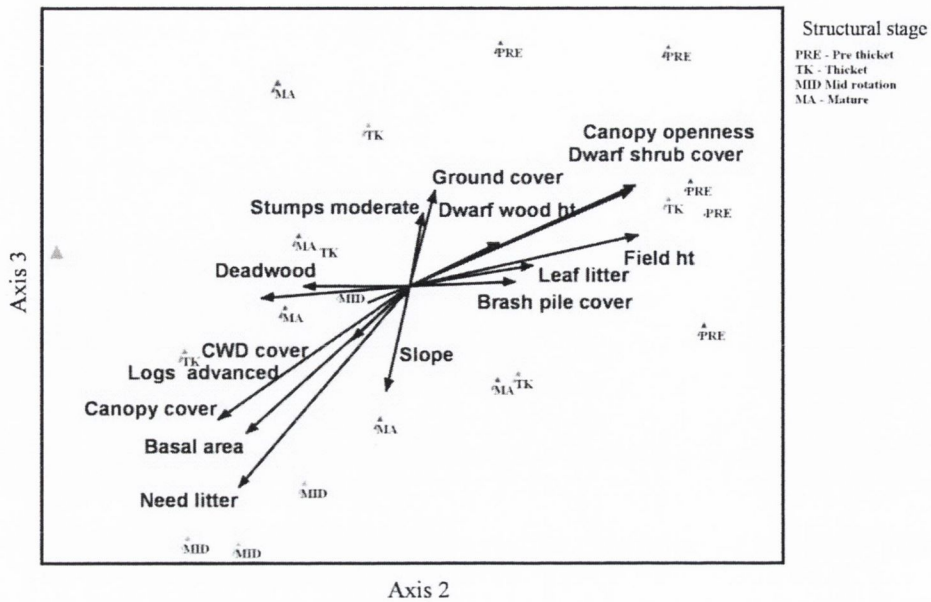


Figure 3. Joint plot of NMS ordination illustrating total ground flora of different structural stages according to their overall species abundances and composition with environmental variables displayed as vectors in ordination space. Final stress for 3-dimensional solution = 8.61, final instability = 0.00045, axis 2 $r^2 = 0.504$, axis 3 $r^2 = 0.182$.

3.4 Structural and functional diversity indicators

Variables that were highly correlated with axes of the NMS ordination were subsequently analysed for correlation with species richness using Spearman's rank correlation coefficient (Table 4). These results indicated four variables as significantly correlated with i.e. more important influences on, ground flora diversity and composition: stand stage, canopy openness, brash pile cover and volume of moderately decayed logs.

Table 4. Correlations between species richness and structural and functional variables. Spearman’s rank correlation coefficient, r_s , is displayed for those that were significant according to p-values from t-statistic (Kent & Coker, 1992).

Correlation variable	SR
Canopy openness	0.766***
Dwarf woody cover	0.699***
Field cover	0.831***
Field height	0.630**
Ground cover	0.592**
Brash pile	0.733***
Logs (moderately decayed)	0.728***

Note: * indicates that the correlation coefficient is significant at the $p < 0.05$ level, ** indicates significance at the $p < 0.01$ level and *** indicates significance at the $p < 0.001$ level. Cover units are per cent coverage and height units are in meters.

There was a significant positive correlation according to Spearman rank correlation coefficient ($r_s = 0.766$, $p < 0.01$) between canopy openness and species richness over the forest cycle (Fig. 4). Owing to this effect on ground flora richness among the Sitka spruce structural groups, canopy openness is a potential indicator of diversity in Sitka spruce stands ($r_s = 0.766$, $p < 0.01$, Fig. 4).

