CORA Cork Open Research Archive
Cartlann Taighde Oscailte Chorcaí

Title	Invertebrate diversity in Irish and British forests
Authors	Fuller, Lauren
Publication date	2013
Original Citation	Fuller, L. 2013. Invertebrate diversity in Irish and British forests. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
Rights	© 2013, Lauren Fuller - http://creativecommons.org/licenses/by-nc-nd/3.0/
Download date	2026-11-06 23:03:32
Item downloaded from	https://hdl.handle.net/10468/1570



UCC
University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Invertebrate Diversity in Irish and British Forests

Lauren Fuller



This thesis is presented to the National University of Ireland, Cork, in candidature for the degree of Doctor of Philosophy

Research supervisors:
Professor John O'Halloran
Dr Tom Kelly

School of Biological, Earth and Environmental Sciences, College of Science, Engineering and Food Science, University College Cork

Head of School: Professor John O'Halloran

August 2013

Table of Contents

Declaration 1

Abstract 2

Chapter 1: Introduction 3

Forests in Ireland and Britain 4

Forest biodiversity 5

Forest management for biodiversity 5

Invertebrate diversity 8

Aims of this research 9

References 11

Chapter 2: The response of ground-dwelling spiders (Araneae) and hoverflies (Diptera: Syrphidae) to afforestation in an agricultural landscape 21

Abstract 22

Introduction 23

Materials and methods 25

Results 32

Discussion 42

References 48

Chapter 3: The importance of young plantation forest habitat and forest road-verges for ground-dwelling spider diversity 57

Abstract 58

Introduction 59

Materials and methods 61
Results 67
Discussion 73
References 78
Chapter 4: Influence of conifer tree species on ground-dwelling spider diversity in plantation forests 84
Abstract 85
Introduction 86
Materials and methods 88
Results 93
Discussion 100
References 105
Chapter 5: Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (*Quercus robur/ Q. petraea*) and Scots pine (*Pinus sylvestris*) 113
Abstract 114
Introduction 115
Materials and methods 117
Results 125
Discussion 133
Acknowledgements 138
References 139

Chapter 6: The application of forest biodiversity indicators across forest stand types and regions 146

Abstract 147

Introduction 148

Materials and methods 150

Results 157

Discussion 161

References 169

Chapter 7: Ground-dwelling spider diversity in rare European oak and yew woodlands and the impact of grazing 181

Abstract 182

Introduction 183

Materials and methods 185

Results 189

Discussion 195

References 200

Chapter 8: Concluding synthesis 207

Main conclusions 208

Forest management recommendations 210

Further research 211

References 213

Acknowledgements 218

Appendix 1 219

Appendix 2 224

Appendix 3 230

Appendix 4 233

Declaration

This work has not previously been accepted in substance for any degree, nor is it being currently submitted in candidature for any other degree, either at University College Cork or elsewhere. This thesis is the result of my own independent work and research, except where otherwise stated.

Signed……L. Fuller……..

Date……16.12.2013……....

Abstract



Robertus lividus from Sitka spruce plantation forest

Ireland and Britain were once covered in natural forest, but extensive anthropogenic deforestation reduced forest cover to less than 1% and 5 %, respectively, by the beginning of the 20th century. Large-scale afforestation has since increased the level of forest cover to 11% in Ireland and 12% in Britain, with the majority of planted forests comprising small monoculture plantations, many of which are of non-native conifer tree species. At present the forest cover of Ireland and Britain generally consists of small areas of remnant semi-natural woodland and pockets of these plantation forests within a predominantly agricultural landscape.

Invertebrates comprise a large proportion of the biodiversity found within forested habitats. In particular, spiders and carabid beetles play an important role in food webs as both predators and prey and respond to small-scale changes in habitat structure, meaning they are particularly sensitive to forest management. Hoverflies play an important role in biological control and pollination and have been successfully used as indicators of habitat disturbance and quality.

This research addressed a number of topics pertinent to the forest types present in the contemporary Irish and British landscapes and aimed to investigate the invertebrate diversity of these forests. Spiders and carabid beetles were sampled using pitfall trapping and hoverflies were sampled using Malaise net trapping. Topics included the impacts of afforestation, the importance of open space, the choice of tree species, and the use of indicators for biodiversity assessment, as well as rare native woodlands and the effect of grazing on invertebrate diversity.

A total of 196 spider species (n = 32,422), 59 carabid beetle species (n = 23,388) and 76 hoverfly species (n = 1,828) were identified during this research. Afforestation in agricultural grasslands had a positive effect on spider and hoverfly diversity. Additionally, hedgerow habitat provides an important contribution to biodiversity in agricultural landscapes and afforested grasslands. Forest road-verges in six year old forests supported ten spider species of conservation importance and a variety of open- and forest-associated species, indicating that the open habitat of forest road-verges are important areas for invertebrate diversity within forests and should be protected as forests mature. Two commonly planted European conifer species, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), were found to support higher spider diversity compared to two commonly planted North American conifer species, Sitka spruce (*Picea sitchensis*) and

lodgepole pine (*Pinus contorta*). These results suggest that planting semi-native tree species or species of European provenance will increase forest biodiversity. Mixed tree species stands did not support higher species richness of spiders and carabid beetles than monoculture stands, indicating that the current ratios of tree species and planting patterns recommended by forest policy for mixed stands do not enhance the diversity of these two species groups. Biodiversity indicators were tested for spiders and ground vegetation species richness in conifer, broadleaf and mixed tree forests in Ireland and England and were found to consistently predict species richness across forest types, but not across countries. These results indicate that biodiversity indicators can support forest management for biodiversity, but a number of other important factors, such as site history and climate, must also be considered. Oak and yew woodlands in Killarney National Park provided important habitat, which is otherwise scarce in Ireland, for five spider species. Deer grazing in these native woodlands was also investigated and found to have a negative effect on spider diversity.

The results are discussed and evidence-based recommendations are made for forest policy and management to protect and enhance invertebrate biodiversity in order to promote sustainable forest management in Ireland and Britain.

Chapter 1

Introduction



Hemispherical photograph of oak woodland in Killarney National Park

Forests in Ireland and Britain

The island of Ireland has historically undergone vast deforestation and modification of its natural environment, as a result of which less than 1% of the natural forest cover remained by the beginning of the 20th century (Anon, 2008). This lack of forest estate led to government policy and grant-aid in support of afforestation which has increased forest cover to approximately 11% over the course of the last century (Forest Europe *et al.*, 2011). Similarly, in Britain the natural forest cover fell to 5% at the beginning of the 20th century and has since increased to 12%, mainly through the establishment of plantation forests (Watts, 2003; Forest Europe *et al.*, 2011). However, both countries still rank among the lowest in terms of forest cover in Europe, where the average is 32% (Forest Europe *et al.*, 2011).

Plantation forests comprise approximately 89% of the current forest estate in Ireland and 77% in Britain (Forest Europe *et al.*, 2011). These forests were originally established with the single goal of timber production and, due to a lack of suitable native tree species, used non-native fast growing species (Pryor, 2000; Anon, 2008). Therefore many of these plantation forests are dominated by non-native tree species and Ireland has one of the highest percentages of introduced species in Europe with 70% of the forests consisting of non-native conifer species (Forest Europe *et al.*, 2011). Only 11% of the total forest cover in Ireland is semi-natural woodland (Forest Europe *et al.*, 2011) and these tend to be small and fragmented, with approximately 68% of woodlands less than 10 ha in size (Perrin *et al.*, 2008). Much of the plantation forests in Britain are also composed of non-native conifers (49%) and only 23% of the total forest cover is semi-natural woodland (Forest Europe *et al.*, 2011).

The long history of deforestation of native woodlands and subsequent reforestation with commercial forests means the forest cover of the contemporary Irish and British landscapes comprises small and fragmented areas of semi-natural woodland and patches of plantation forests set within a predominantly agricultural landscape (Pryor, 2000; Anon, 2008). The current government target in Ireland is to further increase the forest cover to 14% by 2030, mainly through further establishment of plantation forests with non-native conifers (COFORD Council, 2009). However, in Britain no clear target has been specified, although government policy is committed to maintaining or increasing the total forest area (Anon, 2011).

Forest biodiversity

The biodiversity found within non-native plantation forests is of particular interest due to the negative impact of deforestation on global biodiversity and the potential for non-native reforestation to contribute to biodiversity conservation (Carnus *et al.*, 2006; Brockerhoff *et al.*, 2008). Whilst forests represent some of the richest and most biologically diverse habitats of the world (Millenium Ecosystem Assessment, 2005), the highly managed nature of plantation forests means they may support less native biodiversity and fewer species than naturally occurring forest habitats (Moore and Allen, 1999; Palik and Engstrom, 1999; du Bus de Warnaffe and Lebrun, 2004; Hiroaki *et al.*, 2004; Bremer and Farley, 2010). Nevertheless, in countries with very low forest cover and very little naturally occurring forest, these plantation forests offer an important opportunity to provide habitat for forest associated species and enhance overall landscape biodiversity (Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2008).

Biodiversity conservation is a key issue in the global environmental arena at present (Buckley, 2004). The conservation of biodiversity in the world's plantation forests is a key component of sustainable forest management (SFM), which aims to manage forests for a range of ecosystem services, including biodiversity, as well as timber production, and the principles of SFM are included in forestry policies worldwide (United Nations Conference on Environment and Development, 1992; MCPFE, 1993; European Communities, 2003). As members of the European Union (EU) and signatories to the UN Convention on Biological Diversity, Ireland and Britain are committed to the implementation of EU Directives aimed at maintaining and enhancing biodiversity in plantation forests (DAHG, 2011; Anon, 2012b). These directives have been incorporated into Irish and British law through forestry policies such as the Forest Biodiversity Guidelines in Ireland and the Forest and Biodiversity guidelines in Britain (Anon, 2000b; Forestry Commission, 2011).

Forest management for biodiversity

The provision of habitat for biodiversity by plantation forests in landscapes where native woodland has become rare is dependent on appropriate management (Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2008). During the 20th century, afforestation in Ireland was mainly carried out by the semi-state forestry company Coillte (Anon, 2008). However, in recent times this rate of afforestation has slowed, due to the difficulties of acquiring suitable land, and the majority of afforestation is now carried out on

privately owned land, and in particular on farmland (Anon, 2010). Afforestation impacts on biodiversity and the magnitude and direction of the effect is influenced by preceding land use and forest management practices (Hunter, 2000; Carnus *et al.*, 2006). Changes in forest management practices in recent decades reflect the growing importance of ecological considerations, particularly biodiversity conservation, and land-owners undertaking afforestation in Ireland must comply with forestry objectives which form part of a legal and institutional framework. These include not only producing commercial timber but also ecosystem services such as carbon sequestration, improving water quality and increasing biodiversity (Anon, 2012a). Therefore, grant-aided afforestation can provide both a positive incentive for increasing total forest cover as well as an effective regulatory tool for sustainable forest management.

One of the goals of sustainable forest management is the creation of a more natural forest environment which will support higher biodiversity (Angelstam and Dönz-Breuss, 2004). Open spaces are important components of native woodlands that occur naturally in riparian strips, mires, and crags, and should be incorporated into plantation forests to mimic the natural woodland habitat and enhance biodiversity (Ratcliffe and Peterken, 1995; Iremonger *et al.*, 2006). Areas of open space allow light through the canopy which stimulates ground flora diversity thus increasing habitat diversity and supporting open specialist and edge habitat associated species which are not found in the forest interior (Sparks and Greatorex-Davies, 1992; Greatorex-Davies *et al.*, 1994; Stephens, 2005; Gittings *et al.*, 2006; Smith *et al.*, 2007). Although typically associated with negative impacts on biodiversity in extensively forested landscapes (Buckley *et al.*, 2003; Avon *et al.*, 2013), in landscapes with largely fragmented forests, such as that found in Ireland, there is the potential for forest roads to make a positive contribution to forest biodiversity where they increase habitat heterogeneity attracting species that may otherwise be rare or absent (Warren and Fuller, 1993; Mullen *et al.*, 2003; Gittings *et al.*, 2006). Forest roads can be planned and managed so that from the time of planting they make a positive contribution to biodiversity (Warren and Fuller, 1993; Ryan *et al.*, 2004).

The selection and management of the canopy tree species can also have a significant influence on forest biodiversity, altering understory structure and species composition through changes in microclimate, soil chemistry, litter and vegetation (Palik and Engstrom, 1999; Anon, 2000a; Horgan *et al.*, 2003; Hiroaki *et al.*, 2004). Even-aged plantation forests of single conifer species, although fast growing and desirable for production objectives, are

generally considered to support low biodiversity and mainly generalist species compared to broadleaf native woodlands which can support more native forest specialist species (Fahy and Gormally, 1998; du Bus de Warnaffe and Lebrun, 2004; Bremer and Farley, 2010). The use of mixed tree species plantations to improve the biodiversity value of commercial forests has received considerable attention in forest policy and management plans in recent years (Spence *et al.*, 1997; Spiecker, 2003; European Environment Agency, 2008). Forestry guidelines in Ireland and Britain advocate the planting of tree species mixtures, and in particular the inclusion of a broadleaf component, to improve the biodiversity value of plantation forests (Anon, 2000b, a, 2011). Although, recent evidence has highlighted the need for further investigation into the biodiversity benefits conferred by mixed stands, to inform management plans for biodiversity enhancement (Barbier *et al.*, 2008a, b; Cavard *et al.*, 2011; Oxbrough *et al.*, 2012).

Compiling a full inventory of the species in a forest is not generally possible due to financial and time limitations (Lawton, 1998; Lindenmayer, 1999; Larsson, 2001). Therefore methods which can provide a surrogate measure of biodiversity, such as indicators that are correlated with species richness, are often recommended as a means to assess the habitat quality and diversity of forest ecosystems (Noss, 1999; Larsson, 2001; Gardner, 2010). Many sets of functional, structural and compositional indicators have been proposed, however, rigorous testing of biodiversity indicators is required to understand their applicability to different species groups, forest types and structural stages (Noss, 1999), as well as their reliability across different geographical regions. The most useful biodiversity indicators for forests managers will be developed for use at the forest management unit level, as most forest management is carried out at this scale (Similä *et al.*, 2006). Biodiversity indicators must also be cost-effective and easy to assess and interpret by non-experts (Ferris and Humphrey, 1999).

The lack of native forest in Ireland emphasises the importance of the condition and biodiversity of the nation's remaining areas of natural woodland. Killarney National Park in south-west Ireland has been a designated UNESCO biosphere reserve since 1982 (UNESCO, 2001) and contains the most extensive areas of semi-natural woodland in Ireland (NPWS, 2005). Several areas of internationally important and nationally rare woodland are found here, including yew (*Taxus baccata*) and acidophilus sessile oak (*Quercus petraea*), which are priority habitats under Annex I of the EU Habitats Directive (Perrin *et al.*, 2006; National Parks and Wildlife Service, 2008). These woodlands have large populations of red

deer (*Cervus elaphus*) and introduced Asian sika deer (*Cervus Nippon*) (Carden *et al.*, 2011; Carden *et al.*, 2012). Grazing pressure from large ungulates such as deer can have ecological impacts through the reduction of field layer vegetation cover and diversity and the reduction of the survival of tree saplings. This not only changes the species composition of the overstory, but also has a cascading effect on biodiversity, including arthropods, birds and mammals (Côté *et al*., 2004). Considering the rarity of the woodlands types in Killarney National Park, the biodiversity they support and the effects of grazing on biodiversity are of importance for conservation management, as well as informing forest management plans for managing grazing animals.

Invertebrate diversity

Invertebrate species comprise the largest proportion of global biodiversity, occurring in almost every terrestrial and aquatic ecosystem (Kim, 1993; Samways, 1993; Mora *et al.*, 2011), and fulfil a variety of functional roles, maintaining the diversity of ecological processes which are fundamental for life on earth (Samways *et al.*, 2010). In forests they play an integral role in ecosystem functioning and the delivery of ecosystem services, performing important functional roles in food webs, pollination and nutrient cycling (Petersen and Luxton, 1982; Gunnarsson, 1996; Kevan, 1999; Sommaggio, 1999; Sanders *et al.*, 2008; Samways *et al.*, 2010; Cardoso *et al.*, 2011). Therefore the conservation of invertebrate biodiversity is central to the planning and management of forest ecosystems.

Spiders (Araneae) are the dominant invertebrate predator in most terrestrial ecosystems and are one of the most abundant arthropod species groups of the forest floor (Wise, 1993). They play an integral role in the functioning of forest food webs as predators, regulating litter arthropod communities (Clarke and Grant, 1968; Moulder and Reichle, 1972; Wise, 2004), and as prey for many birds and insectivorous mammals (Churchfield *et al.*, 1991; Gunnarsson, 1996). Spiders are sensitive to habitat changes at a small scale, show strong habitat specificity, and are primarily affected by vegetation and litter structure, making them an appropriate focus group for assessing habitat quality (Uetz, 1975; Uetz, 1991; Marc *et al.*, 1999; Oxbrough *et al.*, 2005; Oxbrough *et al.*, 2006).

Carabid beetles (Coleoptera: Carabidae) are another ubiquitous and abundant species group that occupy an important place in forest food webs, mainly as generalist predators, although some species are herbivorous or omnivorous (Lovei and Sunderland, 1996; Pearce and Venier, 2006). Carabids are an interesting group to study as they respond to a range of

environmental parameters such as moisture and ground temperature, soil pH, and litter and vegetation structure, meaning they are particularly sensitive to forest management (Thiele, 1977; Niemela *et al.*, 1992; McGeogh, 1998; Magura *et al.*, 2000; Magura *et al.*, 2001; Paillet *et al.*, 2010).

Hoverflies (Diptera:Syrphidae) play a significant role in the functioning of ecosystem processes, including food webs and pollination (Sommaggio, 1999). Many hoverfly species are predatory on other arthropods and can contribute to the biological control of pests in agricultural and forest ecosystems (Peng *et al.*, 1993; Sommaggio, 1999; Bennewicz, 2011). Furthermore, hoverflies may be the second most important pollinators after wild bees (Larson *et al.*, 2001) and contribute to enhanced pollination services (Fontaine *et al.*, 2006; Albrecht *et al.*, 2012; Jauker *et al.*, 2012). Hoverflies respond to habitat disturbance and can exhibit strong habitat specificity, meaning they are useful indicators of habitat quality and have been successfully used for biodiversity assessments in forests (Smith *et al.*, 2005; Gittings *et al.*, 2006; Speight, 2008).

Monitoring of arthropod diversity in forests can be used to infer overall forest biodiversity and is an effective and cost-effective tool for designing and assessing sustainable forest management plans (Maleque *et al.*, 2009). In particular, the diversity of spiders in a habitat can also be used to infer information on other species groups, such as those involved in predator-prey interactions with spiders, and those which are also affected by habitat across a small scale, such as carabid beetles (Coleoptera: Carabidae) (Niemelä *et al.*, 1996; Marc *et al.*, 1999). Spiders, carabids and hoverflies are often used as biodiversity indicators due to their well-known habitat associations, the ease of trapping and identification, and the availability of reliable species lists (McGeogh, 1998; Kevan, 1999; Marc *et al.*, 1999; Sommaggio, 1999; Niemela *et al.*, 2000; Pearce and Venier, 2006; Meyer *et al.*, 2009).

Aims of this research

This research aimed to investigate a number of topics pertinent to the forest types present in the contemporary Irish and British landscapes, and provide evidence-based recommendations for forest policy and management, to protect and enhance invertebrate biodiversity. The thesis is presented as a series of self-contained chapters in paper style. Chapter 2 presents the first within-site assessment of the changes in ground-dwelling spider and hoverfly diversity following afforestation in agricultural grasslands in Ireland. Chapter 3 investigates whether forest roads make a positive contribution to ground-dwelling spider

diversity and whether road-width is related to spider diversity. Chapter 4 examines the diversity value of semi-native and introduced conifer species used in Irish forestry for ground-dwelling spiders. Chapter 5 is a paper that was produced in collaboration with researchers at Forest Research UK and investigates whether mixed tree species plantations support higher ground-dwelling spider and carabid beetle diversity than monocultures. Chapter 6 tests the reliability of biodiversity indicators for ground vegetation and ground-dwelling spider species richness in a range of forest types in Ireland and England. Chapter 7 presents the first investigation of ground-dwelling spider diversity in an important area of ancient semi-natural woodland and investigates the effect of deer grazing on ground-dwelling spider diversity in this woodland. In Chapter 8 the results of this research are discussed and recommendations for forest management are made based on these findings.

References

Albrecht, M., Schmid, T., Hautier, Y., Müller, C., 2012. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences 7, 4845-4852.

Angelstam, P., Dönz-Breuss, M., 2004. Measuring Forest Biodiversity at the Stand Scale: An Evaluation of Indicators in European Forest History Gradients. Ecological Bulletins 51, 305-332.

Anon, 2000a. Code of best forest practice. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2000b. Forest Biodiversity Guidelines. Department of the Marine and Natural Resources , Government of Ireland.

Anon, 2008. Irish Forests - A Brief History. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2010. Afforestation Statistics. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2011. The UK Forestry Standard. Forestry Commission, Edinburgh.

Anon, 2012a. Afforestation Scheme. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2012b. UK Post-2010 Biodiversity Framework. Joint Nature Conservation Committee and Department for Environment, Food and Rural Affairs, UK.

Avon, C., Dumas, Y., Bergès, L., 2013. Management practices increase the impact of roads on plant communities in forests. Biological Conservation 159, 24-31.

Barbier, S., Gosselin, F., Balandier, P., 2008a. Does mixing tree species promote plant diversity in forests? Revue Forestiere Francaise 60, 159-167.

Barbier, S., Gosselin, F., Balandier, P., 2008b. Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests. Forest Ecology and Management 254, 1-15.

Bennewicz, J., 2011. Aphidivorous hoverflies (Diptera: Syrphidae) at field boundaries and woodland edges in an agricultural landscape. Polish Journal of Ecology. 80, 129-149.

Berndt, L., Brockerhoff, E., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodiversity & Conservation 17, 1171-1185.

Bremer, L., Farley, K., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodiversity & Conservation 19, 3893-3915.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity & Conservation 17, 925-951.

Buckley, D.S., Crow, T.R., Nauertz, E.A., Schulz, K.E., 2003. Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. Forest Ecology and Management 175, 509-520.

Buckley, P., 2004. Development of wildlife conservation policy and legislation in Ireland. Biology & Environment 104B, 107-111.

Carden, R.F., Carlin, C.M., Marnell, F., McElholm, D., Hetherington, J., Gammell, M.P., 2011. Distribution and range expansion of deer in Ireland. Mammal Review 41, 313–325.

Carden, R.F., McDevitt, A.D., Zachos, F.E., Woodman, P.C., O'Toole, P., Rose, H., Monaghan, N.T., Campana, M.G., Bradley, D.G., Edwards, C.J., 2012. Phylogeographic, ancient DNA, fossil and morphometric analyses reveal ancient and modern introductions of a large mammal: the complex case of red deer (*Cervus elaphus*) in Ireland. Quaternary Science Reviews 42, 74-84.

Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. Biological Conservation 144, 2647-2655.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006a. Planted Forests and Biodiversity. Journal of Forestry 104, 65-77.

Cavard, X., Macdonald, E., Bergeron, Y., Chen, H.Y.H., 2011. Importance of mixedwoods for biodiversity conservation: Evidence for understorey plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environmental Reviews 19, 142-161.

Churchfield, S., Hollier, J., Brown, V.K., 1991. The Effects of Small Mammal Predators on Grassland Invertebrates, Investigated by Field Exclosure Experiment. Oikos 60, 283-290.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

COFORD Council, 2009. Forestry 2030. Department of Food, Agriculture and the Marine, Government of Ireland.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological Impacts of Deer Overabundance. Annual Review of Ecology, Evolution, and Systematics 35, 113-147.

DAHG, 2011. Ireland's National Biodiversity Plan 2011-2016. Department of Arts, Heritage and the Gaeltacht.

du Bus de Warnaffe, G., Lebrun, P., 2004. Effects of forest management on carabid beetles in Belgium: implications for biodiversity conservation. Biological Conservation 118, 219-234.

European Communities, 2003. Sustainable Forestry and the European Union. European Union, Belgium.

European Environment Agency, 2008. European Forests – ecosystem conditions and sustainable use. European Environment Agency Report, Copenhagen, Denmark.

Fahy, O., Gormally, M., 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. Forest, Ecology and Management 110, 263-273.

Ferris, R., Humphrey, J., 1999. A review of potential biodiversity indicators for application in British forests. Forestry 72, 313-328.

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLoS Biol. 4, e1.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Forestry Commission, 2011. Forests and Biodiversity. UK Forestry Standard Guidelines. Forestry Commission, Edinburgh.

Gardner, T., 2010. Monitoring Forest Biodiversity: Improving Conservation through Ecologically-Responsible Management. Earthscan.

Gittings, T., O'Halloran, J., Kelly, T., Giller, P.S., 2006a. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management 237, 290-300.

Greatorex-Davies, J.N., Sparks, T.H., Hall, M.L., 1994. The response of Heteroptera and Coleoptera species to shade and aspect in rides of coniferised lowland woods in southern England. Biological Conservation 67, 255-273.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155, 81-95.

Hiroaki, T.I., Shin-ichi, T., Tsutom, H., 2004. Exploring the Relationships Among Canopy Structure, Stand Productivity, and Biodiversity of Temperate Forest Ecosystems. Forest Science 50, 342-355.

Horgan, T., Keane, M., McCarthy, R., Lally, M., Thompson, D., 2003. A Guide to Forest Tree Species Selection and Silviculture in Ireland. COFORD, Dublin.

Hunter, M.L., 2000. Maintaining biodiversity in forest ecosystems. Cambridge University Press, UK.

Iremonger, S., Gittings, T., Smith, G.F., Wilson, M., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D.L., Giller, P., O'Sullivan, A.,

Neville, P., Mitchell, F.J.G., O'Donnell, V., Kelly, T., Dowding, P., 2006. Investigation of experimental methods to enhance biodiversity in plantation forests. In, BIOFOREST Project 3.1.3 Final Report. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology 14, 81-87.

Kevan, P.G., 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture, Ecosystems & Environment 74, 373-393.

Kim, K., 1993. Biodiversity, conservation and inventory: why insects matter. Biodiversity & Conservation 2, 191-214.

Larson, B.M.H., Kevan, P.G., Inouye, D.W., 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. The Canadian Entomologist 133, 439-465.

Larsson, T.B., 2001. Biodiversity evaluation tools for European forests. In, Ecological Bulletins, Blackwell, Oxford.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.H., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification on tropical forests. Nature 391, 72-76.

Lindenmayer, D.B., 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. Forest Ecology and Management 115, 277-287.

Lovei, G.L., Sunderland, K.D., 1996. Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae). Annual Review of Entomology 41, 231-256.

Magura, T., Tóthmérész, B., Bordán, Z., 2000. Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. Biological Conservation 93, 95-102.