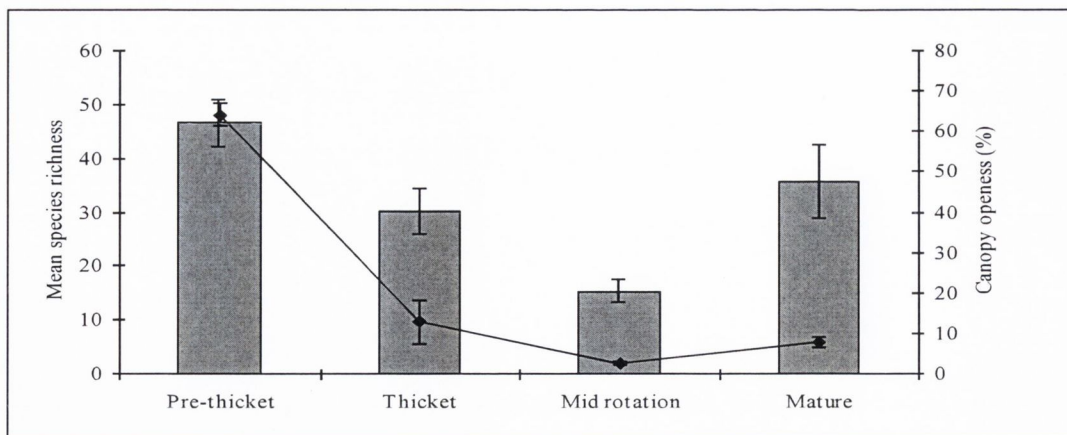


Figure 4. Significant positive correlation ($r_s = 0.766$, $p < 0.001$) between canopy openness and mean species richness over the structural cycle. Error bars indicate $\pm$ standard error. Note: columns represent species richness and line represents canopy openness (%).

The mean volume of decaying wood across the structural cycle was 40 m^3 per ha with most concentrated in the mid rotation to mature stages and with the greatest proportion at an advanced stage of decay. There were varying relationships between species richness and the different classes of deadwood. Non vascular species richness was negatively correlated with total deadwood volume ($r_s = -0.382$, $p > 0.05$; Fig. 5). In fact at mid rotation where deadwood volume is at the highest level during the forest cycle, the non vascular species richness is at the lowest of the cycle. Moreover Figure 5 illustrates that pre-thicket non vascular species richness is equivalent to that of mature stands. Non vascular species richness was significantly positively correlated with brash piles ($r_s = 0.539$, $p > 0.05$).

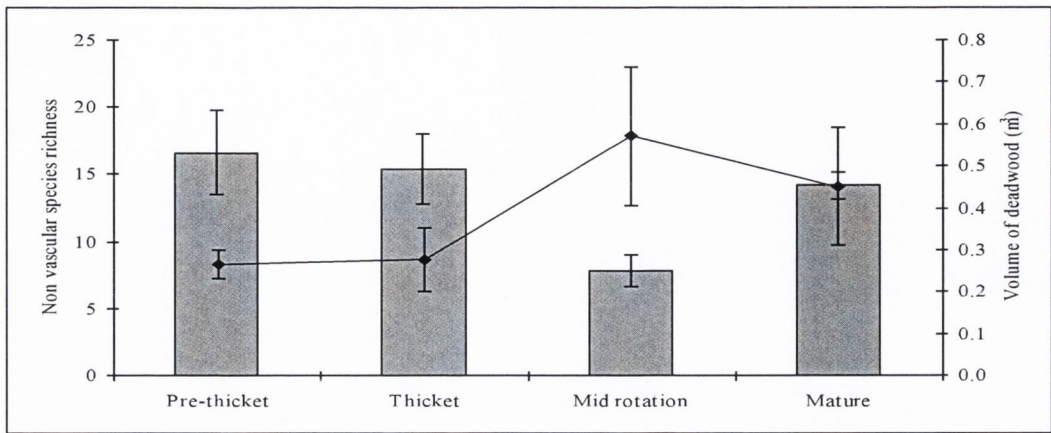


Figure 5. Relationship between non vascular richness and total volume of deadwood ($r_s = -0.382$, $p > 0.05$). Error bars indicate $\pm$ standard error. Note: columns represent non vascular species richness and line represents total deadwood volume (m^3).

4 DISCUSSION

4.1 Ground flora dynamics over the forest cycle

We have found that ground flora diversity vary in Sitka spruce forests across the forest cycle (Fig. 2). Several structural, compositional and functional variables correlated with species richness (Table 4) and have the potential to be used as biodiversity indicators in forest management at the stand scale. Species richness proved to be a suitable ground flora diversity index for Sitka spruce reforestation as per the findings of work on afforestation plantations (French et al. 2008; Smith et al. 2005). ANOVA analysis highlighted species richness as an appropriate diversity index as structural differences between stages were significant (Fig. 2). This index also highlighted differences within stages owing to the environmental variable heterogeneity between sites of the same structural stage.

The results from this study suggest that, with the progression of the reforestation cycle, the impact of stand structural stage on ground flora diversity follows the Franklin diversity

model (1982: as cited in Smith et al. 2007) where diversity peaks during late pre-thicket stage, is at a minimum during the dense canopy stages of thicket and unthinned mid rotation, but peaks again with canopy thinning (opening) during the mature stage (Fig. 2). This model also accurately described the relationship between afforestation ground flora diversity and stand structural stage (French et al. 2008). As reported by Hill (1979) for afforestation stands, plantation vegetation succession in reforestation also involves an initial increase in ground flora diversity following crop planting. In reforestation sites this is clearly evidenced in the high coverage of plants suited to open areas during the pre-thicket stage, such as the dwarf shrub woody layer. *Calluna vulgaris* is the main species of this layer at most of our sites. However, when canopy layer values are high during the unthinned mid rotation phase there is a large reduction in ground flora through shading. When the stand reaches the mature stage, with less shading owing to the thinning regime, the ground flora community biomass and diversity recovers somewhat, but never reaches the levels of pre-thicket. Ferris et al. (2000) also found the pre-thicket stages were closely matched with heath or upland grassland communities, and contained species associated with open conditions such as *C. vulgaris*. The findings of this project support recent British research (Humphrey et al. 2003) that Sitka spruce pre-thicket plots have high values for dwarf shrub layer cover with distinctive communities and are more diverse than later stages which have high canopy cover values and low shrub layer cover.

4.1.1 Afforestation and reforestation non vascular dynamics over the forest cycle

The importance of maturing forests as habitats for bryophytes has been widely reported as bryophytes generally prefer cool, damp, shaded conditions often found in mature stands (Smith et al. 2007; Smith et al. 2005; French, et al. 2008; Humphrey et al. 2003; Ferris et al. 2000). Investigations into the potential value of conifer plantations for non vascular plants, and how they might be managed to improve habitat quality, have focused on the value of deadwood as a substrate for non vascular plants. There is a reported positive correlation between the species-richness of non vascular communities and the type and decay class of deadwood. However, this research found non vascular species richness was not dependent on stand age (i.e. pre-thicket and mature stands had equal richness) and was also significantly negatively correlated with deadwood volume (Fig. 5). These findings indicate that although suitable deadwood substrate is more available in the older than in the younger stands, the light environment is restrictive to non vascular species. Indeed non vascular species richness is negatively correlated with canopy cover. When canopy cover is at its greatest during the forest cycle and the total deadwood volume is at its highest, i.e. at mid rotation, the non vascular species are at their lowest cover of the forest cycle (Fig. 5). The findings of this latest research indicate that deadwood only becomes an important habitat for non vascular species in plantations if other environmental conditions are favourable also e.g. canopy openness. The synergistic effect of these two variables, canopy openness and deadwood, on non vascular richness highlights the importance of an integrated management program for ground flora diversity in plantations. Moreover, it is important that continuity of deadwood supply is maintained (as is the case in natural woodlands) so that there is no catastrophic die off of the communities dependent on deadwood substrate during the forest cycle.

Smith et al. (2005) have reported higher bryophyte species richness beneath the closed canopy stages of afforestation Sitka spruce perhaps owing to lower light intensities and less risk of desiccation. However, the high number of non vascular species reported in the pre-thicket stage in this research contradicts these findings (Fig. 5). In fact, pre-thicket non vascular species richness is equivalent to that of mature stands. The presence of large, complex brash piles (>2m wide and >1m tall) from the previous rotation had a significant impact on the diversity of pre-thicket sites (the only stage where brash piles of those dimensions occurred). The habitat they provided resulted in higher species richness in pre-thicket plots that did have brash piles than in plots where they were absent. Therefore, this research suggests there is a positive effect of large, complex brash piles (left over from previous rotation) on non vascular (and vascular) species richness in pre-thicket by providing suitable habitat and/or reducing desiccation. However, due to a lack of comprehensive site history information (problems obtaining information from some forest managers in time to include in analysis) it is unclear whether this management practice of piling up previous rotation stumps and logs is recent (as only observed in sites < 10 years since planting) or whether it has been common practice since first round of reforestations e.g. did the thicket to mature stages in this study begin with a similar brash pile-diversity dynamic as that recorded by this study at pre-thicket sites?