Magura, T., Tóthmérész, B., Molnár, T., 2001. Forest edge and diversity: carabids along forest-grassland transects. Biodiversity & Conservation 10, 287-300.

Maleque, M.A., Maeto, K., Ishii, H.T., 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Applied Entomology and Zoology 44, 1-11.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems & Environment 74, 229-273.

McGeogh, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73, 181-201.

MCPFE, 1993. Second Ministerial Conference on the Protection of Forests in Europe. Helsinki, Finland.

Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic Applied Ecology 10, 178-186.

Millenium Ecosystem Assessment, 2005. Ecosystems and human well-being: current state and trends. Findings of the condition and trends working group. Island Press, Washington.

Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK., pp. 400-433.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., Worm, B., 2011. How Many Species Are There on Earth and in the Ocean? PLoS Biol. 9, e1001127.

Moulder, B., Reichle, D., 1972. Significance of Spider Predation in the Energy Dynamics of Forest-Floor Arthropod Communities. Ecological Monographs 42, 473-498.

Mullen, K., Fahy, O., Gormally, M., 2003. Ground flora and associated arthropod communities of forest road edges in Connemara, Ireland. Biodiversity & Conservation 12, 87-101.

National Parks and Wildlife Service, 2008. The Status of EU Protected Habitats and Species in Ireland. Department of the Environment, Heritage and Local Government, Ireland.

Niemela, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P., 1992. Small-Scale Heterogeneity in the Spatial Distribution of Carabid Beetles in the Southern Finnish Taiga. Journal of Biogeography 19, 173-181.

Niemelä, J., Haila, Y., Punttila, P., 1996. The Importance of Small-Scale Heterogeneity in Boreal Forests: Variation in Diversity in Forest-Floor Invertebrates across the Succession Gradient. Ecography 19, 352-368.

Niemela, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., New, T., Penev, L., Samways, M., Spence, J., 2000. The search for common anthropogenic impacts on biodiversity: a global network. Journal of Insect Conservation 4, 3-9.

Noss, R.F., 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. Forest Ecology and Management 115, 135-146.

NPWS, 2005. Management Plan for Killarney National Park 2005-2009. Government of Ireland.

Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? Forest Ecology and Management 270, 11-18.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Paillet, Y., BergÈS, L., HjÄLtÉN, J., ÓDor, P., Avon, C., Bernhardt-RÖMermann, M., Bijlsma, R.-J., De Bruyn, L.U.C., Fuhr, M., Grandin, U.L.F., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., MÉSzÁRos, I., SebastiÀ, M.T., Schmidt, W., StandovÁR, T., TÓThmÉRÉSz, B., Uotila, A., Valladares, F., Vellak, K.A.I., Virtanen, R., 2010. Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation Biology 24, 101-112.

Palik, B., Engstrom, R.T., 1999. Species composition. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, pp. 65-94.

Pawson, S.M., Brockerhoff, E.G., Meenken, E.D., Didham, R.K., 2008. Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodiversity & Conservation 17 1127-1148.

Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6, 780-793.

Peng, R.K., Incoll, L.D., Sutton, S.L., Wright, C., Chadwick, A., 1993. Diversity of Airborne Arthropods in a Silvoarable Agroforestry System. Journal of Applied Ecology 30, 551-562.

Perrin, P., Martin, J., Barron, S., O'Neill, F., McNutt, K., Delaney, A., 2008. National Survey of Native Woodlands 2003-2008. National Parks and Wildlife Service, Ireland.

Perrin, P.M., Kelly, D.L., Mitchell, F.J.G., 2006. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Natural regeneration and stand dynamics. Forest Ecology and Management 236, 356-367.

Petersen, H., Luxton, M., 1982. A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. Oikos 39, 288-388.

Pryor, S.N., 2000. Afforestation in Britain: opportunities and obstacles, strategies and targets. In: Weber, N. (Ed.), NEWFOR - New Forest for Europe: Afforestation at the Turn of the Century. European Forest Institute, Freiburg, Germany.

Ratcliffe, P.R., Peterken, G.F., 1995. The potential for biodiversity in British upland spruce forests. Forest Ecology and Management 79, 153-160.

Ryan, T., Phillips, H., Ramsay, J., Dempsey, J., 2004. Forest Road Manual. Department of Food, Agriculture and the Marine, Government of Ireland.

Samways, M., 1993. Insects in biodiversity conservation: some perspectives and directives. Biodiversity & Conservation 2, 258-282.

Samways, M.J., McGeoch, M.A., New, T.R., 2010. Insect Conservation: A Handbook of Approaches and Methods. Oxford University Press, Oxford, UK.

Sanders, D., Nickel, H., Grützner, T., Platner, C., 2008. Habitat structure mediates top-down effects of spiders and ants on herbivores. Basic Applied Ecology 9, 152-160.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L., Huhta, E., 2006. Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? Ecologial Indicators 6, 686-700.

Smith, G.F., Gittings, T., Wilson, M., French, L.J., Oxbrough, A., O'Donoghue, S., Pithon, J., O'Donnell, V., McKee, A.-M., Iremonger, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Giller, P., Kelly, T., 2005. Assessment of Biodiversity at Different Stages of the Forest Cycle. In, Bioforest Final Report, Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S., Mitchell, F.J.G., 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. Biological Conservation 136, 283-294.

Sommaggio, D., 1999. Syrphidae: can they be used as environmental bioindicators? Agriculture, Ecosystems & Environment 74, 343–356.

Sparks, T., Greatorex-Davies, J.N., 1992. The effect of shade in plantation woodland on invertebrate abundance and biodiversity. Aspects of Applied Biology 29, 89-96.

Speight, M.C.D., 2008. Database of Irish Syrphidae (Diptera). Irish Wildlife Manuals 36.

Spence, J.R., Langor, D.W., James Hammond, H.E., Pohl, G.R., 1997. Beetle abundance and diversity in a boreal mixed-wood forest. In: Watt, A.D., Stork, N.E., Huner, M.D. (Eds.), Forests and Insects. Chapman & Hall, p. 424.

Spiecker, H., 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe—temperate zone. Journal of Environmental Management 67, 55-65.

Stephens, P.C., 2005. Managing woodland open space for wildlife. Forestry Commission, UK.

Thiele, H., 1977. Carabid Beetles in their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour. Springer-Verlag, Berlin.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

Uetz, G.W., 1975. Temporal and Spatial Variation in Species Diversity of Wandering Spiders (Araneae) in Deciduous Forest Litter. Environmental Entomology 4, 719-724.

UNESCO, 2001. Biosphere Reserve Information. Ireland. Killarney. UNESCO.

United Nations Conference on Environment and Development, 1992. Agenda 21, the Rio Declaration on Environment and Development, the Statement of Forest Principles, the United Nations Framework Convention on Climate Change and the United Nations Convention on Biological Diversity. Rio de Janeiro.

Warren, M.S., Fuller, R.J., 1993. Woodland Rides and Glades: Their Management for Wildlife. Nature Conservancy Council, Peterborough, UK.

Watts, K., 2003. British Forest Landscapes: The Legacy of Woodland Fragmentation. Forest Research, UK.

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press.

Wise, D.H., 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48, 181-188.

Chapter 2

The response of ground-dwelling spiders (Araneae) and hoverflies (Diptera: Syrphidae) to afforestation in an agricultural landscape



Malaise net trap in afforested agricultural grassland

A manuscript based on this chapter has been published in *Forestry: an International Journal of Forest Research*.

Abstract

Despite extensive global deforestation the area of commercial forests continues to increase and plantation forests now dominate many landscapes. In recent decades forest cover in Ireland has expanded largely due to commercial afforestation with non-native conifers. This study provides the first within-site assessment of the response of two important arthropod groups to afforestation in agricultural grasslands in Ireland. Five sites were studied one year before and seven years after afforestation using pitfall trapping for active ground-dwelling spiders and Malaise trapping for hoverflies. Both species groups were studied in grassland habitat and spiders were also sampled in field boundary hedgerow habitat.

Afforestation had a positive effect on ground-dwelling spider diversity over the first seven years; total species richness increased in open and hedgerow habitats and forest specialist species richness increased in open habitats. This was related to increased canopy cover, field layer vegetation and litter. There was no effect of afforestation on hoverfly species richness over the first seven years, possibly due to confounding effects of hoverfly movements across landscapes. Spider and hoverfly species compositions were also positively affected by afforestation.

These results indicate that afforestation in a predominantly agricultural landscape benefits arthropod diversity by increasing habitat diversity and that hedgerow habitats are an important contributor to biodiversity in forest plantations. Ecologically oriented planning and management of afforestation must consider the influence of habitat quality in forest plantations, including the protection of biodiversity rich habitats and the quality of the land being afforested, to improve the contribution to biodiversity enhancement and conservation. Afforestation in agricultural landscapes has implications for important ecosystem services such as pollination, biological control and biodiversity.

Introduction

With the expansion of commercial plantation forests (European Commission, 2011) there is growing interest in ecologically sound forest planning and management practices (FAO, 2011). At the beginning of the 20th century very little of the once extensive natural forest cover in Ireland remained, and less than 1% of the Irish landscape was forested (Anon, 2008). This lack of forest estate led to government policy and grant-aid in support of afforestation, which has increased forest cover to approximately 11% in Ireland over the course of the last century (Forest Europe *et al.*, 2011). The current target is to further increase this cover to 14% by 2030, mainly through the establishment of plantation forests (COFORD Council, 2009). To achieve this, the government aims to increase the area of forest cover in private as well as state owned land by providing incentive schemes for private land-owners. These schemes include the Afforestation Scheme and the Forestry Environment Protection Scheme which provide grants and annual premiums for establishing forests on private land (Anon, 2012a, b).

The planting of forest on agricultural land is increasing and in Ireland in 2010, 95% of afforestation was carried out on agricultural land (Anon, 2010). Changes in forest management practices in recent decades reflect the growing importance of ecological considerations, particularly biodiversity conservation and land-owners undertaking afforestation in Ireland must comply with forestry objectives which form part of a legal and institutional framework. These include not only producing commercial timber but also providing ecosystem services such as climate change mitigation, improving water quality and increasing biodiversity (Anon, 2012a). Although afforestation in Ireland consists mainly of non-native tree species, these objectives and initiatives mean that new forests are compliant with the principles of sustainable forest management which aims to manage the world's plantation forests in a way that maintains biodiversity and ecosystem functioning whilst providing forest products and services (United Nations Conference on Environment and Development, 1992; MCPFE, 1993).

Afforestation impacts on biodiversity and the magnitude and direction of the effect is influenced by preceding land use and forest management practices (Hunter, 2000; Carnus *et al.*, 2006). In countries such as Ireland, where there is an extensively modified and intensively managed agricultural landscape and native forests have become rare, plantation forestry can benefit landscape biodiversity, particularly when appropriately managed

(Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2008). Changes in biodiversity throughout the forest cycle are well-documented, but in countries undertaking large-scale afforestation the change in land use, and its effect on habitats that are already present, means that the effects on biodiversity in recently planted areas are of particular interest.

The processes involved in preparing a site for afforestation, such as chemical application, soil drainage, and the subsequent changes in vegetation structure and diversity, induce changes in species composition (Gittings *et al.*, 2006; Smith *et al.*, 2006), which is followed by further changes in response to the habitat modification resulting from the planting of trees (Oxbrough *et al.*, 2005; Oxbrough *et al.*, 2006b). Therefore, afforestation is likely to have an impact on the biodiversity of agricultural grasslands and hedgerows contained within this habitat. Hedgerows are woody habitats located at field boundaries and are often the only semi-natural habitat present across large tracts of agricultural land (Marshall and Moonen, 2002). Hedgerows provide an important contribution to ecosystem services, through the conservation of native wildlife, habitat connectivity between forest patches, and for insect pollinators and biological control taxa which utilise this habitat (Landis *et al.*, 2000; Le Coeur *et al.*, 2002; Marshall and Moonen, 2002; Benton *et al.*, 2003; Frank and Reichhart, 2004). The effect of afforestation on the biodiversity of ground vegetation, birds and arthropods has been studied by substituting time for space using a chronosequence approach (Oxbrough *et al.*, 2006b; Smith *et al.*, 2006). However, there has been no reported within site tracking to directly monitor the changes in biodiversity following afforestation in agricultural grasslands.

The diversity of ground-dwelling spiders (Araneae) and hoverflies (Diptera:Syrphidae) in afforested sites is important as they play a significant role in the functioning of ecosystem processes, including food webs and pollination (Clarke and Grant, 1968; Sommaggio, 1999; Meyer *et al.*, 2009). Spiders and many hoverfly species are predatory on other arthropods and can contribute to the biological control of pests in agricultural and forest ecosystems (Sommaggio, 1999; Symondson *et al.*, 2002). Additionally, ground-dwelling spiders respond to changes in vegetation structure which undergo significant changes during the forest cycle (Oxbrough *et al.*, 2005) and hoverflies are useful as indicators of habitat disturbance and quality (Sommaggio, 1999). Spiders and hoverflies are often used as biodiversity indicators due to their well-known habitat associations, the ease of trapping and identification, and reliable species lists (Sommaggio, 1999; Pearce and Venier, 2006).

This study is unique at is the first to examine changes in arthropod diversity following afforestation in agricultural grasslands in the same sites prior to planting and 7 years after planting, as opposed to a chronosequence approach. Specifically, it will examine the change in species richness and composition of ground-dwelling spiders and hoverflies in 1) open grassland habitat found in agricultural fields and 2) hedgerow habitat which is often found at field boundaries, for ground-dwelling spiders only.

Materials and methods

Study sites

Five agricultural grassland sites, which had previously been used for livestock grazing, were studied one year before planting (hereafter called pre-planting), in the summer of 2002, and seven years after planting, in the summer of 2010 (hereafter called post-planting). These sites had a wide geographical spread across Ireland (Figure 1) and each site was planted in 2003 with coniferous and broadleaf tree species including Sitka spruce (*Picea sitchensis*), ash (*Fraxinus excelsior*), maple (*Acer pseudoplatanus*), larch (*Larix kaempferi*) and alder (*Alnus glutinosa*) (Table 1).

The data from the pre-planting survey were collected for the BIOFOREST Project (Smith *et al.*, 2006) and were kindly provided by Anne Oxbrough and Tom Gittings for use in this study. Additionally, the hoverfly identification from the post-planting survey was conducted by Tom Gittings.

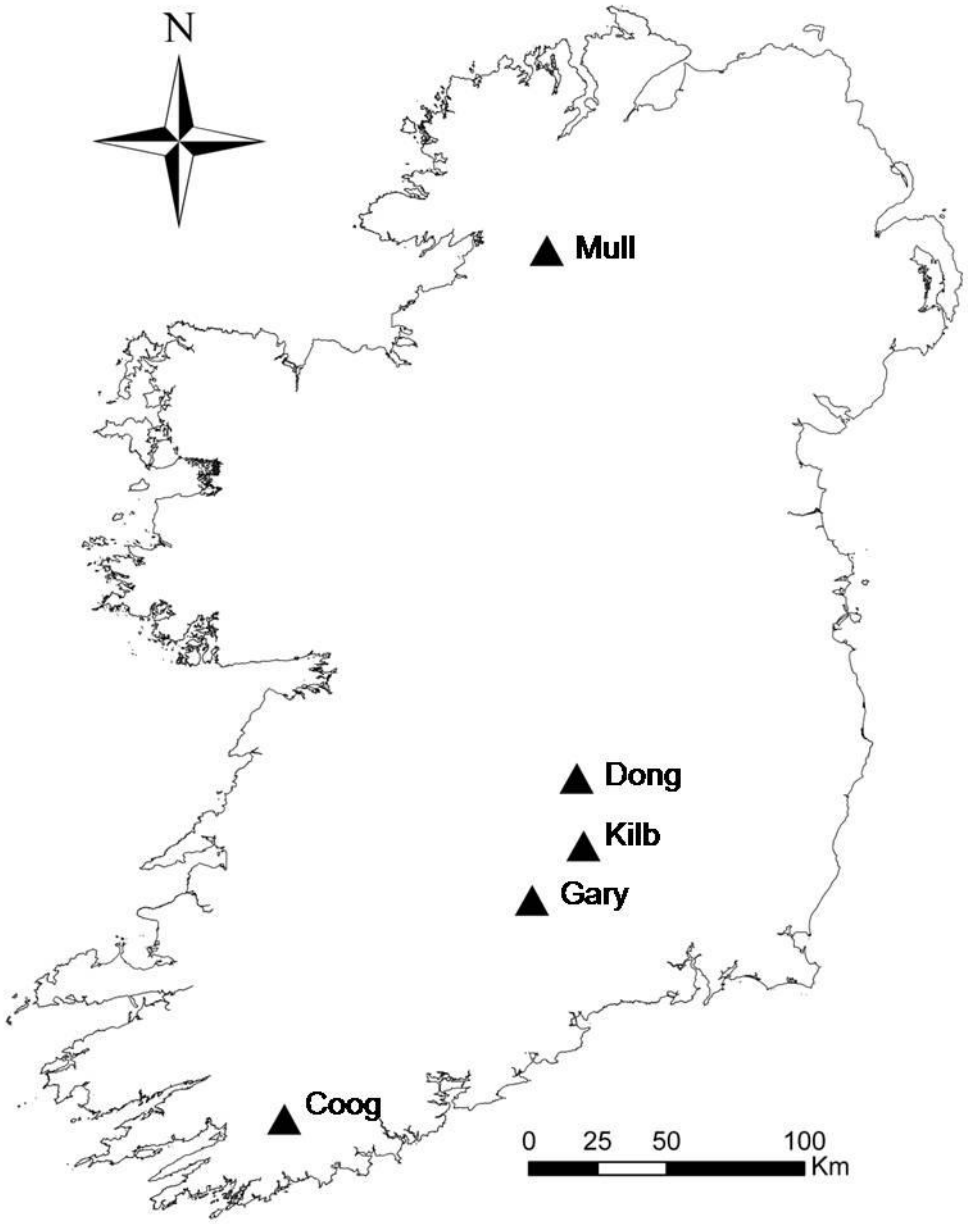


Figure 1. Distribution of the study sites in Ireland.

Table 1. Locations and characteristics of the study sites.

Site code	Grid ref	Size (ha)	Elevation (m)	Soil type	Tree species planted in 2003†
Coog	W209559	6.9	140	Peaty podzol	Ash (F), Alder (F), Larch (F), Oak (O)
Dong	S269797	12.6	92	Brown earth	Maple (A), Ash (A), Sitka spruce (F), Alder (O)
Gary	S107353	16.7	140	Brown earth	Ash (A), Maple (F)
Kilb	S295552	11.4	237	Brown podzol	Sitka spruce (A), Larch (A)
Mull	H162712	23	145	Gley	Sitka spruce (D)

†DAFOR abundance scale: D = dominant, A = abundant, F = frequent, O = occasional, R = rare

Spider sampling

Active ground-dwelling spiders were sampled using a standardised sampling method (Oxbrough *et al.*, 2006b). Pitfall traps were placed in six plots at each site. Three of the plots were located in open grassland habitat and three in hedgerow habitats (hereafter called open and hedgerow plots respectively). At one study site four open plots and two hedgerow plots were established. In each open plot five pitfall traps were placed in a grid arrangement, the four corner traps were spaced four metres apart and one trap was placed in the centre. In each hedgerow plot five pitfall traps were placed in a linear arrangement with traps spaced at two metre intervals.

Plastic cups of approximately 7cm diameter and 9cm high were used as pitfall traps and were dug into the ground so the rim of the cup was slightly below the ground surface. Each trap was filled with ethylene glycol (anti-freeze) to a depth of 3cm and drainage slits were cut 1cm from the top of the cup to prevent flooding. The contents of each pitfall trap were collected every three weeks between May and August, to coincide with the main activity period of Irish spiders (Nolan, 2008), resulting in three collections and a total trapping time of between 62 - 66 days. This length of trapping is sufficient to detect variation in spider diversity for biodiversity assessments (Oxbrough *et al.*, 2006a, 2007). The plastic cup was placed back in the ground and filled with fresh anti-freeze after each collection. The contents of the traps were transferred to labelled sample bottles and stored in 70% ethanol.

Spiders were identified to species level using Roberts (1993), nomenclature follows Platnick (2012), and sub-groups of specialist species which exhibit a preference for open or forest habitats were identified using Nolan (2008).

Hoverfly sampling

Two Malaise net traps were placed in each site in linear areas which act as flight paths for hoverflies, using a standard sampling procedure (Speight, 2000; Smith *et al.*, 2006). The traps were spaced approximately 10m apart in sheltered, un-shaded areas and orientated with the collecting bottles facing south so that they received the maximum amount of sunlight. The collection bottles were filled with 70% ethanol used as a killing agent and a preservative. The contents of each bottle were collected every three weeks from May to August, resulting in a total of three collections and a total of 62 – 68 trapping days. After each collection a new bottle of 70% ethanol was placed back on the trap.

Hoverflies were identified to species level using Stubbs and Falk (1983), van Veen (2004), and Haarto and Kerppola (2007), and species nomenclature follows Speight (2008b). Species were separated into sub-groups of open, woody vegetation and water-associated species using the Database of Irish Syrphidae (Speight, 2008b). The Database of Irish Syrphidae uses the fuzzy coding system which codes habitats with the numbers 1 – 3, where 1 indicates the habitat is low preference and 3 indicates the habitat is maximally preferred by the species. Only species which were coded 3, for maximum preference, were included in the sub-groups for species associated with open, woody vegetation and water habitats.

Habitat variables

The habitat surrounding each pitfall trap was surveyed using 1m x 1m quadrats placed over each trap. The percentage cover of the following variables were recorded: ground vegetation (0 – 10cm), lower field layer vegetation (10 – 50cm), upper field layer vegetation (50 – 200cm), litter and deadwood. The canopy cover in open plots was also recorded from the centre of each pitfall plot using one hemispherical photograph taken at a height of 1.3m and analysed with GLA 2.0 (Frazer *et al.*, 1999).

The habitat categories defined by Gittings *et al.* (2006) which are based on the Syrph the Net microhabitat categories (Speight *et al.*, 2004) were surveyed within a 100m radius of the Malaise traps at each site using the DAFOR (dominant, abundant, frequent, occasional, rare) scale. The categories surveyed were: mature trees, immature/ understory trees, tall shrubs, low shrubs, tussocks, tall herbs, short herbs, submerged sediment/ debris and water-saturated ground. Conifer and broadleaf trees and shrubs were recorded separately and the length of streams and rivers within the 100m radius were also recorded.

Data analysis

Sampling across different years can affect species abundance and richness due to temporal variation, therefore species with 2 or fewer individuals were removed from the spider and hoverfly datasets as they could potentially occur as singletons in both sampling years (Norris, 1999). Data were unavailable for three of the hedgerow spider sampling plots from the pre-planting survey, so these three plots were excluded from the analysis. In the post-planting survey the hedges had been removed from three of the hedgerow spider sampling plots, therefore these three plots were also removed from the analysis. The number of spider sampling plots used in the analysis totalled 16 open plots in both the pre-planting and post-

planting surveys, 11 hedgerow plots in the pre-planting survey and 9 hedgerow plots in the post-planting survey.

Spider species count data were pooled across the five pitfall traps and all three collections for each plot, and plot level data were used as the sample unit in all analysis. Due to trap losses and different sampling period lengths, the species richness for each plot was standardised by computing individual based rarefaction curves based on unstandardized abundance data (Gotelli and Colwell, 2001). The number of individuals along the X axis was then standardised and the species richness for each plot extracted. The number of individuals was standardised using the following formula: $ni / Ti * T$, where ni = the number of individuals at the *ith* plot, Ti = number of traps multiplied by the number of trapping day at the *ith* plot and T = lowest number of traps multiplied by the lowest number of trapping days.

Hoverfly species count data were pooled across the three collections and two Malaise traps per site and these site totals were used as the sample unit in analyses, making 5 replicates each in the pre-planting and post-planting surveys. Species richness required standardisation due to different sampling period lengths and Malaise trap damage. The volume of Malaise trap sample residue and the number of hoverfly species per sample is positively correlated (Gittings *et al.*, 2009), therefore species richness was standardised to the lowest volume of total sample residue. This was calculated using the following formula: $ni / Ti * T$, where ni = the species richness at the *ith* trap, Ti = the trap volume at the *ith* trap and T = the lowest trap volume.

The dominance of each species, expressed as a percentage of the total species, was calculated. This was based on each species overall abundance weighted by its overall frequency of occurrence among plots, using the method developed by Pinzón and Spence (2010). The difference in species richness between pre-planting and post-planting in the open and hedgerow plots was analysed using generalised linear mixed modelling (GLMM). This type of analysis is an extension of linear modelling and allows for plots that are nested within sites, by using site as a random effect (Zuur *et al.*, 2009). This analysis was conducted on total species richness of spiders and hoverflies and also for the identified sub-groups of habitat associated species. GLMM was also used to test the effect of changes in the habitat variables on spider species richness between pre-planting and post-planting in the open and hedgerow plots.

Indicator species analysis (ISA) was used to identify spider and hoverfly species which were strongly associated with either the pre-planting or post-planting habitat within open plots and hedgerow plots. This analysis was also used to identify spider species which were associated with open or hedgerow plots in the pre-planting survey and open or hedgerow plots in the post-planting survey. This analysis uses species count data to calculate the relative abundance and relative frequency with which a species occurs in *a priori* determined groups. An indicator value percentage is then assigned to each species to indicate which group they are associated with (Dufrene and Legendre, 1997). The analysis was run using 4999 permutations followed by a Monte Carlo test of statistical significance.

Redundancy analysis (RDA) was used to examine the relationship between spider species composition, plot type (open or hedgerow), sampling year (pre- or post-planting), and the measured habitat variables. This analysis was also used on hoverfly species composition, sampling year (pre- or post-planting), and the measured habitat variables. This type of analysis tests how much of the variation in species composition can be explained by the constraining variables (ter Braak, 1994). Prior to analysis, the habitat variables were examined for collinearity using Spearman's rho correlations, any which were collinear above 0.7 were removed, the variables were scaled so the mean = 0 and standard deviation = 1, and the species data were Hellinger transformed (Legendre and Gallagher, 2001). Latitude can affect spider species composition in Ireland (Oxbrough *et al.*, 2012), and here longitude also had an effect, therefore partial RDA using latitude and longitude as conditional variables was carried out. Latitude also had an effect on hoverfly species composition and so it was used as a covariable in a partial RDA. Forward selection was used to identify the variables which explained the most variation in species composition among the plots (Blanchet *et al.*, 2008). ANOVA was then used to determine the significance level of the final model and the selected variables.

Habitat variables recorded at the spider sampling plots were compared between pre-planting and post-planting using GLMM. The variables were averaged across the five quadrats in each plot and plot level data was used as the sample unit in the analyses. Percentage cover values were arcsine transformed prior to analysis. Habitat variables recorded for the Malaise traps were in categorical form, so were not suitable for statistical analysis among plots. However, the categories were re-coded from 1 – 5, with 1 representing rare and 5 representing dominant, and these dummy variables were included in the RDA ordination of hoverfly species composition.

ISA was conducted in PC-ORD (McCune and Mefford, 2011). All other analyses were conducted in R (R Core Team, 2012). GLMM used the nlme package (Pinheiro *et al.*, 2013) and the MASS package (Ripley *et al.*, 2013), RDA used the vegan package (Oksanen *et al.*, 2012), and forward selection used the packfor package (Dray *et al.*, 2012).

Results

The effect of afforestation on habitat characteristics

There was a significant increase in canopy cover and a significant decrease in the cover of ground vegetation in open plots following afforestation (Table 2). There was also a notable but non-significant increase in the cover of upper field layer vegetation, bare soil, litter and deadwood in the open plots post-planting. There were no significant differences in the habitat characteristics in hedgerow plots following afforestation. However, there was a notable but non-significant increase in the cover of lower field layer vegetation, litter and deadwood and a decrease in the cover of ground vegetation and upper field vegetation in hedgerow plots post-planting (Table 2).

Table 2. Mean ± standard error of habitat variables (percent cover) from open and hedgerow spider sampling plots pre- and post-planting. Comparison between pre- and post-planting made using GLMM. Statistically significant results are highlighted in bold.

	Pre-planting	Post-planting	GLMM
Open plots			
Ground vegetation	32.90 ± 7.37	13.53 ± 4.51	**$t_{1,15}$ = -2.64, P = 0.02**
Lower field layer	36.72 ± 7.73	48.62 ± 7.79	$t_{1,15}$ = 0.55, P = 0.59
Upper field layer	37.41 ± 6.24	42.03 ± 9.25	$t_{1,15}$ = 2.00, P = 0.06
Bare soil	9.09 ± 0.41	15.10 ± 2.77	$t_{1,15}$ = 2.08, P = 0.05
Litter cover	1.59 ± 0	24.38 ± 7.91	$t_{1,15}$ = 1.59, P = 0.13
Deadwood	2.28 ± 0	5.05 ± 1.09	$t_{1,15}$ = 0.39, P = 0.70
Canopy cover	0 ± 0	66.57 ± 6.52	**$t_{1,15}$ = 7.70, P = 0**
Hedgerow plots			
Ground vegetation	33.55 ± 8.79	18.45 ± 7.09	$t_{1,8}$ = -1.92, P = 0.07
Lower field layer	29.91 ± 4.39	49.23 ± 9.92	$t_{1,8}$ = 2.02, P = 0.06
Upper field layer	61.73 ± 7.97	28.77 ± 9.64	$t_{1,8}$ = -1.81, P = 0.09
Bare soil	21.59 ± 6.92	15.95 ± 3.74	$t_{1,8}$ = -1.05, P = 0.31
Litter cover	3.91 ± 2.76	35.41 ± 11.47	$t_{1,8}$ = 2.06, P = 0.05
Deadwood	5.59 ± 1.96	11.27 ± 7.98	$t_{1,8}$ = 1.15, P = 0.26

The effect of afforestation on ground-dwelling spiders

Pre-planting, a total of 909 adult ground-dwelling spiders from 72 species and 5 families were recorded at the study sites. After omitting species with 2 or fewer individuals a total of 898 adult spiders from 62 species and 5 families were used in the analysis. Of these species, 14 were open habitat specialists, 9 were forest specialists and 39 were habitat generalists. The dominant species in open plots was *Erigone atra* (24%), an open specialist from the Linyphiidae family ('money' spiders), and in hedgerow plots was *Monocephalus fuscipes* (18%), a forest specialist from the Linyphiidae family. Post-planting, a total of 2,186 adult spiders from 93 species and 10 families were recorded. After omitting species with 2 or fewer individuals a total of 2,149 adult spiders from 67 species and 5 families were used in the analysis. Of these species 15 were open habitat specialists, 10 were forest specialists and 42 were habitat generalists. The dominant species in both open and hedgerow plots following afforestation was *Pardosa amentata* (25% and 37% respectively), an open specialist from the Lycosidae family ('wolf' spiders).

There was a significant increase in total spider species richness in open plots post-planting (Table 3), which was influenced by the increase in canopy cover ($t_{1,15} = 4.28$, P = 0.001). There was also a significant increase in total species richness in hedgerow plots post-planting (Table 3), which was associated with increased cover of lower field layer vegetation ($t_{1,8} = 3.88$, P = 0.01) and litter layer ($t_{1,8} = 5.39$, P = 0.003) and decreased cover of upper field layer vegetation ($t_{1,8} = -3.21$, P = 0.02). Forest specialist species richness significantly increased in open plots post-planting, but there was no significant difference in hedgerow plots (Table 3). This increase was associated with decreased cover of ground vegetation ($t_{1,8} = -2.83$, P = 0.02) and increased cover of lower field layer vegetation ($t_{1,8} = 3.06$, P = 0.01), bare soil ($t_{1,8} = -3.79$, P = 0.003), litter layer ($t_{1,8} = 2.36$, P = 0.04) and canopy cover ($t_{1,8} = 3.84$, P = 0.003). Open specialist species richness was not significantly different between pre-planting and post-planting in either the open or hedgerow plots.

Table 3. Mean ± standard error of ground-dwelling spiders and hoverflies pre- and post-planting. Comparison between pre- and post-planting made using GLMM. Statistically significant results are highlighted in bold.

	Pre-planting	Post-planting	GLMM
Spiders open plots			
All species	8.00 ± 0.97	14.38 ± 1.19	**$t_{1,15}$ = 4.48, P = 0.0002**
Open specialists	2.90 ± 0.33	3.86 ± 0.60	$t_{1,15}$ = 1.16, P = 0.26
Forest specialists	0.74 ± 0.17	2.29 ± 0.36	**$t_{1,15}$ = 2.57, P = 0.02**
Spiders hedgerow plots			
All species	6.94 ± 1.29	12.66 ± 1.28	**$t_{1,8}$ = 3.29, P = 0.004**
Open specialists	1.53 ± 0.36	2.78 ± 0.55	$t_{1,8}$ = 1.16, P = 0.26
Forest specialists	1.67 ± 0.34	2.23 ± 0.37	$t_{1,8}$ = 1.62, P = 0.12
Hoverflies			
All species	5.81 ± 1.84	5.19 ± 0.02	$t_{1,4}$ = 0.62, P = 0.56
Water-associated	1.91 ± 0.75	1.90 ± 0.13	$t_{1,4}$ = -0.53, P = 0.62
Open-associated	0.95 ± 0.34	1.15 ± 0.06	$t_{1,4}$ = <0.0001, P = 1
Woody vegetation associated	3.45 ± 1.07	2.16 ± 0.04	$t_{1,4}$ = -0.31, P = 0.77

ISA identified one habitat generalist species and one open specialist species which were associated with open plots pre-planting and 16 species which were associated with open plots post-planting; these were a mixture of open, forest and habitat generalist species (Table 4). No species recorded were associated with pre-planting hedgerow plots; however, 10 species were associated with hedgerow plots post-planting (Table 4). Additionally, more forest specialist species were highly associated with hedgerow plots compared to open plots in both pre-planting and post-planting surveys (Table 5).

Partial RDA of the selected variables produced a significant model ($F_{3,46}$ = 2.82, P = 0.005) which explained 6% of the variation in species composition. The covariable latitude explained a further 2% of the variation ($F_{1,49}$ = 2.91, P = < 0.0001) and longitude also explained 2% of the variation ($F_{1,49}$ = 2.64, P = < 0.0001). Three axes were recommended for plotting the partial RDA and the first two axes which represent 5% of the variation are presented in Figure 2. Canopy cover explained 2% of the variation in species composition ($F_{3,46}$ = 2.91, P = < 0.0001), litter cover explained 2% of the variation ($F_{3,46}$ = 2.90, P = < 0.0001), and plot type (open or hedgerow) explained 2% of the variation ($F_{3,46}$ = 2.65, P = 0.0004). In the pre-planting survey the species composition of open plots was different to the hedgerow plots, but post-planting the species composition among open and hedgerow plots became similar (Figure 2).

Table 4. Indicator Species Analysis of ground-dwelling spider within open plots pre-planting vs. post-planting and within hedgerow plots pre-planting vs. post-planting. Numbers represent Indicator Value percentages: * < 0.05, ** < 0.01, *** < 0.001.

		Open		Hedgerow	
Species	Habitat association	Pre	Post	Pre	Post
Bathyphantes nigrinus	Shade-associated	0	31*	3	49*
Diplocephalus latifrons	Forest specialist	0	38*	4	58*
Dismodicus bifrons	Habitat generalist	0	53**	0	33*
Pachygnatha clercki	Habitat generalist	1	48*	1	31*
Pardosa amentata	Open specialist	9	58*	3	61*
Robertus lividus	Habitat generalist	1	58**	0	53**
Walckenaeria acuminate	Habitat generalist	1	57**	2	49*
Erigone dentipalpis	Open specialist	43*	0	-	-
Lophomma punctatum	Habitat generalist	1	51**	-	-
Monocephalus fuscipes	Forest specialist	0	56**	-	-
Neriene clathrata	Habitat generalist	0	38*	-	-
Oedothorax fuscus	Habitat generalist	46*	6	-	-
Palliduphantes ericaeus	Habitat generalist	0	46*	-	-
Pirata latitans	Open specialist	0	31*	-	-
Pocadicnemis juncea	Open specialist	1	48**	-	-
Pocadicnemis pumila	Open specialist	2	47*	-	-
Saaristoa abnormis	Habitat generalist	0	56***	-	-
Tenuiphantes zimmermanni	Forest specialist	5	63**	-	-
Centromerus sylvaticus	Shade-associated	-	-	0	33*
Oedothorax gibbosus	Habitat generalist	-	-	0	54**
Pardosa pullata	Open specialist	-	-	0	32*

Table 5. Indicator Species Analysis of ground-dwelling spiders within open vs. hedgerow plots pre-planting and within open vs. hedgerow plots post-planting. Numbers represent Indicator Value percentages: * < 0.05, ** < 0.01.

		Pre-planting		Post-planting	
Species	Habitat association	Open	Hedge	Open	Hedge
Bathyphantes gracilis	Habitat generalist	62*	11	-	-
Monocephalus fuscipes	Forest specialist	0	55**	15	65*
Oedothorax fuscus	Habitat generalist	45*	2	-	-
Pardosa pullata	Open specialist	60*	0	-	-
Erigone atra	Open specialist	-	-	61*	0
Erigonella hiemalis	Forest specialist	-	-	0	44*
Oedothorax retusus	Habitat generalist	-	-	51*	1

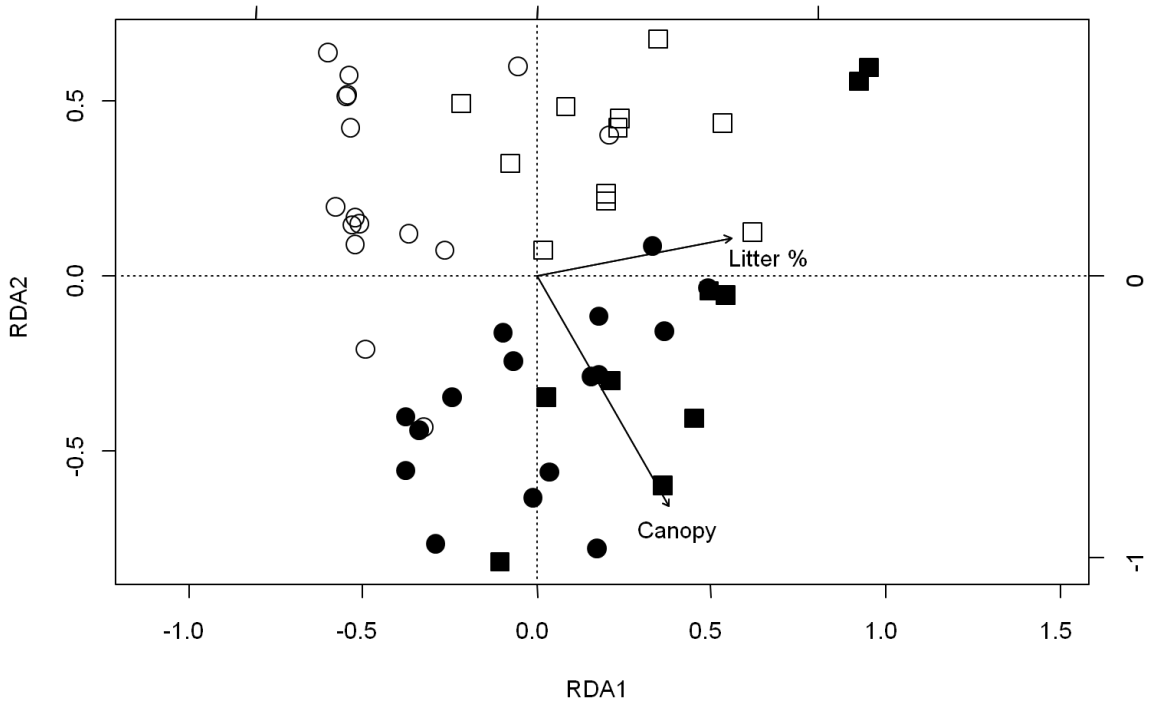


Figure 2. Partial RDA of ground-dwelling spider species composition. Axis 1: $R^2 = 0.03$, $F_{1,46} = 4.18$, P = 0.0002. Axis 2: $R^2 = 0.02$, $F_{1,46} = 2.86$, P = 0.0002. (○) open plots pre-planting, (●) open plots post-planting, (□) hedgerow plots pre-planting, (■) hedgerow plots post-planting.

The effect of afforestation on hoverflies

Pre- planting, a total of 1,211 adult hoverflies from 52 species were recorded. After omitting species with 2 or fewer individuals 1,196 hoverflies from 42 species were used in the analysis. Of these species, 11 were open habitat associated, 15 were woody vegetation associated and 20 were water associated. The dominant species was *Platycheirus clypeatus* (33%), a water-associated species. Post-planting, a total of 617 adult hoverflies from 63 species were recorded. After omitting species with 2 or fewer individuals 600 hoverflies from 50 species were used in the analysis. Of these species, 13 were open associated, 20 were woody vegetation associated and 20 were water associated. The dominant species was *Rhingia campestris* (11%), which is associated with cattle farming in Ireland and woody vegetation in Europe.

Afforestation did not impact on total species richness or species richness of the sub-groups of open, water and woody vegetation associated species (Table 3). ISA identified five species which were associated with the post-planting habitat and were a mixture of open-associated, water-associated and woody vegetation associated species (Table 6). Partial RDA of the selected variables produced a significant model ($F_{1,7}$ = 2.82, P = 0.008) and explained 10% of the variation in species composition, which was due to only one variable: the presence of understory trees post-planting. The covariable latitude explained a further 6% of the variation ($F_{1,7}$ = 2.05, P = 0.01).

Table 6. Indicator Species Analysis of hoverfly species pre-planting vs. post-planting. Numbers represent Indicator Value percentages: * < 0.05.

Species	Habitat association	Pre-planting	Post-planting
Eristalis pertinax	Water-associated	0	60*
Eupeodes luniger	Open-associated	0	50*
Helophilus hybridus	Water-associated	0	60*
Melangyna lasiophthalma	Woody vegetation associated	0	50*
Platycheirus peltatus	Water-associated	1	62*
Xylota sylvarum	Woody vegetation associated	0	50*

Discussion

Before-and-after study methods can be difficult to implement and can present difficulties when trying to control for variation over the course of the study (Gardner, 2010). The sites used in the current study were privately owned and management was not homogenous across sites, particularly in relation to planted tree species. However, this is less likely to affect species composition and diversity in the early stages of the forest cycle compared to later stages (Oxbrough *et al.*, 2005). In the present study, seven years into the forest cycle, the canopy was still quite open and a well-developed understory vegetation was present in both coniferous and broadleaf areas. After forest canopy closure there is a change in ground vegetation, microclimate and light levels which can differ between broadleaf and coniferous forests and may present confounding effects in future studies of these sites (Wallace and Good, 1995; Chen *et al.*, 1999; Humphrey *et al.*, 1999; Oxbrough *et al.*, 2005).

Effect of afforestation on ground-dwelling spiders

Total spider species richness increased in both open and hedgerow plots following afforestation, which was correlated with the changes in habitat, as a result of increased shade provided by canopy cover and increased ground layer structure provided by litter cover. Spider species composition also changed following afforestation and open and hedgerow plots became more similar. These changes were also associated with the litter cover and canopy cover provided by planted trees. Although species richness increased, the sites also retained the open specialist spider fauna of the grassland habitat and continued to support high abundances of open specialist species in the open plots, although the ecology of the dominant species differed. *E. atra* was dominant prior to afforestation and is a pioneer species commonly found in intensively farmed grasslands (Downie *et al.*, 2000; Cole *et al.*, 2003). After afforestation *P. amentata* was the dominant species, which is usually found in the litter layer of humid open habitats (Alderweireldt and Maelfait, 1987; Nolan, 2008). This change in species dominance reflects the initial changes in habitat caused by afforestation. The conversion of grassland to forest habitat was concurrent with the cessation of livestock grazing which reduces ground disturbance and allows the structural diversity of field layer vegetation to increase (Dennis *et al.*, 1998; Oxbrough *et al.*, 2006b). Structural complexity created by vegetation and litter cover increases the habitat for spider diversity, as these habitat characteristics increase web-attachment points, prey abundance

and shelter from predators (Gunnarsson, 1983; Greenstone, 1984; Uetz, 1991; Gunnarsson, 1996; Dennis *et al.*, 1998; Castro and Wise, 2009).

In addition to the open specialist spider fauna that persisted through the habitat change associated with the planting of trees, the afforested sites also supported a greater number of forest specialist species in their open plots. Increased shade and litter cover also positively influenced forest specialist species richness as well as changes in the vegetation layers, where ground vegetation decreased and lower field layer vegetation increased. The shade provided by planted trees during the early stages of canopy development provides adequate shelter, even before complete canopy closure, to stabilize the microclimate and increase the suitability of these sites for forest specialist species (Pollard, 1968; McIver *et al.*, 1992; Oxbrough *et al.*, 2006b).

Prior to afforestation the hedgerows within grasslands supported a different species composition than open habitat plots, with high abundance of forest specialist species such as *M. fuscipes* associated with hedgerows. This finding supports the theory of the importance of field margin hedgerows (Oxbrough *et al.*, 2006b) as a refuge for forest specialist species in predominantly agricultural landscapes. Hedgerows provide important landscape connectivity across small and fragmented forest areas and are an important factor in the capacity of these forests to support biodiversity (Joyce *et al.*, 1999; Hinsley and Bellamy, 2000; Holland and Fahrig, 2000; Pithon *et al.*, 2005).

There were few spider species associated with open or hedgerow plots pre-planting, which supports the conclusion that the species present prior to planting persist within the early post-planting habitat. The additional species present post-afforestation included generalist species which can occur in a variety of open and forested habitats and are less important when considering the value of a habitat for species diversity. However, a number of other species of interest were present. Two of the species associated with the open plots post-planting require damp open habitats: *Lophomma punctatum* is found amongst litter and low vegetation in wetland habitats and *Pirata latitans* occurs in open marsh and fen habitats (Helsdingen, 1996; van Helsdingen, 1998; Nolan, 2008). The vegetation and moisture requirements of these species may mean young afforested sites provide suitable habitat, however, they are unlikely to persist in closed canopy forests where light, moisture and ground vegetation diversity decrease (Anderson *et al.*, 1969; Hill, 1979; Avon *et al.*, 2010). Three forest specialist species, *Diplocephalus latifrons*, *Monocephalus fuscipes* and

Tenuiphantes zimmermanni, and one shade-associated species, *Bathyphantes nigrinus*, which are typically associated with litter in woodland habitats (Roberts, 1993; Harvey *et al.*, 2002; Nolan, 2008), were associated with the open plots post-planting, indicating their increased suitability for species requiring forest habitats. Hedgerow plots shared seven species with open plots, which were associated with the changes in habitat post-planting, including *B. nigrinus* and *D. latifrons*. However, *M. fuscipes* and *Erigonella hiemalis* still showed a higher affinity with hedgerows in the afforested sites compared with the open plots, indicating that hedgerows continue to provide important habitat in young afforested sites and should be retained in afforestation.

The effect of afforestation on hoverflies

The difference in hoverfly species composition following afforestation was associated with increased tree cover, although there was a mixture of open associated, woody vegetation associated and water associated species both pre-planting and post-planting. Prior to afforestation the dominant species was *P. clypeatus*; this species is associated with water habitats provided by undrained land and wet ditches, which could explain its dominance here, where three out of the five sites contained streams and water-saturated ground prior to afforestation (Speight, 2008a). The streams were still present post-afforestation, however surface water habitats, which are important for many hoverfly species, can be affected by forestry practises such as land drainage, which is used to prepare land for afforestation and often results in the reduction and quality of these habitats (Gittings *et al.*, 2006; Smith *et al.*, 2006). The prevalence of *R. campestris* after afforestation reflects the surrounding environment of farmland used for grazing, as the larvae of this species feed almost exclusively on cow dung in Ireland (Speight, 2008a), although adults of this species also forage at woodland edges (Stubbs and Falk, 1983). Therefore planting native broadleaf trees in agricultural land is likely to benefit this species.

There were no hoverfly species associated with the pre-planting habitat suggesting that, similar to the effect seen for ground-dwelling spiders, these species were not lost post-afforestation and that new species were present in the assemblage. *Eristalis pertinax*, *Helophilus hybridus* and *Platycheirus peltatus* occur in wet habitats including wetlands, seasonally-flooded grassland, river banks and water-filled ditches. *H. hybridus* in particular is associated with tall herbaceous vegetation along rivers and streams and *P. peltatus* can occur in the open habitat of young plantations, and where humid open areas occur around

plantation forests. These species are negatively affected by land drainage, which can accompany afforestation; therefore provision for wet habitats in afforestation sites is important. *Xylota sylvarum* is associated with broadleaf forests and is not usually found in conifer plantations or the standard farmland landscape of green fields plus hedges. The presence of this species here reflects the mixture of tree species planted on the sites, which included broadleaf species, and indicates the importance of planting native tree species for biodiversity conservation. *Melangyna lasiophthalma* occurs in most types of woodland and conifer plantations and suburban gardens and *Eupeodes luniger* occurs in a variety of open habitats including crops, grassland and gardens, as well as open areas around deciduous and coniferous forests. The generalist nature and variety of habitats utilised by these two species means they are unlikely to require specific habitat management.

Although there were noticeable changes in hoverfly species composition, there was no detectable difference in species richness pre- and post-planting. At this early stage in the forest cycle there were large gaps in the canopy, meaning the habitat could still be suitable for open associated species. However, the species richness of woody vegetation associated species was expected to increase after planting. Previous research in grassland sites found that five years after afforestation with Sitka spruce the diversity of hoverfly species associated with open habitats decreased and the diversity of woody vegetation associated species increased (Smith *et al.*, 2006). The mixture of open, woody vegetation and water associated species both pre- and post-planting in this study may be related to the confounding effect of adult hoverfly movements across landscapes, where migratory and foraging movement can result in species being recorded outside of their primary habitat (Castella *et al.*, 1994; Branquart and Hemptinne, 2000; Gittings *et al.*, 2006). Four of the five study sites had forested areas within one kilometre before afforestation, meaning that woody vegetation associated species from these areas could have been recorded whilst foraging or passing through grassland habitats. Furthermore, both local habitat factors and landscape factors influence hoverfly species composition, and hoverfly feeding guilds also respond to land use at differing spatial scales (Meyer *et al.*, 2009). Local factors, particularly site management, which can affect vegetation height and the species richness of flowering plants, and important landscape factors, such as road length and forest area, influence hoverfly abundance and diversity in grasslands (Sjödin *et al.*, 2008; Meyer *et al.*, 2009). Therefore, differences in site management, the availability of flowering plants, and the area of forest in the surrounding landscape can all influence hoverfly species composition.

Implications of afforestation in an agricultural landscape

Within the first seven years after planting with trees the habitat of agricultural grassland sites changed to provide a mosaic of open and shaded areas with increased structural variation created by litter and vegetation cover. These sites became suitable for a wider range of ground-dwelling spider species with differing ecological requirements. The habitat change did not impact on hoverfly species in the same way, due to their migratory behaviour and their response to landscape scale factors, which can mask the effect of site level changes. However, in general, afforestation in agricultural landscapes increases the diversity of habitats and available niches which affords these areas the opportunity to increase arthropod biodiversity at both the site and landscape level.

The retention of hedgerow habitats was an important contributor to biodiversity in forest plantations. Protecting and incorporating habitats, such as hedgerows, which enhance biodiversity will contribute to the objectives of sustainable forest management (Gittings *et al.*, 2006; Oxbrough *et al.*, 2006a; Smith *et al.*, 2008). The species of tree selected for planting may influence the biodiversity value of afforested areas, particularly in plantation forests of exotic conifer species, as when canopy closure occurs the species richness of ground-dwelling spiders and hoverflies has been shown to decrease, due to the loss of open specialist species (Gittings *et al.*, 2006; Oxbrough *et al.*, 2006a). Therefore, it is important that afforestation plans consider not only the area and type of habitats but also their quality, and that forest management considers factors related to increased species diversity at all stages of the forest cycle.

The biodiversity benefits of planting forests on agricultural land can also make an important contribution to ecosystem services through the biological control of crop pests and the pollination of arable crops and wildflowers in nearby fields. Forested areas and hedgerows support diverse and abundant populations of predatory arthropods such as spiders and hoverflies, which can disperse into crop fields and may be useful in the biological control of crop pests (Peng *et al.*, 1993; Kajak, 2007; Bennewicz, 2011). Furthermore, hoverflies may be the second most important pollinators after wild bees (Larson *et al.*, 2001) and can contribute to enhanced pollination services (Fontaine *et al.*, 2006; Albrecht *et al.*, 2012; Jauker *et al.*, 2012).

Considering the global expansion of commercial forests and the agricultural landscape in many countries these results provide important evidence for the biodiversity benefits and ecosystem services conferred by afforestation in agricultural grasslands.

References

Albrecht, M., Schmid, T., Hautier, Y., Müller, C., 2012. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences 7, 4845-4852.

Alderweireldt, M., Maelfait, J.P., 1987. Life cycle, habitat choice and distribution of *Pardosa amentata* (Clerck, 1757) in Belgium (Araneae: Lycosidae). Xème Colloque Européen d'Arachnologie, Rennes, France, pp. 7-15.

Anderson, R.C., Loucks, O.L., Swain, A.M., 1969. Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests. Ecology 50, 255-263.

Anon, 2008. Irish Forests - A Brief History. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2010. Afforestation Statistics. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2012a. Afforestation Scheme. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2012b. Forest Environment Protection Scheme (Afforestation). Department of Agriculture, Food and the Marine, Government of Ireland.

Avon, C., Bergès, L., Dumas, Y., Dupouey, J.-L., 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management 259, 1546-1555.