4.2 Diversity indicators

The NMS ordination (Fig. 3) and subsequent correlation analysis (Table 4) indicated stand stage, canopy openness, brash pile cover and volume of moderately decayed logs as important influences (having significant correlations with total species richness) on ground flora diversity and composition. The NMS ordination of the forest stands also highlights the problems of amalgamating discrete quadrat data. Heterogeneity in vegetation composition among quadrats *within* a single stand means that such sites do not fit into a well constrained cluster pattern.

Structural stage or stand age as a diversity indicator is suggested by popular models such as those of Franklin (1982: as cited in Smith et al. 2007) and Hill (1979). However, this research has shown that these proxy measures do not take into the account the hugely important variables *within* a structural stage that impact on that stand's ground flora diversity i.e. gaps in an otherwise closed canopy. Thus, structural stage is not as good a predictor of diversity in this case. Several potential diversity indicators that were highlighted by NMS ordination and correlation analyses are outlined below. It is important to note that, as with diversity indices, no one indicator should be used in isolation. Rather, in practice, these more influential variables should be used as a suite of diversity indicators.

4.2.1 Structural and functional indicators

Owing to its effect on ground flora richness among the Sitka spruce structural groups, canopy openness is a strong indicator of diversity within Sitka spruce structural groups agreeing with previous work (French et al. 2008; Smith et al. 2007 & 2005; Humphrey, et al. 2003; Ferris et al. 2000; Hill, 1979; Fig. 4). Although species richness was not significantly correlated with total volume of deadwood there are classes of deadwood that can act as ground flora diversity indicators, namely large complex brash plies for pre-thicket sites and moderately decayed logs at the more mature stages of the forest cycle.

4.2.2 Compositional indicators

Dwarf woody shrub cover is a good indicator of species richness in pre-thicket stands but its close relationship with species richness lessens as the stand matures. The cover of non vascular flora is a good indicator of total ground flora richness over the entire structural cycle with higher non vascular coverage indicative of more species rich ground flora communities. Vascular species richness is a better predictor of total ground flora richness than non vascular species richness across the forest cycle. This is owing to the fact that there are more vascular species (97) than non vascular species (65) in ground flora communities of Sitka spruce. However, vascular species richness should not be used as a proxy measure of non vascular species richness, and *vice versa*, as the relationship found between them by this research exhibits a large variation possibly due to differing ecological requirements.

4.3 Sustainable Forestry Management implications

The diversity indicators outlined in section 4.2 indicate the sensitivity of Sitka spruce stands to disturbances that are more influential on ground flora diversity than structural stage. As well as acting passively as indicators of diversity they have management implications, as by manipulating the forest structure using these variables, biodiversity within planted conifer stands can be enhanced.

Due to the negative impacts of closed Sitka spruce canopies on ground flora diversity management to increase the structural diversity within plantations is recommended e.g. establishing stands in the plantation that are in close proximity at different times. This research has shown the importance of large, complex brash piles to pre-thicket diversity and the continuation (or extension) of this practice is recommended. Pre-thicket stages have a high complement of species not found through rest of forest cycle stages i.e. heath and grassland community species. Incorporation of this structural stage at regular spatial intervals in the plantation will increase biodiversity at the plantation scale. As suggested in BIOFOREST this could be achieved by minimum time periods between planting adjacent stands (French et al. 2008).

The importance of open spaces for increasing biodiversity was highlighted in this research. Recent research suggests gaps should be between 625–900 m² (Smith et al. 2007). Moreover, early and sufficient thinning is important in preventing canopy closure as this is probably the most important factor affecting ground flora diversity in Sitka spruce plantations. In conclusion, methods of management for enhancing afforestation biodiversity are, generally speaking, directly applicable to reforestation plantations.

5 CONCLUSIONS

Stand structure strongly affects species richness. We have developed a set of provisional, stand-scale indicators of biodiversity for Sitka spruce for use in Ireland; they are likely to be applicable over a wider area with similar climates, such as northern Britain. The indicators can be employed by non-specialists as a first step in identifying potentially high biodiversity stands or assessing the biodiversity implications of management interventions. In practice, as many of these indicators should be used together and never just one used alone. Structural and functional indicators are particularly useful, as their assessment is often relatively simple. Functional indicators can represent management interventions, such as thinning, that can be changed if required; structural indicators can highlight practices for management implement.

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