Bennewicz, J., 2011. Aphidivorous hoverflies (Diptera: Syrphidae) at field boundaries and woodland edges in an agricultural landscape. Polish Journal of Ecology 80, 129-149.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182-188.

Berndt, L., Brockerhoff, E., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodiversity & Conservation 17, 1171-1185.

Branquart, E., Hemptinne, J.-L., 2000. Selectivity in the Exploitation of Floral Resources by Hoverflies (Diptera: Syrphinae). Ecography 23, 732-742.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity & Conservation 17, 925-951.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted Forests and Biodiversity. Journal of Forestry 104, 65-77.

Castella, E., Speight, M.C.D., Obrdlik, P., Schneider, E., Lavery, T., 1994. A methodological approach to the use of terrestrial invertebrates for the assessment of alluvial wetlands. Wetlands Ecology and Management 3, 17-36.

Castro, A., Wise, D.H., 2009. Influence of fine woody debris on spider diversity and community structure in forest leaf litter. Biodiversity & Conservation 18, 3705–3731.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in Forest Ecosystem and Landscape Ecology. Bioscience 49, 288-297.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

COFORD Council, 2009. Forestry 2030. Department of Agriculture, Food and the Marine, Government of Ireland.

Cole, L., McCracken, D., Downie, I.S., Dennis, P., Foster, G., Waterhouse, T., Murhpy, K., Griffin, A., Kennedy, M., 2003. Comparing the effects of farming practices on ground beetle (Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland. Biodiversity and Conservsation 14, 441–460.

Dennis, P., Young, M., Gordon, I., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23, 253–264.

Downie, I.S., Ribera, I., McCracken, D.I., Wilson, W.L., Foster, G.N., Waterhouse, A., Abernethy, V.J., Murphy, K.J., 2000. Modelling populations of Erigone atra and E.

dentipalpis (Araneae: Linyphiidae) across an agricultural gradient in Scotland. Agriculture, Ecosystems & Environment 80, 15-28.

Dray, S., Legendre, P., Blanchet, F.G., 2012. Packfor: Forward Selection with permutation (Canoco p.46). R version 0.0-8.

Dufrene, M., Legendre, P., 1997. Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. Ecological Monographs 67, 345-366.

European Commission, 2011. Forestry in the EU and the world — A statistical portrait. Publications Office of the European Union.

FAO, 2011. The European Forest Sector Outlook Study II: 2010-2030. United Nations Environment Programme.

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLoS Biology 4, e1.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Frank, T., Reichhart, B., 2004. Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. Bulletin of Entomological Research 94, 209-217.

Frazer, G., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University and the Institute of Ecosystem Studies, Millbrook, New York.

Gardner, T., 2010. Monitoring Forest Biodiversity: Improving Conservation through Ecologically-Responsible Management. Earthscan.

Gittings, T., Harrison, S., O'Halloran, J., 2009. The influence of habitat quality, patch size and isolation on the nature conservation value of groundwater wetlands. Unpublished report by the Biochange project, Environmental Protection Agency.

Gittings, T., O'Halloran, J., Kelly, T., Giller, P., 2006. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management 237, 290–300.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379-391.

Greenstone, M.H., 1984. Determinants of web spider species diversity: Vegetation structural diversity vs. prey availability. Oecologia 62, 299-304.

Gunnarsson, B., 1983. Winter Mortality of Spruce-Living Spiders: Effect of Spider Interactions and Bird Predation. Oikos 40, 226-233.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Haarto, A., Kerppola, S., 2007. Suomen kukkakärpaset ja lähialueiden lajeja [Finnish hoverflies and some species in adjacent countries], Otavan Kirjapaino Oy, Keuruu.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155, 81-95.

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Helsdingen, P.J.v., 1996. The Spider Fauna of Some Irish Floodplains. The Irish Naturalists' Journal 25, 285-293.

Hill, M.O., 1979. The development of a flora in even-aged plantations. In: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.), The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, pp. 175-192.

Hinsley, S.A., Bellamy, P.E., 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. Journal of Environmental Management 60, 33-49.

Holland, J., Fahrig, L., 2000. Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agriculture, Ecosystems & Environment 78, 115-122.

Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R., Jukes, M.R., 1999. Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecology and Management 113, 11-21.

Hunter, M.L., 2000. Maintaining biodiversity in forest ecosystems. Cambridge University Press, UK.

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology 14, 81-87.

Joyce, K.A., Holland, J.M., Doncaster, C.P., 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. Bulletin of Entomological Research 89, 523-531.

Kajak, A., 2007. Effects of forested strips on spider assemblages in adjacent cereal fields: dispersal activity of spiders. Polish Journal of Ecology 55, 691-704.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. Annual Review of Entomology 45, 175-201.

Larson, B.M.H., Kevan, P.G., Inouye, D.W., 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. The Canadian Entomologist 133, 439-465.

Le Coeur, D., Baudry, J., Burel, F., Thenail, C., 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. Agriculture, Ecosystems & Environment 89, 23-40.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems & Environment 89, 5-21.

McCune, B., Mefford, M.J., 2011. PC ORD. Multivariate Analysis of Ecological Data. Version 6. In. MjM Software, Gleneden Beach, Oregon, USA.

McIver, J.D., Parsons, G.L., Moldenke, A.R., 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22, 984-992.

MCPFE, 1993. Second Ministerial Conference on the Protection of Forests in Europe. Helsinki, Finland.

Meyer, B., Jauker, F., Steffan-Dewenter, I., 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. Basic and Applied Ecology 10, 178-186.

Nolan, M., 2008. Database of Irish Spiders (Araneae). Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin.

Norris, K.C., 1999. Quantifying Change Through Time in Spider Assemblages: Sampling Methods, Indices and Sources of Error. Journal of Insect Conservation 3, 309-325.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Hendry, M., Stevens, H., Wagner, H., 2012. Vegan: Community Ecology Package. R version 2.0-7.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006a. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006b. The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands. Forest Ecology and Management 237, 478-491.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2007. Biodiversity of the ground-dwelling spider fauna of afforestation habitats. Agriculture, Ecosystems & Environment 120, 433-441.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Pawson, S.M., Brockerhoff, E.G., Meenken, E.D., Didham, R.K., 2008. Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodiversity & Conservation 17 1127-1148.

Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6, 780-793.

Peng, R.K., Incoll, L.D., Sutton, S.L., Wright, C., Chadwick, A., 1993. Diversity of Airborne Arthropods in a Silvoarable Agroforestry System. Journal of Applied Ecology 30, 551-562.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2013. Package 'nlme'. R version 3.1-109.

Pinzón, J., Spence, J., 2010. Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. Journal of Insect Conservation 14, 439-458.

Pithon, J.A., Moles, R., O'Halloran, J., 2005. The influence of coniferous afforestation on lowland farmland bird communities in Ireland: different seasons and landscape contexts. Landscape and Urban Planning 71, 91-103.

Platnick, N.I., 2012. The World Spider Catalog, Version 13.0. The American Museum of Natural History.

Pollard, E., 1968. Hedges. IV. A Comparison Between the Carabidae of a Hedge and Field Site and those of a Woodland Glade. Journal of Applied Ecology 5, 649-657.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ripley, B., Venables, B., Hornik, K., Gebhardt, A., Firth, D., 2013. Package 'MASS'. R version 7.3-27.

Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK.

Sjödin, N.E., Bengtsson, J., Ekbom, B., 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. Journal of Applied Ecology 45, 763-772.

Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Kelly, T., Iremonger, S., McKee, A.-M., Giller, P., 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodiversity & Conservation 17, 991-1015.

Smith, G.F., Gittings, T., Wilson, M., Oxbrough, A., Iremonger, S., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D.L., Pithon, J., O'Sullivan, A., Neville, P., Mitchell, F.J.G.,, Giller, P., O'Donnell, V., Kelly, T., 2006. Biodiversity Assessment of Afforestation Sites. In, Bioforest Final Report. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Sommaggio, D., 1999. Syrphidae: can they be used as environmental bioindicators? Agriculture, Ecosystems & Environment 74, 343–356.

Speight, M.C.D., 2000. Syrph the net: a database of biological information about European Syrphidae (Diptera) and its use in relation to conservation of biodiversity. Biodiversity: the Irish dimension. The Royal Irish Academy, Dublin, pp. 156–171.

Speight, M.C.D., 2008a. Database of Irish Syrphidae (Diptera). Irish Wildlife Manuals 36.

Speight, M.C.D., 2008b. Database of Irish Syrphidae (Diptera). Irish Wildlife Manuals, National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Speight, M.C.D., Castella, E., Sarthou, J.-P., Monteil, C., 2004. The database of European Syrphidae. Syrph the Net Publications, Dublin

Stubbs, A.E., Falk, S.J., 1983. British Hoverflies: An illustrated identification guide. British Entomological and Natural History Society, Reading.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561-594.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

United Nations Conference on Environment and Development, 1992. Agenda 21, the Rio Declaration on Environment and Development, the Statement of Forest Principles, the United Nations Framework Convention on Climate Change and the United Nations Convention on Biological Diversity. Rio de Janeiro.

van Helsdingen, P.J., 1998. The spider fauna of Scragh Bog in Co Westmeath, Ireland (Arachnida: Araneae). Zoologische Verhandelingen 323, 407–415.

van Veen, M.P., 2004. Hoverflies of northwest Europe. KNNV Publishing, Utrecht, The Netherlands.

Wallace, H.L., Good, J.E.G., 1995. Effects of afforestation on upland plant communities and implications for vegetation management. Forest Ecology and Management 79, 29-46.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, LLC, New York, USA.

Chapter 3

The importance of young plantation forest habitat and forest road-verges for ground-dwelling spider diversity



Road-verge in six year old Sitka spruce plantation forest

A manuscript based on this chapter has been published in *Biology and Environment*.

Abstract

The potential of forest roads to enhance habitat diversity within plantation forests is an important conservation issue. If properly managed these open spaces allow structurally diverse vegetation to grow at the road-verges, which may support greater invertebrate abundance and species richness, increasing overall forest biodiversity. In this study the spider diversity along road edges in young plantation forests in Ireland, the influence of road-verge vegetation, and the consequences of doubling the standard forest road-width currently used in Ireland was investigated. Active ground-dwelling spiders were studied in eight Sitka spruce (*Picea sitchensis*) plantations using pitfall trapping one year after planting and five years after planting.

A total of 16,741 spiders were caught, from which 141 species were identified from 14 families. Ten spider species of conservation importance were found in the road-verges demonstrating their importance as habitats for spider diversity. There was no detectable difference in ground-dwelling spider diversity between road-verge and forest interior plots at this stage in the rotation. There was no advantage or disadvantage of increasing the road-width of forest roads for ground-dwelling spider diversity of young plantation forests. The findings of this study are discussed in the context of the management of plantation forests for biodiversity conservation and associated forest policy development.

Introduction

At the beginning of the 20th century forest cover in Ireland had been reduced to less than 1% of the landscape, largely through anthropogenic activity (Anon, 2008). Since this time the area of forest cover has been increasing and today approximately 11% of the landscape is forested (Forest Europe *et al.*, 2011). This increase has mainly been achieved through state funded afforestation with non-native conifer plantation forests and the government aim is to further increase the national forest cover to 14% by 2030 (COFORD Council, 2009).

Biodiversity conservation is a key issue in the global environmental arena at present (Buckley, 2004). As a member of the EU and a signatory to the UN Convention on Biological Diversity, Ireland is committed to the implementation of EU Directives aimed at maintaining and enhancing biodiversity in plantation forests (DAHG, 2011). The biodiversity contained within non-native plantation forests is of particular interest due to the negative impact of deforestation on global biodiversity and the potential for non-native reforestation to contribute to biodiversity conservation (Carnus *et al.*, 2006; Brockerhoff *et al.*, 2008). Plantation forests are expanding worldwide and in countries, such as Ireland and the United Kingdom, where plantation forests comprise a large proportion of the forest estate (Forest Europe *et al.*, 2011), they offer opportunities to contribute to compliance with EU Directives and commitments to biodiversity conservation.

The diversity of invertebrate species is an important component of forest ecosystems and the delivery of ecosystem services, as they play functional roles in food webs, pollination and nutrient cycling (Petersen and Luxton, 1982; Gunnarsson, 1996; Kevan, 1999; Sanders *et al.*, 2008). In particular, ground-dwelling spiders play an important predatory role in terrestrial food webs as generalist predators and regulate the litter invertebrate communities in forest ecosystems (Clarke and Grant, 1968; Moulder and Reichle, 1972). They also respond to habitat structural diversity and are useful indicators for changes in the ground layer habitat of forests (Uetz, 1991; Oxbrough *et al.*, 2005), particularly as they are a large, taxonomically well-known group of invertebrates which are easily sampled (Pearce and Venier, 2006).

Until recently there was little information available on the ecology and distribution of this important species group in Irish forests and much of the information on Ireland's spiders came from open habitats, such as bogs, fens, grasslands and heathlands (Higgins, 1985; Helsdingen, 1996; Nolan, 2002). Increasing interest in sustainable forest management and

biodiversity conservation has revealed gaps in our knowledge of forest spider communities and a number of studies have been undertaken in recent years (Smith *et al.*, 2005; Iremonger *et al.*, 2006; O'Halloran *et al.*, 2011). Recent publications on species distributions (van Helsdingen, 1996) and ecology (Nolan, 2008) have also provided more information on Irish spiders, although the conservation status of most spider species is still not known in sufficient detail to plan for the conservation of priority species.

The capacity of plantation forests to enhance and maintain biodiversity and associated ecosystem function is dependent on appropriate forest planning and management, including the creation or retention of features which influence biodiversity (Carnus *et al.*, 2006). Stand level management for biodiversity should not be based only on total abundance and species richness, but should include management for individual species of conservation priority which may be present in the assemblage, which will also increase the contribution of forests to landscape biodiversity.

Invertebrate species richness and abundance is positively correlated with increased light availability which stimulates ground flora diversity thus increasing habitat heterogeneity (Sparks and Greatorex-Davies, 1992; Greatorex-Davies *et al.*, 1994; Sparks *et al.*, 1996). This effect is seen within 5m of the road, providing new habitat for invertebrate species within forest plantations (Watkins *et al.*, 2003; Avon *et al.*, 2013). Forests roads increase overall spider abundance and species richness through their contribution to open space within plantations (Oxbrough *et al.*, 2006a). In landscapes with largely fragmented forests, such as that found in Ireland, there is the potential for forest roads to make a positive contribution to forest biodiversity where they increase habitat heterogeneity attracting species that may otherwise be rare or absent (Warren and Fuller, 1993; Mullen *et al.*, 2003; Gittings *et al.*, 2006).

Grant aided afforestation in Ireland requires that at least 15% of the planted forest area is designated as an 'Area for Biodiversity Enhancement' and should include 5-10% retained habitat such as hedgerows and native broadleaf trees and 5-10% open space, which may include forest roads and rides (Anon, 2000). The Forest Road Scheme in Ireland aims to improve the environmental and biodiversity value of the forests through grant aiding for the construction of harvest roads (Anon, 2012). Forest roads can be planned and managed so that from the time of planting they make a positive contribution to biodiversity (Warren and Fuller, 1993; Ryan *et al.*, 2004). The standard minimum road-width currently recommended

in Ireland by the Forest Service is 15m, including a 5m wide road surface and the verges up to the tree bases on each side of the road (Ryan *et al.*, 2004). However, there is usually very little undisturbed open space in the road-verges as branches from maturing trees can directly shade this area and the space is also used for positioning of drains and banks (Iremonger *et al.*, 2006). Previous research in Britain has recommended that forest roads should be 1 – 1.5 times as wide as the height of the trees, to prevent shading of the verges (Kirby, 1992; Warren and Fuller, 1993). In an Irish context, Mullen *et al.* (2003) recommend a combined width of 20-30m for the road-verge and road in Sitka spruce plantations, yet there are no studies published to describe spider communities in roads of different width in Ireland.

In light of the inclusion of forest roads in Irish forest policy and the potential to increase forest open space through increasing the road-width, the contribution of forest roads to spider diversity must be assessed from an ecological standpoint. This study set out to investigate: 1) whether forest roads support species of conservation value in plantation forests, 2) whether forest roads make a positive contribution to spider diversity, 3) whether increasing the width of forest roads impacts on spider diversity.

Materials and methods

Experimental design

Eight experimental study sites were selected in second rotation Sitka spruce (*Picea sitchensis*) plantation forests (Figure 1). A base-line survey was carried out in 2005 when the trees were one year old and a repeat survey was undertaken in 2010, six years into the forest cycle. The data from the base-line survey were collected for the BIOFOREST Project (Iremonger *et al.*, 2007) and were kindly provided by Anne Oxbrough for use in this study.

In each site, one 400m long section of the road which was located at least 50m from the edge of the forest was used for study. The first 200m of these road sections were the standard 15m treatment width, including a 5m wide road and 5m of road-verge either side (hereafter referred to as standard). The other 200m was widened to a 30m treatment width, including a 5m wide road and 12.5m road-verge either side (hereafter referred to as wide). Three sampling plots were established in each treatment at 50m, 100m, and 150m, making a total of three sampling plots per treatment and two treatments per site.

The sampling plots were placed on the south facing side of the road, and each consisted of three plot positions: Open 1, Open 2 and Forest (Figure 2). The standard road-width

treatment was arranged so that Open 1 was parallel to the road edge, halfway between the road edge and the tree line. Open 2 was also placed halfway between the road edge and the tree line; this was approximately 2.5 – 3m from the trees. There was a gap of 2m between Open 1 and Open 2. The Forest plot was placed 5m into the forest after the tree line. The wide treatment was arranged so that Open 1 was placed halfway between the road edge and the tree line. Open 2 was placed 2.5 - 3m before the tree line to match Open 2 in the standard treatment. The Forest plot was placed 5m into the forest after the tree line. Open 1 sampled spider assemblages utilising the middle of the road-verge, Open 2 sampled spider assemblages which may be subject to shading and Forest plots were used as a reference point to compare changes in the road-verge habitat and associated spider assemblages to those in the forest.

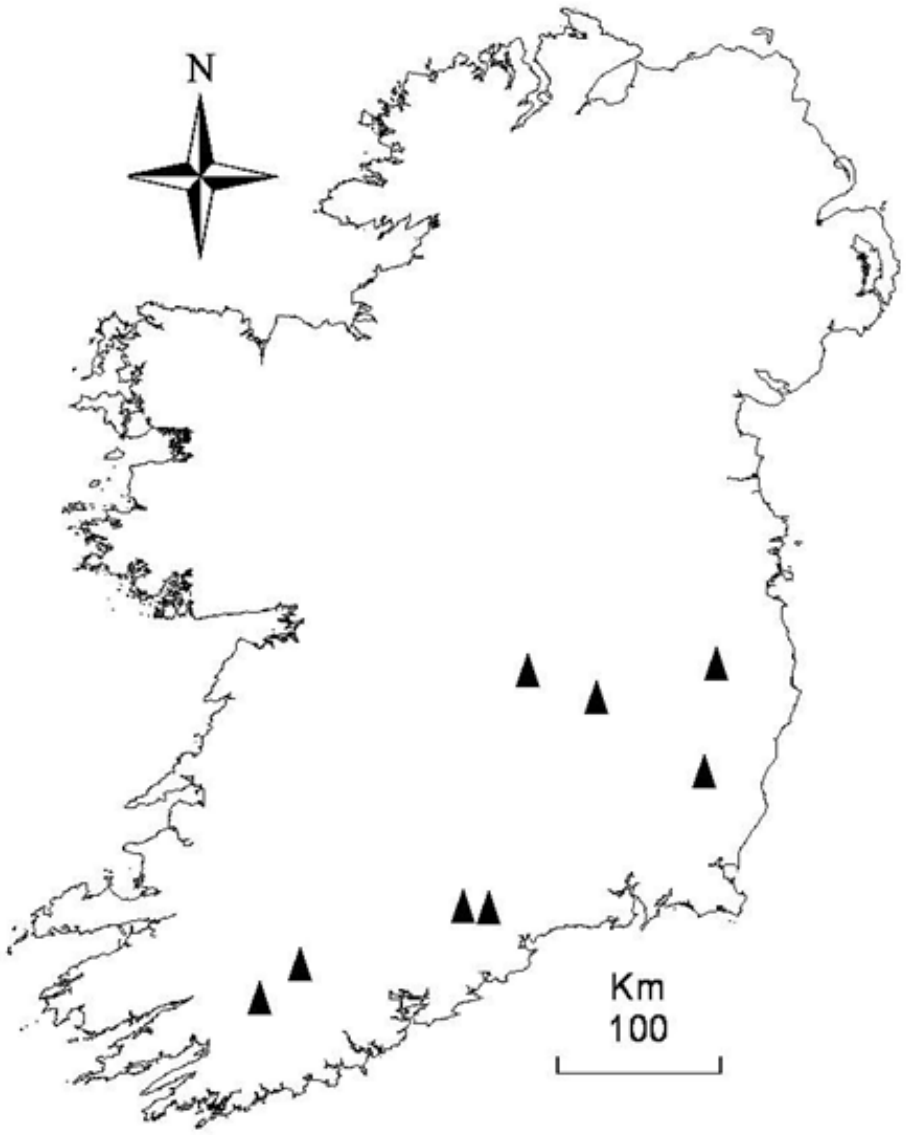


Figure 1. Distribution of study sites across Ireland.

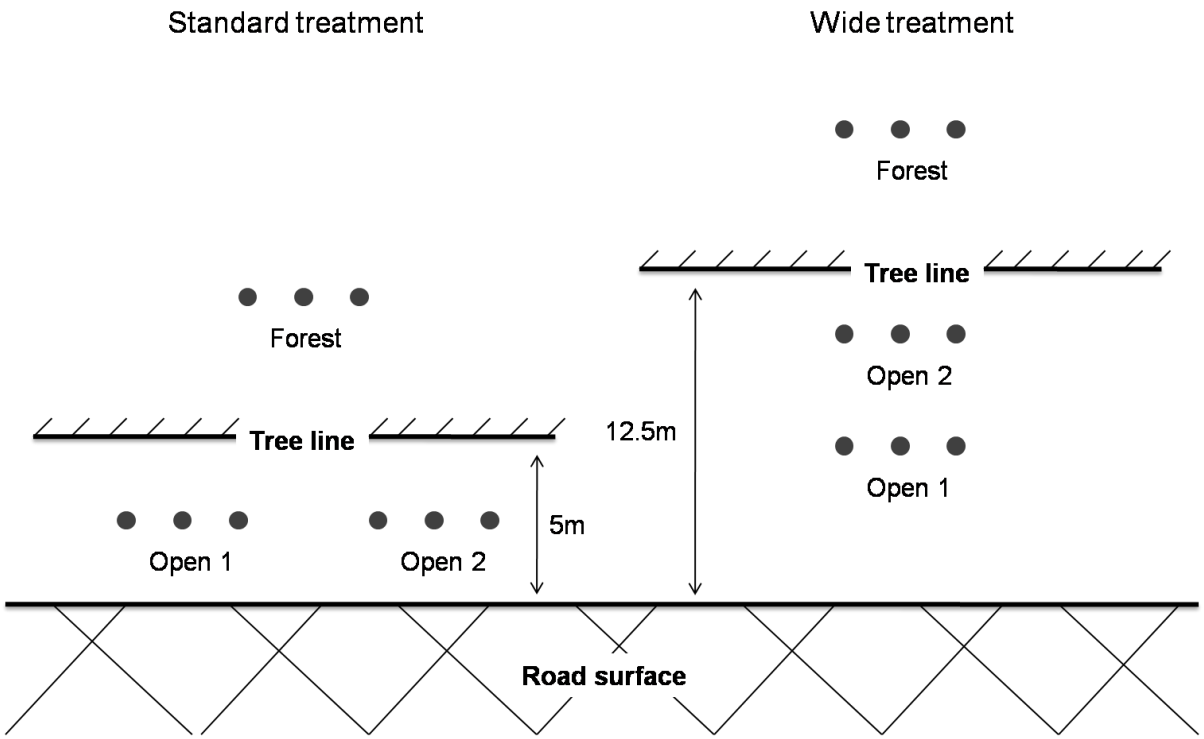


Figure 2. Plot (Open 1, Open 2 and Forest) configuration for sampling spiders in the road-verges and forest interior of standard and wide road-width treatments.

Spider sampling

Pitfall traps, filled with 3cm of ethylene glycol (anti-freeze), were used to sample active ground-dwelling spiders. Traps were plastic cups of approximately 7cm diameter and 9cm high and had drainage slits were cut 1cm from the top of the cup. Traps were dug into the ground the so the rim was just below the surface. In each plot position (Open 1, Open 2 or Forest) two pitfall traps were placed in a line, with a 2m gap between each trap. The contents of each pitfall trap were collected every three weeks from May to July totalling three collections and 63 trapping days. The plastic cup was placed back in the ground and filled with fresh anti-freeze after each collection. The contents of the traps were transferred to labelled sample bottles and stored in 70% ethanol.

Adult spiders were identified to species level using Roberts (1993) and nomenclature follows Platnick (2012), juveniles were counted but not identified due to difficulties with species level identification. Each species was assigned to a feeding guild (web-spinning or cursorial) and habitat specialist species which are associated with open or forest habitats were determined based on Nolan (2008). Conservation status of rare species was assigned based on Nolan (2008), which uses British records by Dawson *et al.* (2008), as there is little information on the status of many spider species in Ireland.

Environmental variables

Habitat was surveyed using the Braun-Blanquet scale (Mueller-Dombois and Ellenberg, 1974) to determine the percentage cover of vegetation (+ = <1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-100%), using a $1m^2$ quadrat placed over both pitfall traps in each plot. Vegetation was classed as ground vegetation (0-10cm), lower field layer (>10cm-50cm) and upper field layer (>50cm-200cm). The cover of deadwood, leaf litter, bare soil and stone was also recorded using the same method. Deadwood was split into two categories: deadwood under 10cm in diameter was classed as fine woody debris and deadwood over 10cm in diameter was classed as coarse woody debris, this included snags and tree stumps. Leaf litter type (i.e. broadleaf or coniferous) and depth was also recorded. The percentage of canopy cover was also calculated at each plot in the repeat survey, using GLA 2.0 from a hemispherical photograph (Frazer *et al.*, 1999) which was taken at the centre of each plot at a height of 1.3m.

Data analysis

The two pitfall traps were pooled at each plot position (Open 1, Open 2 and Forest) and across all collection periods and the three sampling plots in each treatment per site, and site level data was used in all analyses.

Species richness and abundance were tested for normality and compared between plot position and treatment within each sampling year. This analysis was carried out using paired t-tests for normally distributed data and paired Wilcoxon signed rank tests for non-normally distributed data. The species richness of habitat specialists, feeding guilds and rare species were also compared in this way.

The effect of plot position and road-width treatment on the composition of spider assemblages within each sampling year was compared with a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). The analysis was performed on Hellinger transformed species abundance data (Legendre and Gallagher, 2001), using the Bray-Curtis dissimilarity measure and 4999 permutations.

Variation partitioning (Peres-Neto *et al.*, 2006) was used to examine how much of the variation in species assemblages in the road-verges was explained by the subsets of the measured variables: habitat structure, treatment and plot position. Redundancy analysis was then used to examine the effect of significant subsets on species composition. This is a constrained ordination which tests how much of the variation in species assemblage is explained by the variables (ter Braak, 1994). The habitat variables were checked for strong correlations and any that had a variance inflation factor above 10 were examined and if necessary removed (Borcard *et al.*, 2011). Forward selection of the habitat variables was used to choose those which explained the most variation in the species dataset before using variation partitioning and redundancy analysis (Blanchet *et al.*, 2008). Species abundance data were Hellinger transformed, the variance of continuous explanatory variables was adjusted so that the mean = 0 and standard deviation = 1, and the analysis used 4999 permutations.

All statistical analysis was carried out using R (R Core Team, 2012). Hellinger transformations, PERMANOVA, and RDA were performed using the vegan package (Oksanen *et al.*, 2012) and forward selection used the Packfor package (Dray *et al.*, 2012).

Results

A total of 16,741 spiders were caught during the baseline and repeat surveys. Juveniles constituted 3,067 (18%) of this total and 13,674 (82%) constituted adult spiders from which 141 species were identified from 14 families. Twenty nine of these species were classified as forest and shade associated species, 35 were classified as open specialists and 77 as habitat generalists. Two families comprised the majority of the assemblage: Linyphiidae (47%) and Lycosidae (45%). The dominant species caught was *Pardosa pullata* (33%) which is an open specialist from the Lycosidae family.

Rare spider species

Ten rare species were recorded during this study. *Jacksonella falconeri* (n = 1) and *Meioneta mollis* (n = 1) are classed as endangered species in Britain. *Agyneta subtilis* (n = 410), *Erigonella ignobilis* (n = 2), *Hypselistes jacksoni* (n = 5), *Maro minutus* (n = 72), *Saaristoa firma* (n = 13), *Taranucnus setosus* (n = 25), *Trochosa spinipalpis* (n = 3) and *Walckenaeria dysderoides* (n = 51) are classed as vulnerable species in Britain. See Appendix 1 for details on the site location, road-width treatment, plot position and sampling year these species were caught in.

Spider diversity in forest road-verges

Species assemblages did not differ between the plot positions (Open 1, Open 2 and Forest) of the road-verge and forest in either the baseline survey ($F_{2,42}$ = 0.41, P = 1.00) or the repeat survey ($F_{2,42}$ = 0.46, P = 0.10). There was also no effect of plot position on any of the species metrics measured in the baseline or repeat surveys. Variation partitioning of the measured variables revealed that habitat structure explained 19% of the variation in species composition in the road-verges ($F_{6,57}$ = 3.42, P = 0.005) whilst treatment and plot position had no influence and produced values of <0% (Figure 3). There was also no shared variation explained by combinations of habitat and treatment (0%) or plot position and treatment (0%), and the combination of habitat and plot position produced a value of <0%. When minus values are produced by this analysis it means that the explanatory variable performs worse than random at explaining the variation in species composition (Borcard *et al.*, 2011). RDA of the habitat variables revealed that shrub and herb vegetation cover were the most influential habitat variables on spider species assemblages in the road-verges (Table 1).

Effect of road-width on spider diversity

The baseline survey, one year after planting, found no effect of road-width treatment on species assemblage ($F_{1,42}$ = 0.84, P = 0.64). There was also no effect on relative abundance, species richness of forest specialists, open specialists or cursorial spiders (Table 2). However, in Open 1 plots the species richness of rare species was significantly greater in the wide treatment, and in Forest plots overall species richness and web-spinning spider species richness was significantly greater in the standard road-width treatment than in the wide treatment (Table 2). The repeat survey also found no effect of road-with treatment on species assemblage ($F_{1,42}$ = 1.39, P = 1.00) and there was no effect of road-width on any of the species metrics measures (Table 3).

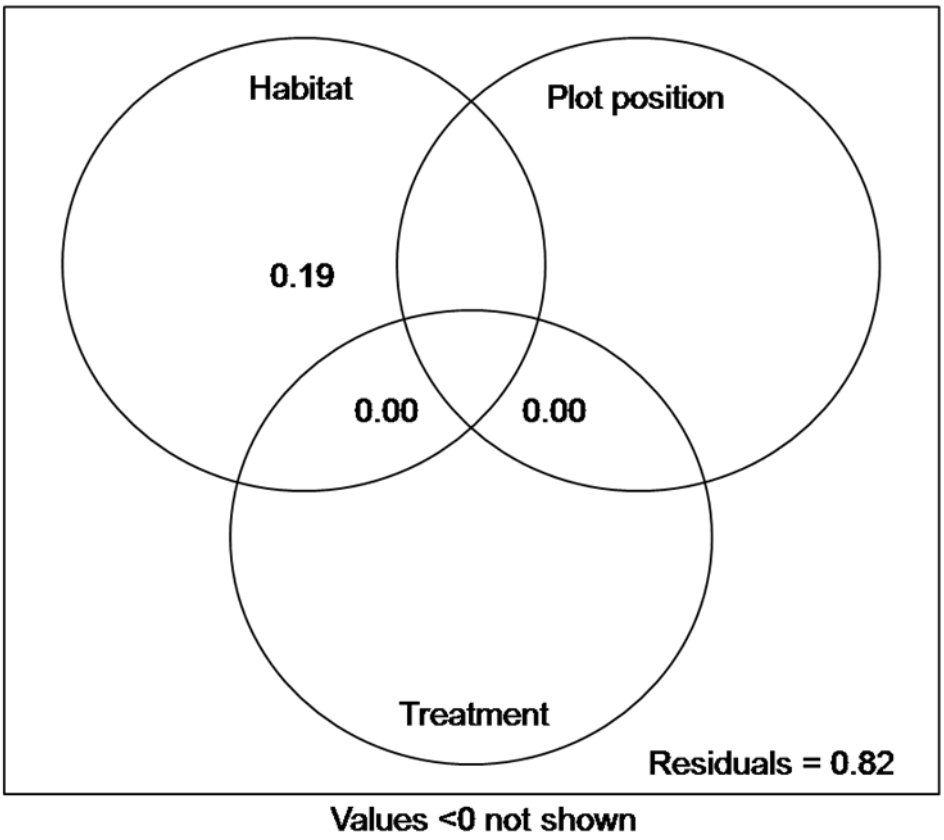


Figure 3. Variation partitioning of spider species assemblages in the road-verges.

Table 1. Redundancy analysis results of the effect of habitat variables on spider species assemblages in the road-verges.

Habitat variable	$F_{1,57}$	P
Shrub vegetation (50-100cm)	7.83	< 0.001
Herb vegetation (10-50cm)	3.87	< 0.001
Deadwood	2.82	< 0.001
Leaf litter	2.42	<0.001
Bare soil	1.82	0.02
Ground vegetation (0-10cm)	1.78	0.02

Table 2. Mean abundance and richness of species, habitat specialists and feeding guilds in each treatment x plot combination ± standard error during the baseline survey in 2005. Significant comparisons of species metrics between treatments are indicated in **bold**. Comparisons between plot positions were non-significant (P = >0.05).

	Standard			Wide		
	Open 1	Open 2	Forest	Open 1	Open 2	Forest
Abundance	203.9 ± 48.3	221.0 ± 51.9	241.8 ± 62.8	200.9 ± 37.3	195.4 ± 31.1	204.9 ± 36.6
Total species richness	30.88 ± 1.92	33.00 ± 11.67	**33.88 ± 2.02** [a]	31.88 ± 2.29	29.50 ± 2.09	**28.75 ± 3.07** [a]
Forest specialist species richness	6.75 ± 0.80	7.88 ± 0.55	7.63 ± 0.63	7.50 ± 0.73	7.00 ± 0.46	6.38 ± 0.68
Open specialist species richness	8.50 ± 0.85	8.88 ± 0.79	9.63 ± 1.08	8.50 ± 0.96	7.63 ± 0.73	7.88 ± 1.08
Web-spinning spider species richness	24.63 ± 1.63	26.13 ± 2.00	**26.88 ± 1.42** [b]	26.13 ± 1.61	23.63 ± 1.70	**22.63 ± 2.27** [b]
Cursorial spider species richness	5.75 ± 0.53	6.25 ± 1.01	6.25 ± 0.80	5.38 ± 0.80	5.38 ± 0.75	5.75 ± 0.96
Rare species richness	**1.5 ± 0.19** [c]	1.63 ± 0.26	1.63 ± 0.42	**2.13 ± 0.13** [c]	1.88 ± 0.23	2.13 ± 0.35

[a] $t_{1,7} = 3.30$, P = 0.01, [b] $t_{1,7} = 2.82$, P = 0.03, [c] $U_{1,7} = 0$, P = 0.04

Table 3. Mean abundance and richness of species, habitat specialists and feeding guilds in each treatment x plot combination ± standard error during the repeat survey in 2010. Comparisons of species metrics between treatment and plot position were non-significant (P = >0.05).

	Standard			Wide		
	Open 1	Open 2	Forest	Open 1	Open 2	Forest
Abundance	65.9 ± 11.9	70.9 ± 12.3	72.4 ± 9.5	79.6 ± 13.7	76.4 ± 8.7	76.4 ± 9.8
Total species richness	29.88 ± 3.22	30.5 ± 3.03	32.50 ± 2.31	31.5 ± 3.42	33.13 ± 2.05	32.13 ± 2.39
Forest specialist species richness	7.00 ± 0.87	7.50 ± 0.82	8.25 ± 0.84	8.88 ± 0.93	9.13 ± 1.04	8.13 ± 0.97
Open specialist species richness	8.63 ± 1.07	8.63 ± 0.68	8.25 ± 1.03	7.50 ± 0.89	8.50 ± 0.60	8.63 ± 0.80
Web-spinning spider species richness	24.63 ± 2.28	24.63 ± 2.68	27.13 ± 1.92	26 ± 2.67	27.13 ± 1.68	26.63 ± 1.81
Cursorial spider species richness	4.88 ± 1.08	5.25 ± 0.45	4.88 ± 0.67	5.00 ± 0.71	5.63 ± 0.50	5.13 ± 0.77
Rare species richness	2.13 ± 0.35	1.50 ± 0.33	1.75 ± 0.25	1.38 ± 0.26	2.00 ± 0.38	1.88 ± 0.48

Discussion

Rare spider species

The retention of small patches of non-forest habitat within forest plantations may provide a 'life-boat' function for species of conservation concern (Johansson *et al.*, 2013). The potential for road-verges to contribute to forest biodiversity conservation in Irish plantation forests was investigated in this manner. Two species of endangered spider and eight vulnerable spider species were recorded in the road-verges in young plantation forests in this study, indicating their importance as habitats for species of conservation priority.

Jacksonella falconeri is an endangered species and a habitat generalist found in litter in wetlands, grassland, heathland and forests. *Meioneta mollis* is an endangered species and included in the UK Biodiversity Action plan (Anon, 2013c), it is an open specialist found in low vegetation and litter in grasslands. *Agyneta subtilis* is a vulnerable species which is a habitat generalist found in moss and low vegetation and is associated with coniferous forests, as well as raised bog, fen, moist meadows and heathland. *Erigonella ignobilis* is a vulnerable species which is a habitat generalist and found in damp marshy habitats in damp litter and vegetation at pool edges. *Hypselistes jacksoni* is a vulnerable species which is an open specialist and found in wet heathland and wet grassland. *Maro minutus* is a vulnerable species which is a habitat generalist found on the soil surface and very low vegetation in grassland, coastal and dune systems, and forests. *Saaristoa firma* is a vulnerable species and included in the UK Biodiversity Action plan (Anon, 2013c), it is a habitat generalist found in moss, leaf litter and pine needles in damp broadleaf and coniferous forests. *Taranucnus setosus* is a vulnerable species and an open specialist found in well developed vegetation in open, undisturbed damp or wet habitats. *Trochosa spinipalpis* is a vulnerable species and open specialist found in low vegetation in damp habitats. *Walckenaeria dysderoides* is a vulnerable species found in shaded habitats and moss and litter in forests.

Recommended management for *J. falconeri* and *M. mollis* include preventing the loss of exposed habitats with short vegetation, particularly heathland and grassland (Anon, 2013a, b). *E. ignobilis*, *H. jacksoni*, *T. setosus* and *T. spinipalpis* rely mainly on open habitats with well-developed vegetation and the latter four species in particular require the presence of damp habitats (Helsdingen, 1996; van Helsdingen, 1998; Nolan, 2008). The vegetation and moisture requirements of these species means it is unlikely that they would be found in the forest interior of Sitka spruce plantation forests, particularly after canopy closure where the

ground vegetation diversity is typically reduced, due to the decreasing availability of light, nutrients and moisture (Anderson *et al.*, 1969; Hill, 1979; Avon *et al.*, 2010). The vulnerable and endangered species found in the open habitat of these young plantation forests indicate that open areas within plantation forests support rare species. These findings support the retention of road-verges in plantation forests, and demonstrate the importance of this open habitat for rare spider species. Forest management should include consideration of the importance of these areas for forest biodiversity.

Spider diversity in forest road-verges

The construction of roads through large, otherwise, undisturbed forests, may bring about negative changes in biodiversity by increasing fragmentation, which alters the physical and chemical environment, increasing disturbance and the spread of invasive species (Buckley *et al.*, 2003; Avon *et al.*, 2013; Johansson *et al.*, 2013). However, in fragmented landscapes of plantation forest, that are devoid of open spaces in the absence of active management, roads may provide the opportunity to enhance biodiversity (Warren and Fuller, 1993; Smith *et al.*, 2007), and the design and management of forest roads is crucial for sustainable forest management (Lindenmayer *et al.*, 2006). The inclusion of open spaces, including forest roads, is an objective of forest management for biodiversity conservation in Ireland (Anon, 2000).

The forest road-verges in this study supported a similar ground-dwelling spider fauna as the forest interior, with the majority of species recorded being open specialists and habitat generalists. Forest and shade associated species, such as *Monocephalus fuscipes* and *Tenuiphantes zimmermanni*, were still present in the road-verges and open specialists, such as *Pardosa amentata* and *P. pullata* were present in the forest interior. The road-verges had well developed ground, herb and shrub layers and still experienced full sunlight, making the conditions ideal for many open specialist species. However, the forest interior also had well-developed vegetation, although the trees were tall enough in the repeat survey to cast more shade here than in the road-verges. This mixture of open and forest specialist species is common where species composition remains similar to the pre-planting habitat until the time of canopy closure, as forest specialists and shade-associated species can be remnant populations from the previous rotation (Oxbrough *et al.*, 2010). Additionally, even at this early stage in the forest cycle forest specialists may start to colonise (Oxbrough *et al.*, 2006b; Oxbrough *et al.*, 2010).

Habitat explained more variation in species composition than treatment or plot position, although as the forest matures these are likely to be inter-correlated. Only 19% of the variation in spider assemblages found in the road-verges was explained by the measured habitat variables suggesting that other factors are also influencing species assemblages here. This is common when using multivariate analysis of ecological data where many species and many explanatory variables produce background noise (McCune, 1997). However, shrub and herb cover were shown to have the strongest influence over spider diversity in the road-verges and these vegetation types could be shaded out once the forest matures. The effect of road-verges on ground vegetation favours fast-growing, nutrient and light-demanding non-forest species at distances of less than 5m from the road edge in forests (Watkins *et al.*, 2003; Avon *et al.*, 2010).

As plantation forests mature the road-verges have a lower canopy cover than the forest interior and the increased light levels can result in a ground vegetation community that is different to the forest interior (Watkins *et al.*, 2003; Avon *et al.*, 2010). Consequently, the response of ground vegetation structure to the presence of roads may change as the forest matures, suggesting that the findings of this work cannot be extrapolated to all stages of the forest cycle. The trees in this study were approximately 2m tall and so cast little shade and the ground flora was well-developed along the road-verges. Repeat surveys of this experiment are recommended for all stages of the forest cycle in order to determine how spider diversity is affected by changes in canopy cover and habitat succession in plantation forest road-verges.

This study clearly demonstrates the importance of forest road-verges for open specialists and habitat generalists. As the forest cycle progresses the subsequent change in habitat, including a decrease in ground vegetation and increase in litter cover, leads to a fundamental change in ground-dwelling spider species composition and a decrease in species richness (Oxbrough *et al.*, 2005). Forest roads may then be expected to provide a refuge for open specialist spider species that would not otherwise persist in the forest interior.

Effect of road-width on spider diversity

The effect of forest roads on ground-dwelling spiders is mediated primarily through effects of light penetration, which is greater at forest roads than it is in the forest interior (Mullen *et al.*, 2003; Watkins *et al.*, 2003). The effect of light penetration is reduced as forests mature due to the increasing shade provided as the trees grow taller (Warren and Fuller, 1993;

Avon *et al.*, 2010). The standard road-width in Irish plantation forests at present is 15m, which if increased, may improve the contribution of open spaces along forest roads to forest biodiversity (Smith *et al.*, 2007).

There was no advantage or disadvantage for ground-dwelling spider diversity in young plantation forests of increasing the road-width of forest roads. During the first five years of the forest cycle increasing the width of forest road-verges had no detectable effect on the species composition of ground-dwelling spiders and there was little effect on the species richness of spiders in the road-verges. Forest plots in the standard treatment had higher species richness, which was driven by a greater species richness of web-spinning spiders. This was not expected as Forest plots in both treatments were in areas that had always been in forest interior habitat. The reason for higher web-spinning species richness in the standard Forest plots one year after planting is unclear and this difference did not persist until the time of the repeat survey.

Many of the species recorded in this study were from the Linyphiidae family, which are highly capable aerial dispersers and could potentially move between the two different road-width treatments and confound the results. However, even good dispersers, such as the Linyphiids, are strongly influenced by habitat structure and show strong habitat specificity at the scale of 2 – 3m in Irish forests (Oxbrough *et al.*, 2006a). Therefore it is expected that any differences in habitat which may emerge between the treatments as the forest cycle progresses would also affect spider diversity, regardless of dispersal ability.

Natural regeneration of Sitka spruce trees was observed along the road-verges during the repeat survey at several of the forests in this study. Therefore management of forest roads is required to prevent regeneration of trees along road-verges. If a wider road-width is found to be beneficial to spider diversity at later stages of the forest cycle it will be important to actively manage the road-verges and remove any regeneration of the planted tree species that may cause shading.

Conclusions

The effect of forest roads on forest biodiversity is an important conservation and management issue. Forest road-verges provide important open habitat for ground-dwelling spider diversity in Sitka spruce plantation forests. Their importance extends to species of conservation importance, where they make a valuable contribution to the conservation of

spider diversity, providing further support for their inclusion in forest management plans. Increasing the width of the road-verge had no advantage or disadvantage for ground-dwelling spider diversity during the first five years of the forest cycle. However, the present study provides important baseline data against which future surveys of the effect of road-width treatment on the diversity of road-verges can be monitored.

The importance of investigating the biodiversity of young plantation forests is particularly relevant in countries, such as Ireland and Britain, which are undertaking large-scale afforestation programmes and where non-native tree species comprise a larger proportion of the forest estate (Forest Europe *et al.*, 2011). A significant proportion of forested areas in these countries will be newly established or young second and third rotations. Therefore research into methods of maximising biodiversity in these young forests is required to inform policy development and forest management.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32-46.

Anderson, R.C., Loucks, O.L., Swain, A.M., 1969. Herbaceous Response to Canopy Cover, Light Intensity, and Throughfall Precipitation in Coniferous Forests. Ecology 50, 255-263.

Anon, 2000. Forest Biodiversity Guidelines. Department of the Marine and Natural Resources, Government of Ireland.

Anon, 2008. Irish Forests - A Brief History. Department of Food, Agriculture and the Marine, Government of Ireland.

Anon, 2012. Forest Roads Scheme. Department of Food, Agriculture and the Marine, Government of Ireland.

Anon, 2013a. Summary for *Jacksonella falconeri* (Araneae). British Arachnological Society.

Anon, 2013b. Summary for *Meioneta mollis* (Araneae). British Arachnological Society.

Anon, 2013c. UK BAP priority terrestrial invertebrate species. Joint Nature Conservation Committee.

Avon, C., Bergès, L., Dumas, Y., Dupouey, J.-L., 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management 259, 1546-1555.

Avon, C., Dumas, Y., Bergès, L., 2013. Management practices increase the impact of roads on plant communities in forests. Biological Conservation 159, 24-31.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89, 2623-2632.

Borcard, D., Legendre, P., Gillet, F., 2011. Numerical Ecology with R. Springer, New York, USA.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity & Conservation 17, 925-951.

Buckley, D.S., Crow, T.R., Nauertz, E.A., Schulz, K.E., 2003. Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. Forest Ecology and Management 175, 509-520.

Buckley, P., 2004. Development of wildlife conservation policy and legislation in Ireland. Biology & Environment 104B, 107-111.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. Journal of Forestry. Journal of Forestry 104, 65-77.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

COFORD Council, 2009. Forestry 2030. Department of Food, Agriculture and the Marine, Government of Ireland.

DAHG, 2011. Ireland's National Biodiversity Plan 2011-2016. Department of Arts, Heritage and the Gaeltacht.

Dawson, I., Harvey, P., Russell-Smith, T., 2008. A national Status Review - the draft results. Spider Recording Scheme News 112, 18-24.

Dray, S., Legendre, P., Blanchet, F.G., 2012. Packfor: Forward Selection with permutation (Canoco p.46). R version 0.0-8.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Frazer, G., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0. Simon Fraser University and the Institute of Ecosystem Studies, Millbrook, New York.

Gittings, T., O'Halloran, J., Kelly, T., Giller, P.S., 2006. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management 237, 290-300.

Greatorex-Davies, J.N., Sparks, T.H., Hall, M.L., 1994. The response of Heteroptera and Coleoptera species to shade and aspect in rides of coniferised lowland woods in southern England. Biological Conservation 67, 255-273.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Helsdingen, P.J.v., 1996. The Spider Fauna of Some Irish Floodplains. The Irish Naturalists' Journal 25, 285-293.

Higgins, D., 1985. Invertebrates of Irish Midlands raised bogs. Bulletin of the Irish Biogeographical Society 8, 91-97.

Hill, M.O., 1979. The development of a flora in even-aged plantations. In: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.), The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, pp. 175-192.

Iremonger, S., Gittings, T., Smith, G.F., Wilson, M., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D.L., Giller, P., O'Sullivan, A., Neville, P., Mitchell, F.J.G., O'Donnell, V., Kelly, T., Dowding, P., 2006. Investigation of experimental methods to enhance biodiversity in plantation forests. In, BIOFOREST Project 3.1.3 Final Report. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Johansson, T., Hjältén, J., de Jong, J., von Stedingk, H., 2013. Environmental considerations from legislation and certification in managed forest stands: A review of their importance for biodiversity. Forest Ecology and Management 303, 98-112.

Kevan, P.G., 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture, Ecosystems & Environment 74, 373-393.

Kirby, P., 1992. Habitat Management for Invertebrates: A Practical Handbook. Royal Society for the Protection of Birds, Bedfordshire, UK.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433-445.

Maleque, M.A., Maeto, K., Ishii, H.T., 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Applied Entomology and Zoology 44, 1-11.

McCune, B., 1997. Influence of noisy environmental data on canonical correspondance analysis. Ecology 78, 2617-2623.

Moulder, B., Reichle, D., 1972. Significance of Spider Predation in the Energy Dynamics of Forest-Floor Arthropod Communities. Ecological Monographs 42, 473-498.

Mueller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. Wiley and Sons, New York.

Mullen, K., Fahy, O., Gormally, M., 2003. Ground flora and associated arthropod communities of forest road edges in Connemara, Ireland. Biodiversity & Conservation 12, 87-101.

Nolan, M., 2002. Spiders (Araneae) of montane blanket bog in County Wicklow, Ireland. Bulletin of the Irish Biogeographical Society 26, 39-59.

Nolan, M., 2008. Database of Irish Spiders (Araneae). Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin.

O'Halloran, J., Irwin, S., Kelly, D.L., Kelly, T.C., Mitchell, F.J.G., Coote, L., Oxbrough, A., Wilson, M., Fox, H., French, V., Martin, R.D., Moore, K., Sweeney, O., Dietzsch, A.C., Walsh, A., Keady, S., Kopke, K., Keane, M., Neville, P., 2011. Management of biodiversity in a range of Irish forest types. In, Report prepared for the Department of Agriculture, Fisheries and Food, Ireland.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Hendry, M., Stevens, H., Wagner, H., 2012. Vegan: Community Ecology Package. R version 2.0-7.

Oxbrough, A., Irwin, S., Kelly, T., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111–2121.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006a. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006b. The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands. Forest Ecology and Management 237, 478-491.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6, 780-793.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87, 2614-2625.

Petersen, H., Luxton, M., 1982. A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. Oikos 39, 288-388.

Platnick, N.I., 2012. The World Spider Catalog, Version 13.0. The American Museum of Natural History.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK.

Ryan, T., Phillips, H., Ramsay, J., Dempsey, J., 2004. Forest Road Manual. Department of Food, Agriculture and the Marine, Government of Ireland.

Sanders, D., Nickel, H., Grützner, T., Platner, C., 2008. Habitat structure mediates top-down effects of spiders and ants on herbivores. Basic and Applied Ecology 9, 152-160.

Smith, G.F., Gittings, T., Wilson, M., French, L.J., Oxbrough, A., O'Donoghue, S., Pithon, J., O'Donnell, V., McKee, A.-M., Iremonger, S., O'Halloran, J., Kelly, D.L., Mitchell,

F.J.G., Giller, P., Kelly, T., 2005. Assessment of Biodiversity at Different Stages of the Forest Cycle. In, Bioforest Final Report, Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S., Mitchell, F.J.G., 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. Biological Conservation 136, 283-294.

Sparks, T., Greatorex-Davies, J.N., 1992. The effect of shade in plantation woodland on invertebrate abundance and biodiversity. Aspects of Applied Biology 29, 89-96.

Sparks, T.H., Greatorex-Davies, J.N., Mountford, J.O., Hall, M.L., Marrs, R.H., 1996. The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. Forest Ecology and Management 80, 197-207.

ter Braak, C.J.F., 1994. Canonical community ordination. Part 1: Basic theory and linear methods. Ecoscience 1, 127-140.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

van Helsdingen, P.J., 1996. The county distribution of Irish spiders, incorporating a revised catalogue of the species. The Irish Naturalists' Journal 25, 1-87, 89-92.

van Helsdingen, P.J., 1998. The spider fauna of Scragh Bog in Co Westmeath, Ireland (Arachnida: Araneae). Zoologische Verhandelingen 323, 407–415.

Warren, M.S., Fuller, R.J., 1993. Woodland Rides and Glades: Their Management for Wildlife. Nature Conservancy Council, Peterborough, UK.

Watkins, R.Z., Chen, J., Pickens, J., Brosofske, K.D., 2003. Effects of Forest Roads on Understory Plants in a Managed Hardwood Landscape. Conservation Biology 17, 411-419.

Chapter 4

Influence of conifer tree species on ground-dwelling spider diversity in plantation forests



Pitfall traps in lodgepole pine plantation forest

A manuscript based on this chapter has been submitted for peer-reviewed publication in an international journal.

Abstract

Forest policies worldwide now incorporate sustainable forest management, which aims to manage plantation forests for a range of benefits, including biodiversity, in addition to wood products. The selection and management of the canopy tree species in production forests is intrinsically linked to their biodiversity value, by influencing light levels, micro-climate, the litter layer and understory vegetation. Invertebrate species comprise a large proportion of forest biodiversity and spiders are one of the most abundant forest-floor arthropods. Spiders play an important role in terrestrial food webs and are primarily affected by the structural variation of a habitat, meaning they are a useful group for assessing the influence of canopy tree species on forest biodiversity. The diversity of active ground-dwelling spiders was examined in four conifer plantation types used in production forests in Ireland. Pitfall trapping was carried out in Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) forests between the months of May and July and the effects of factors including litter cover, vegetation layer cover and canopy cover on spider diversity were investigated.

Results indicate that semi-native Scots pine and introduced European Norway spruce forests had the highest species richness of ground-dwelling spiders compared with the two introduced North American species, Sitka spruce and lodgepole pine. Scots pine forests had the highest species richness of open-associated species and the greatest range of associated families, feeding guilds and habitat specialist species. Norway spruce forests had significantly higher species richness of forest-specialist spiders compared with Sitka spruce and lodgepole pine. The spider species composition of Scots pine and Norway spruce forests were different, and lodgepole pine and Sitka spruce forests formed a group which also differed. These differences were associated with higher canopy openness and vegetation cover and structure in Scots pine and Norway spruce forests, as well as the historical presence of these forest types in the Irish landscape. These results indicate that planting native tree species or species of European provenance offers potential benefits for biodiversity in plantation forests. Managing conifer plantations to increase canopy openness and the cover and structural diversity of ground vegetation will increase the number and variety of microhabitats, which will benefit ground-dwelling spider diversity.

Introduction

Whilst forests represent some of the richest and most biologically diverse areas of the world (Millenium Ecosystem Assessment, 2005), the highly managed nature of plantation forests means they may support less native biodiversity and fewer species than naturally occurring forests (Fahy and Gormally, 1998; Moore and Allen, 1999; Palik and Engstrom, 1999; Lindenmayer and Hobbs, 2004). Nevertheless, in countries with very low forest cover and very little naturally occurring forest, these plantation forests offer an important opportunity to provide habitat for forest associated species and enhance overall landscape biodiversity (Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008; Pawson *et al.*, 2008). The conservation of biodiversity in the world's plantation forests is a key component of sustainable forest management (SFM) and the principles of SFM are included in forestry policies worldwide (United Nations Conference on Environment and Development, 1992; MCPFE, 1993; European Communities, 2003). Forest biodiversity can be influenced by a number of factors, including the selection and management of the canopy tree species, which can alter understory structure and species composition through changes in microclimate, soil chemistry, litter and vegetation (Palik and Engstrom, 1999; Anon, 2000; Horgan *et al.*, 2003).

Plantation forests are the dominant forest type in many European countries, comprising approximately 90% of the forest estate in Iceland and Ireland and 80% of the forest estate in the United Kingdom and Denmark (Forest Europe *et al.*, 2011). Many of these plantation forests are dominated by non-native tree species and Ireland has one of the highest percentages of introduced species in Europe, with almost 70% of the forests consisting of exotic conifer species (Forest Europe *et al.*, 2011). The most commonly planted tree species in Ireland are Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) (Forest Europe *et al.*, 2011). Both of these species were introduced from North America in the 19th century, are suited to the soils and climate of Ireland, and are highly productive, meaning they are favoured by forest managers (Carey and Hendrick, 1986; Farrelly *et al.*, 2009). Norway spruce (*Picea abies*) is another introduced species from Europe and was first planted in Ireland in the 16th century (Anon, 2013). Although it requires more specialised conditions, it is suitable for use in frost prone areas which may be detrimental to other species (Anon, 2013). Another, less commonly planted, conifer species used in production forestry in Ireland is Scots pine (*Pinus sylvestris*), which is considered to be semi-native and is regarded as the only naturally occurring conifer with forestry potential (Anon, 2000). The

only other native conifer tree species in Ireland is yew (*Taxus baccata*) which comprises only 0.007% of the total forest area and is not suited to forestry (Anon, 2007). However, the native status of Scots pine is debated as it appears to have become extinct and was subsequently reintroduced. It was present in Ireland from 9500 BP until the early 1st century (Bradshaw and Browne, 1987; Cross, 1998; Mitchell, 2006), although there is evidence that it may have continued to exist here until medieval times (Nelson and Walsh, 1993). Furthermore, whether Scots pine underwent a total extinction or continued to grow in isolated patches is also subject to debate (Roche *et al.*, 2009). However, the majority of Scots pine grown in Ireland today is of Scottish origin, which was reintroduced during the 18th century (Roche *et al.*, 2009). Considering the global expansion of plantation forestry (European Commission, 2011) and the high percentage of introduced species used, research which directly compares different types of plantation forests is required to address knowledge gaps and inform policy for biodiversity conservation (Carnus *et al.*, 2006).

Spiders (Araneae) are one of the most abundant arthropod species groups of the forest floor (Wise, 1993). They play an integral role in the functioning of forest food webs as predators, regulating litter arthropod communities (Clarke and Grant, 1968; Moulder and Reichle, 1972; Wise, 2004) and as prey for many birds and insectivorous mammals (Churchfield *et al.*, 1991; Gunnarsson, 1996). Spiders are sensitive to habitat changes at a small scale and are primarily affected by vegetation and litter structure, which are influenced by canopy structure, making them an appropriate focus group for assessing habitat quality (Uetz, 1975; Marc *et al.*, 1999; Oxbrough *et al.*, 2005). The diversity of spiders in a habitat can also be used to infer information on other species groups, such as those involved in predator-prey interactions with spiders, and those which are also affected by habitat across a small scale, such as carabid beetles (Coleoptera: Carabidae) (Niemelä *et al.*, 1996; Marc *et al.*, 1999).

This research examined the biodiversity value of semi-native and introduced European and North American conifer species used in Irish forestry, using spiders as a model group. To achieve this, the active ground-dwelling spider diversity was investigated in four forest types: Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*) and links to environmental characteristics which might explain differences were examined.

Materials and methods

Study sites

Four replicate stands each of lodgepole pine, Norway spruce, Scots pine and Sitka spruce production forests were selected for study across Ireland (Figure 1). These 16 stands were even-aged, commercially mature monocultures (Table 1). Three sampling plots were located in each stand, a minimum of 50m apart and a minimum of 50m from the forest edge and selected to represent the stand as a whole, in homogenous areas. The Norway spruce stands were sampled in the summer of 2008, the Sitka spruce stands and one lodgepole stand were sampled in the summer of 2010 and the remaining three lodgepole pine and all Scots pines stands were sampled in the summer of 2011.

The data from the Norway spruce stands were collected for the FORESTBIO Project (O'Halloran *et al*., 2011) and were kindly provided by Anne Oxbrough for use in this study.

Spider sampling

Active ground-dwelling spiders were sampled using a standardised sampling method (O'Halloran *et al*., 2011). Pitfall traps were dug into the ground and positioned so the rim of the cup was slightly below the ground surface. The traps were plastic cups, 7cm in diameter and 9cm in depth, filled with 3cm of anti-freeze. Traps which were vulnerable to animal disturbance were covered with a 10cm x 10cm lid which was positioned 3cm above the ground. In each plot five traps were set 2 m apart in a linear arrangement. The contents of each trap were collected every three weeks from May to July, to coincide with the main activity period of Irish spiders (Nolan, 2008), totalling three collections and 62 – 64 trapping days. Spiders were identified to species level using Roberts (1993) and nomenclature follows Platnick (2012). Species with particular habitat associations or specialism's were determined based on information by Nolan (2008) and families were assigned to broad feeding guilds of web-spinning and cursorial hunters based on Uetz *et al.* (1999).

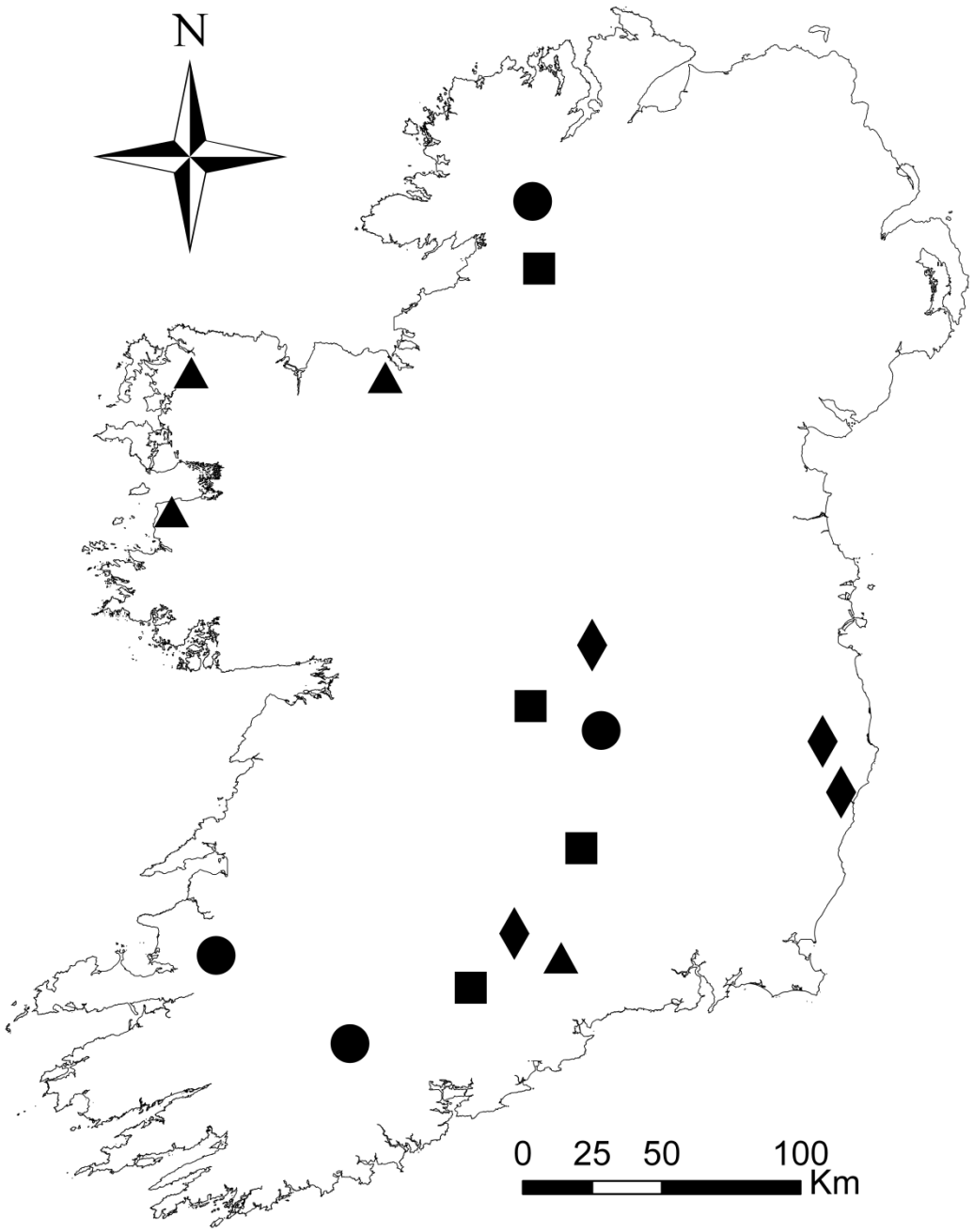


Figure 1. Locations of the 16 study sites: lodgepole pine (▲), Norway spruce (■), Scots pine (◆), Sitka spruce (●).

Table 1. Site characteristics of stands sampled.

Forest type	Mean age (range)	Mean stand size ha (range)	Mean elevation (range)	Soil types (number of stands)
Lodgepole pine	29 (28 – 31)	11 (5 – 16)	175 (37 – 385)	Peat (3), podzol (1)
Norway spruce	41 (38 – 48)	10 (3 – 19)	95 (50 – 140)	Brown earth (1), gley (1), peat (2)
Scots pine	64 (62 – 65)	13 (6 – 20)	127 (57 – 163)	Brown earth (1), brown podzolic (1), gley (1), podzol (1)
Sitka spruce	34 (30 – 37)	6 (3 – 11)	237 (165 – 353)	Brown earth (1), peat (3)

Habitat surveys

Habitat surveys were carried out at each plot using a $1m^2$ quadrat placed over each pitfall trap. The percentage covers of the following environmental variables were recorded: leaf and needle litter, fine woody debris (<10cm diameter), coarse woody debris (>10cm diameter), ground vegetation (0 – 10cm), lower field vegetation (10 – 50cm) and upper field vegetation (50 – 100cm). The mean percentage cover for each variable was calculated at the plot level. One soil sample was taken from each corner and the centre of a 10m x 10m plot adjacent to each pitfall trap plot. The soils were pooled for each plot and soil pH and organic carbon content were measured. Organic carbon content was measured as percent loss on ignition at 550ºC for 5 hours. The percentage of canopy cover was also calculated using GLA 2.0 from a hemispherical photograph (Frazer *et al.*, 1999) taken at the centre of each 10m x 10m plot at a height of 1.3 m.

Data analysis

Traps and collection periods were pooled at each plot and plot level data were used as the sample unit in all analyses. Three plots experienced 16%, 20% and 22% trap losses due to animal disturbance and so were omitted from the analyses. Sampling across different years can result in variation in the abundance of species which could affect analysis of species diversity (Norris, 1999). In order to ensure that observed differences were due to the forest type and not sampling year, rare species were omitted; these were defined as species which were represented by 3 or fewer individuals and were excluded from the analyses as a species could potentially be present as a singleton in each of the three years in which sampling was carried out.

The effect of forest type on the species richness of ground-dwelling spiders was examined with generalised linear mixed modelling (GLMM), using the Poisson distribution and stand as a random effect (Zuur *et al.*, 2009). Where appropriate this was followed by post-hoc tests adjusted for multiple comparisons. This analysis was carried out on 1) total species richness, 2) forest-associated species, 3) open-associated species, 4) web-spinning spiders and 5) cursorial spiders. The environmental variables were also compared between forest types using the same GLMM protocol, except that percentage cover values were arcsine transformed before analysis and the Gaussian distribution was used.

Indicator species analysis (ISA) was used to identify species which exhibited a strong affinity with a particular forest type, out of the four types investigated. This analysis uses species count data to assess the relative abundance and relative frequency with which a species occurs in each forest type. A percentage, called an indicator value, is calculated for each species to indicate which forest type they most abundantly and frequently occur in (Dufrene and Legendre, 1997). The analysis was run using 4999 permutations followed by a Monte Carlo test of statistical significance.

Multivariate regression tree analysis (MRT) (De'ath, 2002) was used to explore and predict the effect of forest type on species composition. This was performed on Hellinger transformed species count data (Legendre and Gallagher, 2001) and used the Bray-Curtis distance measure. The analysis was run 50 times and the tree with the lowest cross-validation error was chosen (De'ath, 2002). Redundancy analysis (RDA) was used to examine the relationship between species composition, forest type, and the measured habitat variables. This type of analysis tests how much of the variation in species composition can be explained by the constraining variables (ter Braak, 1994). Prior to analysis, the habitat variables were examined for collinearity using Spearman's rho correlations, any which were collinear above 0.7 were removed, the variables were scaled so the mean = 0 and standard deviation = 1, and the spider species data were Hellinger transformed (Legendre and Gallagher, 2001). Latitude can affect spider species composition in Ireland (Oxbrough *et al.*, 2012), therefore partial RDA using latitude as a conditional variable was carried out. Forward selection was used to identify the variables which explained the most variation in spider species composition among the plots (Blanchet *et al.*, 2008). ANOVA was then used to determine the significance level of the final model and the selected variables.

GLMM, MRT and RDA were calculated using the statistical analysis program R (R Core Team, 2012). GLMM was calculated using the nlme package (Pinheiro *et al.*, 2013) and the lme4 package (Bates *et al.*, 2012), multiple comparisons used the multcomp package (Hothorn *et al.*, 2013), MRT used the mvpart package (Therneau *et al.*, 2013), RDA used the vegan package (Oksanen *et al.*, 2012) and forward selection used the packfor package (Dray *et al.*, 2012). ISA was carried out in PC-ORD version 6 (McCune and Mefford, 2011).

Results

A total of 3,291 adult ground-dwelling spiders were recorded from 79 species, 49 genera and 12 families. After omitting species with 3 or fewer individuals a total of 3,096 adult ground-dwelling spiders were used in the analysis from 53 species, 36 genera and 7 families. Of these species, 17 were forest specialists, 3 were open specialists and 33 were habitat generalists. The dominant family was the Linyphiidae (94%) and the dominant species were *Tenuiphantes alacris* (19 %), *Tenuiphantes zimmermanni* (15%) and *Tenuiphantes tenebricola* (10 %). All three of these species are forest specialist Linyphiids and the latter two species are commonly sampled in conifer forests (Oxbrough *et al.*, 2010; Oxbrough *et al.*, 2012).

Differences in environmental characteristics between conifer types

Norway spruce plantations had significantly higher soil pH compared with the other three plantation forest types (Table 2). Fine woody debris cover was greater in Sitka spruce compared with Norway spruce. Scots pine had greater cover of upper field vegetation compared with the three other forest types. Canopy cover was significantly lower in Scots pine and Norway spruce compared with Sitka spruce and lodgepole pine.

Differences in spider diversity between conifer types

Total spider species richness and web-spinning spider species richness was similar between Scots pine, Norway spruce and Sitka spruce plantations. Total species richness and web-spinning spider species richness was significantly higher in Norway spruce and Scots pine compared with lodgepole pine plantations (Table 3). Forest specialist species richness was significantly higher in Norway spruce plantations compared with Lodgepole pine and Sitka spruce plantations. Forest specialist species richness was also significantly higher in Scots pine compared with Lodgepole pine plantations. The species richness of open specialist and cursorial spiders was higher in Scots pine compared with the other three plantation types, although they were found in low numbers.

Table 2. Mean ± standard error of environmental variables. Differences between forest types tested using GLMM: n.s. = non-significant, * < 0.01.

	Lodgepole pine	Norway spruce	Scots pine	Sitka spruce	GLMM
Soil pH	3.8 ± 0.1[a]	4.4 ± 0.1[A]	4.0 ± 0.1[a]	4.0 ± 0.1[a]	**$F_{3,41}$ = 6.58***
Organic carbon content	79.1 ± 7.1	47.3 ± 10.9	38.3 ± 8.7	51.8 ± 10.7	$F_{3,41}$ = 1.37, n.s.
Litter cover %	96.7 ± 1.7	42.0 ± 11.6	77.0 ± 12.6	87.7 ± 0.3	$F_{3,41}$ = 2.20, n.s.
Fine woody debris %	26.2 ± 4.4	3.6 ± 0.7[a]	23.7 ± 5.7	43.5 ± 8.5[A]	**$F_{3,41}$ = 6.35***
Coarse woody debris %	0.5 ± 0.5	4.3 ± 2.0	2.1 ± 0.7	6.5 ± 2.3	$F_{3,41}$ = 1.21, n.s.
Ground vegetation %	52.6 ± 10.2	57.1 ± 11.9	61.3 ± 7.8	72.1 ± 5.5	$F_{3,41}$ = 0.33, n.s.
Lower field vegetation %	11.5 ± 7.2	29.5 ± 12.6	44.0 ± 10.0	3.5 ± 1.7	$F_{3,41}$ = 2.10, n.s.
Upper field vegetation %	0 ± 0[a]	0 ± 0[a]	50.1 ± 11.3[A]	0 ± 0[a]	**$F_{3,41}$ = 6.71***
Canopy cover %	90.2 ± 0.8[A]	75.8 ± 3.0[a]	77.3 ± 2.4[a]	92.4 ± 0.8[A]	**$F_{3,41}$ = 9.85***

[A] is significantly greater than [a]

Table 3. Mean ± standard error of ground-dwelling spider species richness. Differences between forest types tested using GLMM: * < 0.05, ** < 0.01, *** < 0.001.

	Lodgepole pine	Norway spruce	Scots pine	Sitka spruce	GLMM
All species	7.9 ± 1.1^{a}	15.8 ± 1.1^{A}	14.5 ± 0.6^{A}	12.4 ± 1.2	$F_{3,41} = 5.64^{*}$
Forest specialists	4.2 ± 0.4^{a}	8.2 ± 0.6^{AB}	6.4 ± 0.5^{A}	5.7 ± 0.4^{b}	$F_{3,41} = 7.43^{**}$
Open specialists	0 ± 0^{a}	0.2 ± 0.1^{a}	0.7 ± 0.2^{A}	0.2 ± 0.1^{a}	$F_{3,41} = 3.11^{*}$
Web-spinning spiders	7.8 ± 1.0^{a}	15.3 ± 1.0^{A}	13.0 ± 0.4^{A}	11.9 ± 1.2	$F_{3,41} = 5.06^{*}$
Cursorial spiders	0.1 ± 0.1^{a}	0.4 ± 0.2^{a}	1.5 ± 0.3^{A}	0.5 ± 0.2^{a}	$F_{3,41} = 3.27^{*}$

^{A} is significantly greater than ^{a}, ^{B} is significantly greater than ^{b}

Differences in species composition between conifer types

Indicator species analysis did not identify any species with an affinity for lodgepole pine forests. Scots pine had the highest number of associated species, which included four habitat generalists, two forest specialists and two open specialists (Table 4). Five habitat generalist species had an affinity with Sitka spruce and one habitat generalist species was associated with Norway spruce.

MRT split the spider species composition into three terminal nodes (Figure 2), explaining 27% of the variation in species assemblage (1 – Error * 100) and having 17% predictability (1 – CV Error * 100). The nodes first separated Norway spruce forests from lodgepole pine, Scots pine and Sitka spruce forests and then separated Scots pine forests from the lodgepole pine/ Sitka spruce forest group.

Partial RDA of the selected environmental variables produced a significant model ($F_{7,36}$ = 3.49, P = 0.001) which explained 21% of the variation in species composition. The covariable latitude explained a further 2% of the variation ($F_{1,50}$ = 2.03, P = 0.03). Seven axes were recommended for plotting the partial RDA and the first two axes which represent 12% of the variation are presented in Figure 3. Forest type explained 13% of the variation in species composition ($F_{3,36}$ = 5.02, P = < 0.001) and showed that Scots pine, Norway spruce and Sitka spruce formed separate, although slightly overlapping, clusters and lodgepole pine plots were spread across Norway spruce and Sitka spruce plots. The vegetation layers also explained some of the variation in species composition; 2% was explained by upper field layer vegetation cover ($F_{1,36}$ = 2.79, P = 0.002), 2% was explained by ground vegetation ($F_{1,36}$ = 2.51, P = 0.002) and 2% was explained by lower field layer vegetation cover ($F_{1,36}$ = 2.09, P = 0.02). Organic carbon content also explained 2% of the variation in species composition ($F_{1,36}$ = 2.00, P = 0.03).

Table 4. Indicator values and habitat association of spider species with a high affinity for the forest types investigated. Significance tested by Monte Carlo test: * < 0.05, ** < 0.01, ** < 0.01, *** < 0.001.

Species	Family	Lodgepole pine	Norway spruce	Scots pine	Sitka spruce	Habitat association
Gongylidiellum vivum	Linyphiidae	1	**46*** **	0	1	Habitat generalist
Bathyphantes nigrinus	Linyphiidae	0	0	**20***	0	Habitat generalist
Dismodicus bifrons	Linyphiidae	1	1	**67*** **	0	Habitat generalist
Gonatium rubellum	Linyphiidae	0	0	**60*** **	0	Forest-associated
Maso sundevalli	Linyphiidae	0	0	**30****	0	Habitat generalist
Pardosa saltans	Lycosidae	0	0	**50*** **	0	Forest-associated
Pardosa pullata	Lycosidae	0	0	**40****	0	Open-associated
Pocadicnemis juncea	Linyphiidae	0	0	**30****	0	Open-associated
Pocadicnemis pumila	Linyphiidae	0	0	**50*** **	0	Habitat generalist
Walckenaeria vigilax	Linyphiidae	0	0	**40****	0	Habitat generalist
Bathyphantes gracilis	Linyphiidae	1	1	0	**33****	Habitat generalist
Palliduphantes ericaeus	Linyphiidae	1	7	0	**25***	Habitat generalist
Pirata uliginosus	Linyphiidae	0	0	0	**42****	Habitat generalist
Porrhomma montanum	Linyphiidae	0	0	0	**33***	Habitat generalist
Tenuiphantes tenuis	Linyphiidae	0	0	9	**35***	Habitat generalist

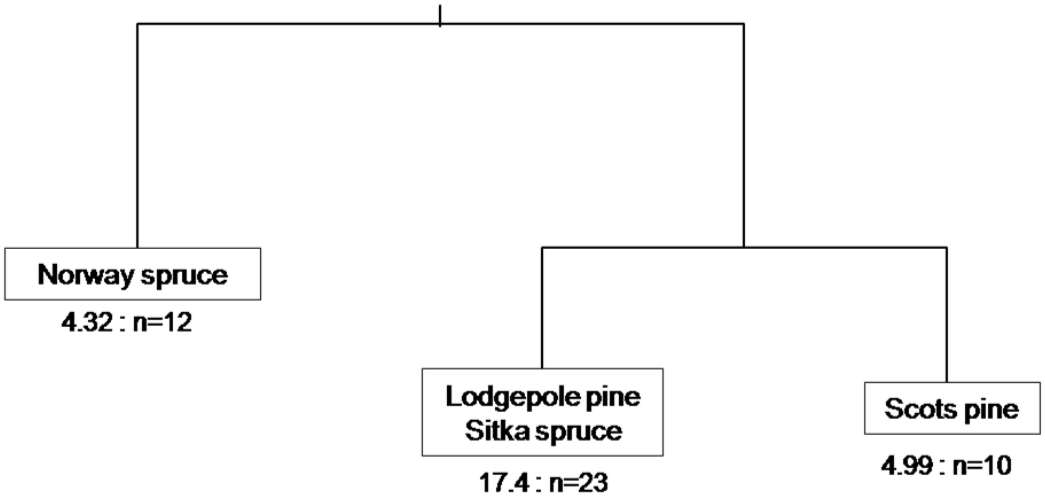


Figure 2. MRT of ground-dwelling spider species composition grouped by forest type. Error = 0.729, cross-validation error = 0.828 and standard error = 0.093.

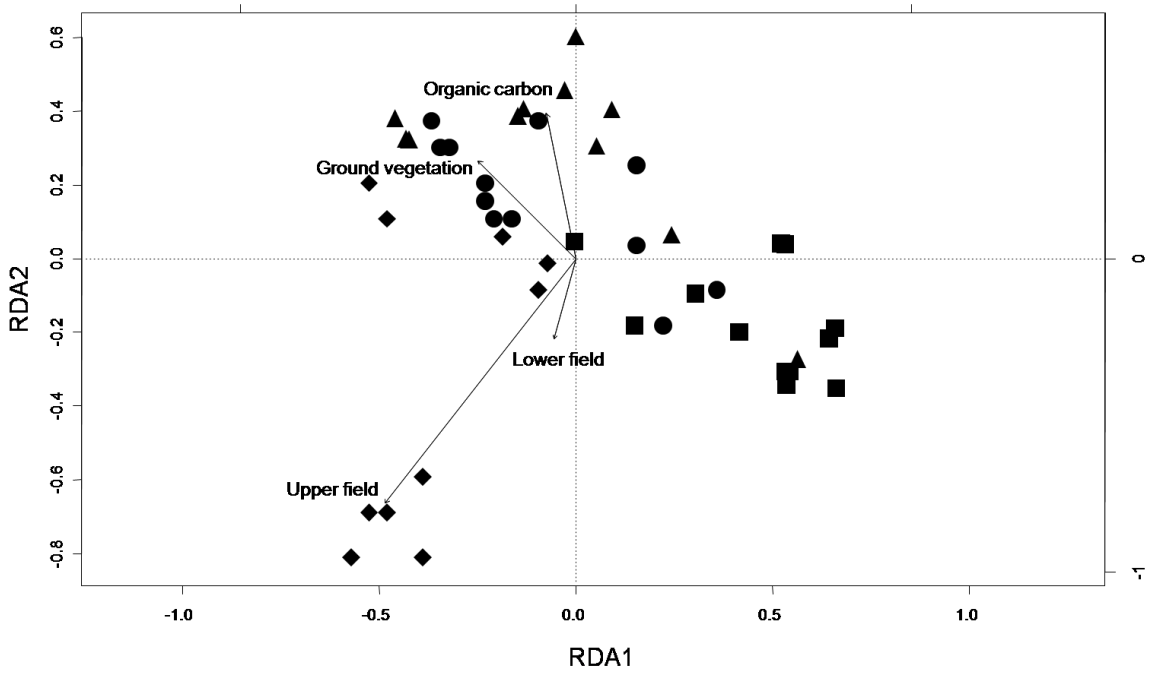


Figure 3. Partial RDA of ground-dwelling spider species composition. Axis 1: $R^2 = 0.08$, $F_{1,36} = 9.18$, P = 0.0002. Axis 2: $R^2 = 0.04$, $F_{1,36} = 4.25$, P = 0.0002. Lodgepole pine (▲), Norway spruce (■), Scots pine (◆), Sitka spruce (●).

Discussion

Total spider species richness was similar between Scots pine, Norway spruce and Sitka spruce forests. However, total species richness alone does not account for the importance of diversity among functional groups. Species of the same functional group, for example feeding guild, perform the same ecological function and in order to increase overall biodiversity and stable ecosystem functioning representatives of many different functional groups are required (Tilman *et al.*, 1997; Hooper *et al.*, 2002). Therefore the species richness of sub-groups of feeding guilds and species with particular habitat associations were also examined. These results revealed that Scots pine, Norway spruce and Sitka spruce forests also support similar levels of web-spinning spider species richness. Web-spinning Linyphiids were the dominant family in all forests in this study and are commonly the most abundant and speciose family in mature coniferous forests (Stratton *et al.*, 1978; Docherty and Leather, 1997; Oxbrough *et al.*, 2005). However, forest specialist species richness was significantly higher in Norway spruce forests compared with Sitka spruce forests, and this difference was driven by differences in the number of Linyphiid species. The species richness of total, web-spinning and forest specialist spiders was lowest in lodgepole pine forests compared with Scots pine and Norway spruce forests, but Sitka spruce forests supported similar species richness of these groups.

Scots pine forests also had the highest species richness of open specialist and cursorial spiders compared with the other forest types. Shade tolerant and forest specialist spider species are adapted to the shade created by canopy cover but open specialists and many cursorial species are negatively affected by this, which can reduce overall spider diversity in forests (McIver *et al.*, 1992). Additionally, many open specialist and cursorial spider species hunt prey associated with shrubs and tall herbaceous vegetation, which were present only in the Scots pine sites, whereas most ground-active forest specialist spiders hunt in the litter layer (McIver *et al.*, 1992; Wise, 1993). Scots pine forests had a greater cover of upper field vegetation compared with all three of the other conifer types due to the presence of bilberry (*Vaccinium myrtillus)*, bramble (*Rubus fruticosa*) and ferns (*Dryopteris dilatata* and *Pteridium aquilinum*). This was probably due to increased light availability from the more open canopy which benefits plant diversity in forests (Thomas *et al.*, 1999; Ferris *et al.*, 2000a). Therefore the more open canopy and presence of upper field layer vegetation in Scots pine forests is likely to benefit open specialist and cursorial spider species. Although Norway spruce forests had similar canopy openness to Scots pine, the cover of lower field

and upper field vegetation was not significantly higher compared to Sitka spruce and lodgepole pine forests. Therefore, other environmental factors not measured here may be affecting the vegetation layers in Norway spruce forests.

The structural variation in a habitat influences spider species richness and composition, and increased cover and structural heterogeneity of vegetation benefits spider diversity by providing web-attachment points, prey abundance, and shelter from inter and intra-specific predators (Larcher and Wise, 1985; Uetz, 1991; McIver *et al.*, 1992; Wise, 1993; Dennis *et al.*, 1998; Oxbrough *et al.*, 2005). Previous research has also indicated that Scots pine forests support greater spider diversity than lodgepole pine forests, which was related to the more closed canopy conditions and therefore depauperate vegetation in lodgepole pine forests (Docherty and Leather, 1997). Species richness is the most common and universally employed measure of diversity (Magurran, 2004). Therefore, in terms of species richness, Scots pine and Norway spruce forests had the greatest diversity value for ground-dwelling spiders, Sitka spruce forests had an intermediate level of diversity value, and lodgepole pine forests had the lowest diversity value.

Lodgepole pine, Norway spruce and Sitka spruce forests were not favoured by any spider species with forest or open habitat associations. Several habitat generalist species were associated with Norway spruce and Sitka spruce forests, however, these generalist species can utilise many habitat types and are less important when considering the value of a habitat for species diversity. The species with a high affinity for Scots pine forests represented a range of families and feeding guilds, which are associated with a number of different microhabitats. *Gonatium rubellum* and *Pocadicnemis juncea* are sheet web-spinners from the Linyphiidae family and both species are found in litter and low vegetation; however the former is forest-associated whereas the latter is associated with a variety of open habitats (Nolan, 2008). *Pardosa saltans* and *Pardosa pullata* are both active hunters from the Lycosidae family, *P. saltans* is found amongst woodland litter whereas *P. pullata* is a more generalist open species found in low vegetation in open grassland and heathland habitats, as well as at forest edges and in clearings (Nolan, 2008). The prevalence of *P. saltans* in the Scots pine forests is particularly interesting as this species is associated with old broadleaf woodlands, and suggests that Scots pine forests may provide old-growth and broadleaf characteristics associated with higher levels of biodiversity (Peterken *et al.*, 1992; Harvey *et al.*, 2002; Nolan, 2008). In Britain, *G. rubellum* is also associated with old woodlands,

although in Ireland this species is found in a variety of forest types (Harvey *et al.*, 2002; Nolan, 2008).

The diversity of spider species associated with Scots pine forests indicates that they may provide a greater number of suitable microhabitats for a variety of species and functional groups compared with the other conifer plantation types. A number of other studies have also shown that Scots pine forests support a natural and diverse fauna and flora. Longhorn beetles (Coleoptera: Cerambycidae), sawflies (Diptera: Symphyta) and hoverflies (Diptera: Syrphidae) show a small but significant difference in species associated with Scots pine compared with other introduced conifers in Ireland (Speight, 1985). A study of the vegetation communities supported by Scots pine forest habitat concluded that they exhibit a semi-natural character and a wide diversity of native plant species (Roche *et al.*, 2009). This phenomenon seems also to hold true for higher trophic groups and a study of the native red squirrel (*Sciurus vulgaris)* in Ireland found that it thrives in conifer plantations which contain a large proportion of Pinus species (Lurz *et al*., 1995).

Scots pine is considered a semi-native species, and Norway spruce was introduced into Ireland 400 years before Sitka spruce and lodgepole pine. It is therefore possible that, due to their European provenance and being present in Ireland for a longer period of time, these ground-dwelling spiders may be more adapted to the forest conditions of Scots pine and Norway spruce forests, than the two more recently introduced North American conifer species (Kennedy and Southwood, 1984; Evans and Jukes, 2008).

Scots pine forests in Scotland surveyed by Docherty and Leather (1997) shared 16 out of the 50 identified spider species with the Scots pine forests used in this study, all of which were common forest species such as *Tenuiphantes tenuis*, *Tenuiphantes zimmermanni* and *Monocephalus fuscipes*. Therefore, although Scots pine forests may support a more diverse spider species assemblage they may also have a lack of associated specialist spider fauna. To the authors knowledge there are no published research on ground-dwelling spider diversity in Norway spruce forests in introduced situations. However, a study in Germany, where it is a native tree species, found a similar number of species, but a greater range of families, than this study (Huber *et al.*, 2007). This study also shared only nine species with the list recorded by Huber *et al.* (2007), which is, in part, likely due to the differences in geographical distributions of spider species. However, two of the dominant species, *Tapinocyba pallens* and *Agyneta ramosa*, were also present in the forests studied here, but

in very low abundance. The lack of specialist species in Scots pine and Norway spruce forests in Ireland may reflect the lack of a developed conifer specialist fauna in Ireland, which could be a result of the low number of native conifer tree species and the long history of deforestation.

These differences in species richness indicate that Scots pine and Norway spruce may be the two most naturalized and highest diversity value conifer species used for forestry in Ireland, compared with the two North American species. However, the semi-native Scots pine and introduced European Norway spruce forests exhibited distinct species compositions from each other and from the North American lodgepole pine/ Sitka spruce group. Previous research has found that tree species has a profound effect on spider assemblages, although stands with similar levels of vegetation cover and canopy openness also affect species composition regardless of the tree species cover (Ziesche and Roth, 2008). However, it seems that in this study the tree species is the most important factor acting on spider species composition, despite the similarities of canopy openness and greater cover of lower field vegetation in Scots pine and Norway spruce forests, compared with Sitka spruce and lodgepole pine forests. Macro-fungal, carabid beetle and canopy Coleoptera communities have also shown distinct differences in species composition between Scots pine and Norway spruce forests in England (Ferris *et al.*, 2000b; Jukes and Peace, 2003). Furthermore, the two spruce forest types, Sitka spruce and Norway spruce, also exhibited distinct species compositions (Jukes and Peace, 2003). In terms of carabid beetles these differences were attributed to the dry open habitat of pine and the moist shady habitat of spruce favouring different species.

Differences in the cover of vegetation layers and organic content also affected species composition across plots, rather than between the *a priori* designated forest types. The ground vegetation in these forests mainly consisted of bryophyte species, which commonly occurs in conifer plantation forests where vegetation is shaded out after canopy closure (Hill, 1979). As a result forest-dwelling spiders are commonly found among this vegetation layer (Harvey *et al.*, 2002; Nolan, 2008) and are likely to be affected by differences in cover. Collembola comprise a large proportion of the diet of forest ground-dwelling spiders and are known to be more concentrated in areas with high organic content, which can influence patterns of spider species composition and abundance in forests (Clarke and Grant, 1968; Petersen and Luxton, 1982; Chen and Wise, 1999; Lawrence and Wise, 2000; Eaton *et al.*, 2004). The cover of lower and upper field vegetation also affected species

composition, although the upper field vegetation layer was only present in the Scots pine stands. Therefore these results indicate that appropriate management of the habitat to increase vegetation cover and structural diversity could benefit ground-dwelling spider diversity and composition in low diversity forest types, such as lodgepole pine.

Conclusions and implications for forest management

Both species richness and functional trait diversity of spiders are important when considering the biodiversity value of forest habitats. Scots pine forests provide a greater number of microhabitat niches, supporting a variety of spider species that fulfil different ecological functions. Plantation forests of another European tree species, Norway spruce, also supported a diverse range of forest spider species; whereas the two most commonly used North American conifer tree species supported the lowest ground-dwelling spider diversity. The use of native or semi-native tree species or species of European provenance in plantation forests could enhance ground-dwelling spider diversity.

Scots pine requires a longer rotation length before reaching commercial maturity and more specialised soil and climate conditions making it a less favourable forestry species in Ireland (Anon, 2012). However, the habitat changes that occur as a result of this longer rotation are probably also the reason for Scots pine's higher diversity value (Lust *et al.*, 1998). Increasing canopy openness and promoting the growth of ground vegetation by either managing forests to mimic these changes or allowing them to naturally succeed will improve their diversity value for spiders. These results have implications for forest policy and clearly demonstrate that longer rotation lengths will benefit ground-dwelling spider diversity in conifer production forests (Peterken *et al.*, 1992; Quine and Humphrey, 2003).

While trade-offs between timber yield and biodiversity are inevitable, the findings of the present study in the context of current interest in using a mix of tree species in plantation forests, suggests that Scots pine might be beneficial as a secondary species in a mix (Lust *et al.*, 1998) due to the advantages it confers on forest biodiversity value. However, this would require further research to determine the proportions and planting patterns which would provide the optimum benefits to biodiversity.

References

Anon, 2000. Code of best forest practice. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2007. National Forest Inventory: Republic of Ireland Results. Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2012. Scots pine (*Pinus sylvestris*). Department of Agriculture, Food and the Marine, Government of Ireland.

Anon, 2013. Norway spruce. Department of Agriculture, Food and the Marine, Government of Ireland.

Bates, D., Maechler, M., Bolker, B., 2012. Package 'lme4'. Linear mixed-effects models using S4 classes. R version 0.999999-2.

Berndt, L., Brockerhoff, E., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodiversity & Conservation 17, 1171-1185.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89, 2623-2632.

Bradshaw, R.H.W., Browne, P., 1987. Changing Patterns in the Post-Glacial Distribution of Pinus sylvestris in Ireland. Journal of Biogeography 14, 237-248.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity & Conservation 17, 925-951.

Carey, M.L., Hendrick, E., 1986. Lodgepole pine in the Republic of Ireland I. Site types, ground preparation and nutrition. Forest Ecology and Management 15, 301-317.

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. Journal of Forestry 104, 65-77.

Chen, B., Wise, D.H., 1999. Bottom-Up Limitation of Predaceous Arthropods in a Detritus-Based Terrestrial Food Web. Ecology 80, 761-772.

Churchfield, S., Hollier, J., Brown, V.K., 1991. The Effects of Small Mammal Predators on Grassland Invertebrates, Investigated by Field Exclosure Experiment. Oikos 60, 283-290.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

Cross, J.R., 1998. An outline and map of the potential natural vegetation of Ireland. Applied Vegetation Science 1, 241-252.

De'ath, G., 2002. Multivariate Regression Trees: A New Technique for Modeling Species-Environment Relationships. Ecology 83, 1105-1117.

Dennis, P., Young, M., Gordon, I., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23, 253–264.

Docherty, M., Leather, S., 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. Forest Ecology and Management 95, 197-207.

Dray, S., Legendre, P., Blanchet, F.G., 2012. Packfor: Forward Selection with permutation (Canoco p.46). R version 0.0-8.

Dufrene, M., Legendre, P., 1997. Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. Ecological Monographs 67, 345-366.

Eaton, R.J., Barbercheck, M., Buford, M., Smith, W., 2004. Effects of organic matter removal, soil compaction, and vegetation control on Collembolan populations. Pedobiologia 48, 121-128.

European Commission, 2011. Forestry in the EU and the world — A statistical portrait. Publications Office of the European Union.

European Communities, 2003. Sustainable Forestry and the European Union. European Union, Belgium.

Evans, H.F., Jukes, M.R., 2008. The role of niche availability as a factor determining the diversity and abundance of invertebrates on Scots pine, *Pinus sylvestris*. Investigacion Agraria, Sistemas y Recursos Forestales: Fuera de Serie, 273-295.

Fahy, O., Gormally, M., 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. Forest Ecology and Management 110, 263-273.

Farrelly, N., Ní Dhubháin, A., Nieuwenhuis, M., Grant, J., 2009. The distribution and productivity of Sitka spruce (*Picea sitchensis*) in Ireland in relation to site, soil and climatic factors. Irish Forestry 64, 51-73.

Ferris, R., Peace, A.J., Humphrey, J.W., Broome, A.C., 2000a. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. Forest Ecology and Management 136, 35-51.

Ferris, R., Peace, A.J., Newton, A.C., 2000b. Macrofungal communities of lowland Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karsten.) plantations in England: relationships with site factors and stand structure. Forest Ecology and Management 131, 255-267.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Frazer, G., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University and the Institute of Ecosystem Studies, Millbrook, New York.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155, 81-95.

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Hill, M.O., 1979. The development of a flora in even-aged plantations. In: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.), The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, pp. 175-192.

Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchmann, N., Degrance, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., van Peer, L., 2002. Species diversity, functional diversity and ecosystem functioning. In: Inchausti, P., Loreau, M., Naeem, S. (Eds.), Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK, pp. 195-208.

Horgan, T., Keane, M., McCarthy, R., Lally, M., Thompson, D., 2003. A Guide to Forest Tree Species Selection and Silviculture in Ireland. COFORD, Dublin.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., 2013. Package 'multcomp'. R version 1.2-18.

Huber, C., Schulze, C., Baumgarten, M., 2007. The effect of femel- and small scale clear-cutting on ground dwelling spider communities in a Norway spruce forest in Southern Germany. Biodiversity & Conservation 16, 3653-3680.

Jukes, M., Peace, A., 2003. Invertebrate communities in plantation forests. In: Humphrey, J.W., Ferris, F., Quine, C.P. (Eds.), Biodiversity in Britain's Planted Forests. Forestry Commission, Edinburgh, pp. 1–118.

Kennedy, C.E.J., Southwood, T.R.E., 1984. The number of species of insects associated with British trees: a re-analysis. Journal of Animal Ecology 53, 455-478.

Larcher, S.F., Wise, D.H., 1985. Experimental Studies of the Interactions between a Web-Invading Spider and Two Host Species. Journal of Arachnology 13, 43-59.

Lawrence, K.L., Wise, D.H., 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44, 33-39.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Lindenmayer, D.B., Hobbs, R.J., 2004. Fauna conservation in Australian plantation forests – a review. Biological Conservation 119, 151-168.

Lurz, P.W.W., Garson, P.J., Rushton, S.P., 1995. The ecology of squirrels in spruce dominated plantations: implications for forest management. Forest Ecology and Management 79, 79-90.

Lust, N., Muys, B., Nachtergale, L., 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodiversity & Conservation 7, 249-260.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems & Environment 74, 229-273.

McCune, B., Mefford, M.J., 2011. PC ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.

McIver, J.D., Parsons, G.L., Moldenke, A.R., 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22, 984-992.

MCPFE, 1993. Second Ministerial Conference on the Protection of Forests in Europe. Helsinki, Finland.

Millenium Ecosystem Assessment, 2005. Ecosystems and human well-being: current state and trends. Findings of the condition and trends working group. Island Press, Washington.

Mitchell, F., 2006. Where Did Ireland's Trees Come From? Biology & Environment: Proceedings of the Royal Irish Academy 106, 251-259.

Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK., pp. 400-433.

Moulder, B., Reichle, D., 1972. Significance of Spider Predation in the Energy Dynamics of Forest-Floor Arthropod Communities. Ecological Monographs 42, 473-498.

Nelson, E.C., Walsh, W.F., 1993. Trees of Ireland: native and naturalized. The Lilliput Press, Dublin.

Niemelä, J., Haila, Y., Punttila, P., 1996. The Importance of Small-Scale Heterogeneity in Boreal Forests: Variation in Diversity in Forest-Floor Invertebrates across the Succession Gradient. Ecography 19, 352-368.

Nolan, M., 2008. Database of Irish Spiders (Araneae). Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin.

Norris, K.C., 1999. Quantifying Change Through Time in Spider Assemblages: Sampling Methods, Indices and Sources of Error. Journal of Insect Conservation 3, 309-325.

O'Halloran, J., Irwin, S., Kelly, D. L., Kelly, T. C., Mitchell, F. J. G., Coote, L., Oxbrough, A., Wilson, M. W., Martin, R. D., Moore, K., Sweeney, O., Dietzsch, A. C., Walsh, A., Keady, S., French, V., Fox, H., Kopke, K., Butler, F. and Neville, P. 2011 Management of biodiversity in a range of Irish forest types. Report prepared for the Department of Agriculture, Fisheries and Food, Government of Ireland.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Hendry, M., Stevens, H., Wagner, H., 2012. Vegan: Community Ecology Package. R version 2.0-7.

Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? Forest Ecology and Management 270, 11-18.

Oxbrough, A., Irwin, S., Kelly, T., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111–2121.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2007. Biodiversity of the ground-dwelling spider fauna of afforestation habitats. Agriculture, Ecosystems & Environment 120, 433-441.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Palik, B., Engstrom, R.T., 1999. Species composition. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, pp. 65-94.

Pawson, S.M., Brockerhoff, E.G., Meenken, E.D., Didham, R.K., 2008. Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodiversity & Conservation 17 1127-1148.

Peterken, G.F., Ausherman, D., Buchenau, M., Forman, R.T.T., 1992. Old-growth Conservation within British Upland Conifer Plantations. Forestry 65, 127-144.

Petersen, H., Luxton, M., 1982. A Comparative Analysis of Soil Fauna Populations and Their Role in Decomposition Processes. Oikos 39, 288-388.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2013. Package 'nlme'. R version 3.1-109.

Platnick, N.I., 2012. The World Spider Catalog, Version 13.0. The American Museum of Natural History.

Quine, C.P., Humphrey, J., 2003. The future management of plantation forests for biodiversity. In: Humphrey, J.W., Ferris, F., Quine, C.P. (Eds.), Biodiversity in Britain's Planted Forests. Forestry Commission, Edinburgh, pp. 1-118.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK.

Roche, J., Mitchell, F.G., Waldren, S., 2009. Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland. Biodiversity & Conservation 18, 2185-2203.

Speight, M.C.D., 1985. The Extinction of Indigenous *Pinus sylvestris* in Ireland: Relevant Faunal Data. The Irish Naturalists' Journal 21, 449-453.

Stratton, G.E., Uetz, G.W., Dillery, D.G., 1978. A Comparison of the Spiders of Three Coniferous Tree Species. Journal of Arachnology 6, 219-226.

ter Braak, C.J.F., 1994. Canonical community ordination. Part 1: Basic theory and linear methods. Ecoscience 1, 127-140.

Therneau, T.M., Atkinson, B., Ripley, B., Oksanen, J., De'Ath, G., 2013. Package 'mvpart'. R version 1.6-1.

Thomas, S.C., Halpern, C.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant Diversity in Managed Forests: Understory Responses to Thinning and Fertilization. Ecological Applications 9, 864-879.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277, 1300-1302.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

Uetz, G.W., 1975. Temporal and Spatial Variation in Species Diversity of Wandering Spiders (Araneae) in Deciduous Forest Litter. Environmental Entomology 4, 719-724.

Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild Structure of Spiders in Major Crops. Journal of Arachnology 27, 270-280.

United Nations Conference on Environment and Development, 1992. Agenda 21, the Rio Declaration on Environment and Development, the Statement of Forest Principles, the United Nations Framework Convention on Climate Change and the United Nations Convention on Biological Diversity. Rio de Janeiro.

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press.

Wise, D.H., 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48, 181-188.

Ziesche, T.M., Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? Forest Ecology and Management 255, 738-752.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, LLC, New York, USA.

Chapter 5

Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (*Quercus robur/ Q. petraea*) and Scots pine (*Pinus sylvestris*)

Authors: Nadia Barsoum, Lauren Fuller, Francis Ashwood, Katy Reed, Anne-Sophie Bonnet-Lebrun, Felix Leung



Oak plantation forest edge

A manuscript based on this chapter has been published in *Forest Ecology and Management.*

Abstract

A mixed tree species composition is frequently proposed as a way to increase habitat heterogeneity and support greater biodiversity in commercial forests. However, although international forest policy is increasingly advocating stands of mixed tree species, there is evidence to question the biodiversity benefits conferred by such forests. Using active ground-dwelling spiders and carabid beetles as biodiversity indicator taxa, we investigated the effect of forest stand composition on spider and carabid beetle community structure and composition. We conducted pitfall trapping in the summer of 2011 in 42 plantation forest stands across three different geographical regions in the UK and Ireland. Three common plantation forest stand types were examined: oak monocultures, Scots pine monocultures, and intimate Scots pine and oak mixtures (oak $\leq$ 40% cover). Forest stand type had a weak effect on spider and beetle species richness, with no significant differences in mixed stands compared with monocultures. There were few differences in species composition between the stand types in each region and indicator species analysis found few species specifically affiliated with any of the forest stand types. Land use history is hypothesised to have contributed, at least in part, to the observed important regional differences in spider and beetle assemblages. Our results do not support the perception that intimate mixtures of dominant tree species benefit biodiversity in plantation forest stands. Further research is required to determine the optimum percentages and planting patterns required for mixtures of canopy tree species in order to support forest biodiversity.

Introduction

European plantation forests are typically coniferous monocultures, which are generally considered to support limited forest biodiversity due to homogenous habitat provision (Peterken, 1993; Lust *et al.*, 1998; Dhôte, 2005; Fuller *et al*., 2008), and in some cases due to a non-native tree species composition (Forest Europe, 2011). By comparison, mixed species stands comprising two or more prominent canopy layer tree species are increasingly being considered to achieve a diversity of ecological, forest resilience and productivity goals (Koricheva *et al*., 2006; Cavard *et al*., 2011; Pérot and Picard, 2012). For example, oak combined with Scots pine is being revived as a recommended mixture in many regions including central France (Morneau *et al*., 2008), northern Spain (Del Rio and Sterba, 2009) and increasingly in Ireland where it has been specifically promoted in recent years in forestry grant schemes (Guest and Huss, 2012). Traditionally, Scots pine has been considered to act as a temporary nurse crop for oak, serving to protect young oaks from temperature extremes, wind exposure and competition from ground vegetation, whilst at the same time, helping to improve growth form (Brown, 1992; Kerr *et al*., 1992; Dannatt, 1996). Today, the mixture is gaining interest because of the wide distribution, but also the high ecological and socio-economic value of both tree species (Del Rio and Sterba, 2009). Oaks are known in particular, to support high associated species diversity (e.g. 423 phytophagous insect and mite species are associated with oak; in contrast, Scots pine supports 173 associated species; Kennedy & Southwood, 1984). United Kingdom, Irish and wider European forest policy specifically promotes the inclusion of broadleaf components for this added ecological value; e.g. the UK Forestry Standard Guidelines call for a minimum of 5% broadleaved trees or shrubs in conifer plantations (Forest Service, 2000; European Environment Agency, 2008; Forestry Commission, 2011).

Biological diversity has been demonstrated to increase with structural diversity, and therefore niche availability (Simpson, 1949; Lack, 1969; Kostylev, 2005). Tews *et al*. (2004) found in a meta-analysis of habitat heterogeneity and species richness, that the majority of studies reviewed (85%) showed a positive correlation between species richness and vegetation structural variables. The structural complexity of plant communities has, as a result, frequently been used as an indicator of diversity in other taxa (e.g. Winter and Möller, 2008 draw relationships between the complexity of mature tree microhabitats and saproxylic beetle species diversity). In forest plantations, increasing the number of tree species is thought to potentially increase the diversity of microhabitat types and related food

resources. The addition of native tree species is also hypothesised to modify physical conditions (soil and microclimate) and create microhabitats that bear a greater resemblance to semi-natural stands, thereby providing niches for specialist native flora and fauna (Benton, 2003; Tews *et al*., 2004; Brockerhoff *et al*., 2008; Fahrig *et al*., 2010; Oxbrough *et al*., 2012). However, there are few studies conducted in forest settings that confirm or refute these hypotheses. A small number of recent studies have demonstrated that mixed woods may not always possess higher species diversity than monocultures or support a greater array of forest generalist and specialist species (Cavard *et al*., 2011; Oxbrough *et al*., 2012).

In this study, we investigate the effects of stand composition on the abundance and richness of two taxa: ground-dwelling spiders and carabid beetles. Spiders are recognised as potentially useful indicators of forest management impacts as they are influenced by vegetation structure, have a broad geographic range and can be sampled and identified effectively (Uetz 1979, 1991; Oxbrough *et al*., 2005). Spiders are considered to be good bioindicators of changes within forest ecosystems caused by anthropogenic influences (Pearce and Venier, 2006; Malaque *et al*., 2008) and occupy a key role in forest food webs (Clarke and Grant, 1968; Gunnarsson, 1983; Wise, 2004). Carabid beetles are also often used in studies of forest invertebrate diversity as their taxonomy and ecology are well known and they can be efficiently collected using pitfall traps. Furthermore, they are potentially suitable bioindicators of invertebrate biodiversity as they are distributed over broad habitat and geographical ranges, are sensitive to environmental change and consist of both specialist and generalist species indicating the diversity of other arthropods (McGeoch, 1998; Cameron & Leather, 2012). Carabid beetles have been extensively studied within broadleaved and coniferous forests, with many studies indicating comparatively low carabid community diversity in coniferous plantations (Niemelä *et al*., 1992; Jukes *et al*., 2001; Magura *et al*., 2002; Fuller *et al*., 2008).

In our study, we compare ground-dwelling spider and carabid beetle species assemblages, and richness in mixed and monoculture stands in three geographically separate regions by combining comparable data that have been collected in the three regions using two separate sampling strategies. The following research hypothesis was addressed: plantation forest stands with mixed tree species composition support greater species richness and a different species composition of ground-dwelling spiders and carabid beetles compared with monocultures. Our study also asked the following questions: 1) are any observed effects of

forest tree species composition on spider and beetle assemblages consistent across regions and 2) do any species have a high affinity with specific forest stand types?

We measured a range of environmental parameters expected to potentially influence spider and carabid species composition in mixed and monoculture stands to investigate whether they differ significantly between forest stand types. We discuss the implications of our findings for forest management practice aimed at enhancing biodiversity in forest plantations.

Materials and methods

Study areas

We selected three forest stand types for study: oak (*Quercus robur / Q. petraea*) monocultures, Scots pine (*Pinus sylvestris*) monocultures and intimate Scots pine and oak (*Q. robur/ petraea*) mixtures. A total of 42 forest stands were selected, located in two forested regions of England (Thetford Forest, East Anglia $0^0$51' E; $52^0$27' N and the New Forest, Hampshire $1^0$38' W; $50^0$47' N) and across a wider area in central and eastern regions of the Republic of Ireland (Figure 1). In both Thetford Forest and the New Forest five $\geq$1.5ha homogenous stands within larger woodland blocks were selected from each of the three different forest stand types; in these two forest regions, the selected mixed stands always comprised at least 40% oak. In Ireland, four $\geq$5.5 ha stands of each of the three different forest stand types were also selected within larger woodland blocks. The four mixed stands comprised 10% (n=2), 15% (n=1), and 20% (n=1) oak. Forest stands were situated across similar altitudes in the New Forest (20-85 m a.s.l.) and Thetford Forest (10-40 m a.s.l.), but across a wider range in Ireland (57-234 m a.s.l.) (Table 1). All three regions of study have a temperate maritime climate; although the 30 year average for annual precipitation is lowest in the most easterly forest region (391-833 mm in Thetford Forest), intermediate in the New Forest region (455-1232 mm) and highest in the stands located in Ireland (750-1400mm) (Harris *et al*., 2012; Walsh, 2012). Edaphic conditions also differ in the three regions, with a patchy mixture of acidic and calcareous brown earths in Thetford Forest (pH in top 40cm ranging from 3 to 7), heavier surface-water gley and clay soils in the New Forest (pH in top 40cm ranging from 4 to 5) and brown earth and podzolic soils in Ireland (pH in top 10cm ranging from 3.5 to 5.5). The majority of the forest stands were planted between the 1930's and 1950's. In the case of Thetford Forest, planting was typically on areas of former heathland in an area that currently comprises plantations of

Scots pine, Corsican pine (*Pinus nigra* subsp. *laricio*) and smaller patches of oak and beech plantation (Randall and Dymond, 1996). The New Forest is a renowned area of ancient woodland pasture with diverse plantation types intermingled with ancient woodland dominated by oak or beech. The New Forest is actively used for grazing by cattle, horses and ponies (Grant and Edwards, 2008) (Table 1). *Q. robur/ petraea* is a native species of Ireland and Great Britain, while the native status of *P. sylvestris* is less certain. Pollen records indicate that Scots pine was once present and well established in all three regions of study, but disappeared from the landscape for long periods of time (>1000 years) (Randall and Dymond, 1996; Grant and Edwards, 2008; Roche *et al*., 2009).

Table 1. Summary characteristics of stands in the three study regions (NF=New Forest, TF= Thetford Forest, Eire=central and eastern Ireland) and three stand types (SP=Scots pine monoculture, SP/OK mix= Scots pine and oak mixtures, OK= oak monoculture). Land cover classes include conifer woodland (C), broadleaf woodland (B), conifer and broadleaf mixed woodland (C/B mix), undefined woodland (W) and non-wooded areas (Bare) that could in some cases be areas of heathland.

Forest stand	Site history		Current stand type	Planting year	Stand area (ha)	Altitude (m)	Soil type
	Landcover 1870's	Landcover 1905 - 1910					
Denny Lodge	C	C/B mix	SP	1930	3.94	20	Surface water gley
Burley (2512)	C/B mix	C/B mix	SP	1927	6.4	45	Surface water gley
Burley (2520a)	Bare	C/B mix	SP	1948	6.61	35	Surface water gley
Milkham (2135)	C	C	SP	1953	5.3	90	Surface water gley
Milkham (2136)	C	C	SP	1953	3.68	80	Surface water gley
Denny Wood	Bare	C/B mix	OK	1900	3.29	20	Surface water gley
Denny Lodge	C	C/B mix	OK	1928	2.66	20	Surface water gley
Ladycross	C/B mix	C/B mix	OK	1940	4.84	25	Surface water gley
Rhinefield	B	B	OK	1951	2.72	35	Brown earth
Holidays Hill	B	C/B mix	OK	1923	1.52	40	Brown earth
Parkhill (4311a)	C	C/B mix	SP/OK mix	1950	12.05	40	Surface water gley
Parkhill (4309b)	C	C/B mix	SP/OK mix	1952	5.5	30	Surface water gley
Wootton Coppice	C/B mix	C/B mix	SP/OK mix	1930	5.46	35	Surface water gley
Burley	C/B mix	C/B mix	SP/OK mix	1929	3.55	35	Surface water gley
Bramshaw	B	C/B mix	SP/OK mix	1936	5.29	85	Surface water gley
Scotch Plantation	Bare	Bare	SP	1937	7.13	35	Calcareous brown earth
Hockham (3345)	Bare	Bare	SP	1932	5.17	40	Brown earth
West Harling (4751)	C/B mix	C/B mix	SP	1967	3.61	30	Brown earth

Roundham Heath	Bare	Bare	SP	1956	1.61	30	Typical podzol
Big Wood	Bare	Bare	SP	1930	1.73	30	Brown earth
West Harling (4714a)	Bare	Bare	OK	1934	4.87	25	Calcareous brown earth
Bridgham (3548b)	Bare	Bare	OK	1934	2.41	35	Brown earth
West Harling (4722)	Bare	Bare	OK	1933	2.91	20	Brown earth
Hockham (3335)	Bare	Bare	OK	1932	6.75	40	Brown earth
Didlington	Bare	Bare	OK	1954	4.73	10	Loamy texture
West Harling (4716a)	C/B mix	C/B mix	SP/OK mix	1934	5.15	20	Calcareous brown earth
Bridgham (3548a)	Bare	Bare	SP/OK mix	1934	4.46	30	Brown earth
Hockham (3324a)	Bare	Bare	SP/OK mix	1935	5.21	40	Ground water gley
Mundford (3021a)	C/B mix	C/B mix	SP/OK mix	1941	4.85	25	Brown earth
Mundford (3009b)	C/B mix	C/B mix	SP/OK mix	1932	3.38	15	Brown earth
Ballydrehid	-	Bare	SP	1946	29.1	163	Podzol
Ballard	-	Bare	SP	1946	15.1	139	Brown earth
Durrow Abbey	-	Bare	SP	1949	12.5	57	Gley
Killeagh	-	Bare	SP	1948	19.8	147	Brown podzolic
Bansha West	-	W	OK	1939	12	122	Brown earth
Demesne (Donadea)	-	Bare	OK	1938	8.6	88	Brown earth
Grangemockler	-	W	OK	1936	6.2	155	Brown podzolic
Jenkinstown	-	W	OK	1860	7.2	82	Brown earth
Ballymanus	-	W	SP/OK mix	1932	5.5	234	Brown podzolic
Brittas	-	W	SP/OK mix	1940	8.8	131	Brown earth
Carrick	-	W	SP/OK mix	1946	9.8	166	Podzol
Kilshane	-	W	SP/OK mix	1940	13.3	192	Podzol

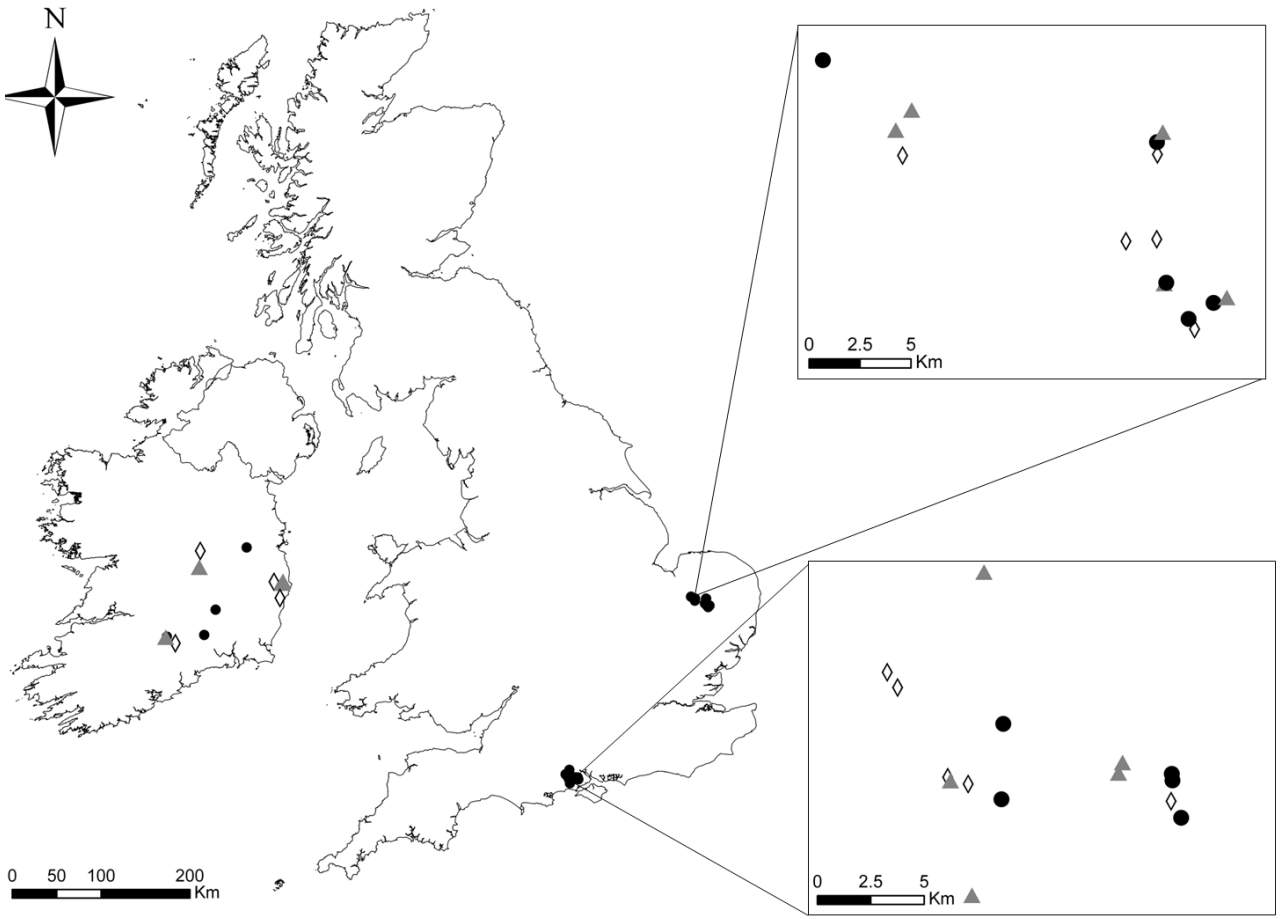


Figure 1. Locations of the stands in each of the three regions studied. Oak monoculture stands (●), Scots pine monoculture stands (◊), Scots pine and oak mixed stands (▲).

Arthropod sampling

We used pitfall traps to sample active ground-dwelling spider and carabid beetle fauna. Pitfall traps were installed using a soil auger to create a well-defined hole of 7-8cm diameter with minimum disturbance to the surrounding area. Plastic cups were inserted into these holes to a depth of 9-11cm. Care was taken to ensure that the rims of each of the pitfall traps were level with the ground and that there were no gaps along the sides of the trap into which invertebrates could fall. About 2-3 cm of 50-70% diluted ethandiol (blue antifreeze) was poured into the cups as a temporary preservative. Drainage holes at the top of plastic cups allowed water to escape and prevent flooding of the traps. Forestry Commission and University College Cork staff collected the contents of each pitfall trap every 2-3 weeks from May to August 2011, totalling 84-90 trapping days. Non-identical pitfall sampling designs were adopted between the UK and Irish sites, as described in further detail below.

Pitfall trapping - English stands

A single pitfall trap was installed within eight 10m x 10m sampling plots per forest stand. These eight sampling plots were arranged equidistantly around the perimeter of a 50m x 50m quadrat positioned within the centre of each stand. Sampling plots were always at least 25m from the forest stand edge and 15m apart from one another. To account for microhabitat heterogeneity, within each of the eight 10m x 10m sampling plots a single pitfall trap was installed in one of two microhabitat types; either the open forest floor, or at the base of a tree. At the four open forest floor microhabitat locations, pitfall traps were located in the open spaces between trees, avoiding stumps, piles of deadwood, and areas of dense vegetation or disturbance. The four pitfall traps that were located at tree bases were always positioned on the north-facing side of a Scots pine or oak tree and as close as possible to the base of the tree. In the forest stands comprising mixtures of Scots pine and oak, two of the pitfall traps installed at tree base microhabitats were positioned at the base of oak trees and two were positioned at the base of Scots pine trees. Each trap was covered by a 19cm x 19cm square steel lid that was positioned 3cm above the ground. Lids each had 15cm-wide entrance holes at all four corners which were kept clear of leaf litter and any other debris.

Pitfall trapping - Irish stands

Three sampling transects were used per forest stand, each consisting of five pitfall traps set 2m apart in a linear arrangement of 10m total length. Transects were established a minimum of 50m apart and a minimum of 50m from the edge of the forest and any large areas of open space. Sampling of different microhabitat types was not included as a feature of the Irish arthropod sampling procedure. A lid was only placed on traps vulnerable to disturbance from animals.

Species identification

Adult ground-dwelling spiders and carabid beetles were identified to species level due to the difficulties of identifying juveniles. Spiders were identified using Roberts (1993) following the nomenclature of Platnick (2012), and habitat specialists designated based on Nolan (2008) and Harvey *et al*. (2002). Carabid identification was conducted using the key of Luff (2007); with habitat preference determined using Jukes *et al*. (2001), Luff (2007) and Thiele (1977).

Environmental parameters

In all of the forest stands a range of environmental parameters were assessed in 10m x 10m sampling plots. In England, eight 10m x10m sampling plots were positioned around each of the eight pitfall traps and in Ireland, three 10m x 10m sampling plots were positioned adjacent to each of the three pitfalls plots. The volume of coarse woody debris (CWD) $\geq$10cm at it widest point, was assessed in each 10m x 10m sampling plot. The CWD considered included: (i) logs and large branches ($\geq$45 degree departure from vertical), (ii) snags (<45 degrees departure from vertical, $\geq$1m tall) and stumps (<1m tall). Measurements used to estimate volume for each of the categories of CWD included the length and diameter at the centre for logs and large branches, the height and diameter at breast height (DBH) (1.3m) for snags, and the height, top diameter and bottom diameter for stumps. The percentage cover of vegetation in three distinct vertical layers was assessed in each 10m x 10m sampling plot. These layers included (1) an understory layer: woody vegetation with a height of between 2m and 5m, (2) a shrub layer: Woody vegetation <2m tall, including brambles and climbing plants and (3) a herb layer: Vascular herbs, including graminoids, grasses, rushes, sedges and ferns but excluding climbing plants, bramble and woody species. The percentage cover of litter and bare ground were additionally measured within each of

the 2m x 2m quadrats in the English stands. Canopy openness was measured at the four corners of each of the 10m x 10m sampling plots using a canopy scope (Brown *et al*., 2000). Soil pH was estimated by collecting soil samples to a depth of 10cm (litter and fermentation layers excluded) from the four corners of each of the 10m x 10m sampling plots. These samples were pooled at the stand level. 5g of soil was diluted in 20mL of distilled water and pH was measured using a Metrohm Titrino pH probe with an autosampler.

Statistical analysis

Data from each region (New Forest, Thetford Forest, and Ireland) were analysed separately. For all analyses, data were pooled across collection periods and forest stands. Data from four missing pitfall traps in Thetford and one in the New Forest were replaced with trap averages.

To test our hypothesis that mixed plantation stands support a greater richness of ground-dwelling spiders and carabids than monocultures, we analysed the effect of stand type on the species richness of all species, habitat generalist species, forest specialist species, and open specialist species with Kruskal-Wallis rank sum tests. We followed significant Kruskal-Wallis tests with post-hoc tests of individual factor levels using Wilcoxon pairwise rank sum tests with Bonferroni corrected p-values for multiple comparisons.

Species composition was examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), to determine if there were any differences in the species composition of ground-dwelling spiders and carabid beetles between each stand type in each region. Species data were Hellinger transformed prior to analysis (Legendre and Gallagher, 2001) and 4999 permutations were used. Latitude can affect species composition (Oxbrough *et al*., 2012); therefore this was used as a control covariate in the analysis where it was found to have an effect. Where stand type was found to have an effect, post-hoc pairwise comparisons were conducted with Bonferroni corrected p-values for multiple comparisons.

We carried out indicator species analysis to identify species that have a high affinity for the different stand types. This analysis assesses the relative abundance and relative frequency of a species across groups; in this case, stand type. The analysis assigns each species an indicator value in the form of a percentage to indicate in which group or groups they are most abundantly and frequently found. A Monte Carlo test of statistical significance follows

(Dufrene & Legendre, 1997). We ran the analysis using the 'indicspecies' package of R, with 4999 permutations (De Caceres & Legendre, 2009). Because the number of significant species was low when the probability was set to <.05, and because we were interested in broad trends in species composition, we chose to report species significant at probability <0.1.

We calculated the stand level average for each environmental variable from the plots and carried out the same Kruskal-Wallis testing procedure as described above.

We carried out all analyses in R 2.15.2 (R Core Team, 2012).

Results

Ground-dwelling spiders

Patterns in species abundance and richness

During the sampling period, the total number of individual ground-dwelling spiders trapped in the New Forest, Thetford Forest and Ireland was 2,279, 3,418 and 2,463, respectively. In the same order by region, these comprised a total of 81, 86 and 81 spider species (Appendix 2). Of these species, in the New Forest, forest specialists constituted less than half (44%) of all spiders captured, while in Thetford Forest there were fewer, at only 27% of all identified spiders. Forest specialist spiders dominated the Irish forest stands, comprising 70% of all spiders captured. Habitat generalist ground-dwelling spiders constituted most of the remaining fraction of spiders in each region, with very few open habitat specialist species occurring in any of the regions (i.e. 4%, 1% and 1% of all spiders in the New Forest, Thetford Forest and Irish stands, respectively).

In the New Forest, Kruskal-Wallis tests showed that there was no significant effect of stand type on the species richness of spiders. In Thetford Forest, however, species richness in Scots pine monocultures was 46% greater than in oak monocultures and 26% greater than in mixed stands. Kruskal-Wallis tests confirmed a positive influence of Scots pine monocultures on species richness of all ground-dwelling spider species compared with mixed stands or oak monocultures (X2 (2) = 9.05, P = 0.01) (Table 2). Habitat generalist spider species richness was similarly affected by stand type (X^2 (2) = 8.86, P = 0.01) in Thetford Forest, although the Mann-Whitney post-hoc test showed only a marginally significant increase in species richness in Scots pine compared with mixed stands (P =

0.06). Stand type also affected forest specialist spiders in Thetford Forest (X^2 (2) = 7.98, P = 0.02), with a marginally higher species richness in Scots pine monocultures compared with mixed stands (P = 0.06). Kruskal-Wallis tests showed that stand type did not affect species richness in Ireland and this was when considering all species, habitat generalists only, or forest specialists only. However, stand type did affect open habitat specialists (X^2 (2) = 7.97, P = 0.02), with richness in Irish Scots pine monoculture stands marginally greater than in mixed or oak monocultures.

Species composition

There was no effect of stand type on the species composition of ground-dwelling spiders in the New Forest ($F_{2,12}$ = 1.42, P = 0.06) or in Ireland ($F_{2,9}$ = 1.21, P = 0.24). In Thetford Forest there was a significant effect of stand type on species composition ($F_{2,12}$ = 2.02, P = 0.004); pairwise comparisons revealed that species composition was significantly different between Scots pine monocultures and oak monocultures ($F_{1,8}$ = 3.54, P = 0.03), marginally different between Scots pine monocultures and mixed stands ($F_{1,8}$ = 1.88, P = 0.05), but did not differ between oak monocultures and mixed stands ($F_{1,8}$ = 0.84, P = 1.00).

Pirata hygrophilus, Pardosa saltans, Tenuiphantes flavipes and *Tenuiphantes zimmermanni,* and *Ozyptila trux* were the five most frequently caught species in the New Forest. *P. hygrophilus* and *O. trux* are habitat generalists, while the others are forest specialists. These species occurred in all stand types, although only 3 individuals of *O. trux* were caught in New Forest mixed stands. These five species comprised 73% of the New Forest total catch. Thetford Forest shared its three most frequently caught spiders, *P. hygrophilus, P. saltans*, and *T. flavipes* with the New Forest. *Microneta viaria* and *Macrargus rufus,* which are both forest specialists, were the fourth and fifth most trapped species. These five species were trapped in all stand types, and comprised 76% of the catch in Thetford Forest. The five most commonly caught species in the Irish stands were, in order of frequency of occurrence, *Tenuiphantes alacris, T. zimmermanni, Monocephalus fuscipes, Walckenaeria acuminata,* and *Tenuiphantes tenebricola*. With the exception of *W. acuminata,* these are forest specialists. These species occurred across all stand types, and constituted 57% of the total catch in Ireland.

Indicator species analysis

Thetford Forest had the highest number of significant indicator species. Two were affiliated with oak monocultures only, four with Scots pine monocultures only, three with both oak monocultures and mixed stands and one with both Scots pine monocultures and mixed stands (Table 3). The New Forest had the lowest number of significant indicator spider species; one was affiliated only with oak monocultures, another with both oak monocultures and mixed stands, and two with both Scots pine monocultures and mixed stands. In Ireland, three species were significantly associated only with Scots pine monocultures, and one with both oak monocultures and mixed stands. The forest specialist species *Diplocephalus picinus* and *Microneta viaria* were found to have the same forest stand type affiliations; they occurred frequently in oak and mixed stands but not in Scots pine stands, in both Ireland and Thetford Forest.

Table 2. Median ± interquartile range of ground-dwelling spider and carabid beetle species richness in oak monoculture, Scots pine monoculture, and Scots pine and oak mixture in each region. Differences between forest types within each region analysed using Kruskal-Wallis tests.

	New Forest			Thetford Forest			Ireland		
	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
Spiders									
All species	16 ± 6	21 ± 2	18 ± 18	22 ± 3[a]	32 ± 4[A]	20 ± 6[a]	25 ± 10	31 ± 3	31 ± 10
Habitat generalists	9 ± 1	13 ± 2	10 ± 9	12 ± 2	19 ± 2[A]	10 ± 5[a]	13 ± 8	17 ± 1	18 ± 9
Forest specialists	7 ± 2	7 ± 2	8 ± 2	10 ± 1	12 ± 2[A]	8 ± 1[a]	11 ± 2	11 ± 3	12 ± 2
Open specialists	1 ± 2	2 ± 0	1 ± 4	1 ± 1	3 ± 2	2 ± 1	1 ± 1[a]	3 ± 1[A]	1 ± 1[a]
Carabids									
All species	8 ± 2	4 ± 2	6 ± 4	16 ± 4[A]	9 ± 4[a]	14 ± 2	8 ± 7	9 ± 4	6 ± 4
Habitat generalists	6 ± 2	3 ± 1	5 ± 4	10 ± 2	7 ± 3	10 ± 3	5 ± 5	5 ± 3	4 ± 3
Forest specialists	1 ± 1	1 ± 0	1 ± 0	2 ± 0[A]	1 ± 1[a]	1 ± 0[a]	1 ± 0	2 ± 2	2 ± 1
Open specialists	0 ± 0	0 ± 0	0 ± 0	2 ± 2	1 ± 1	2 ± 2	3 ± 2	2 ± 2	0 ± 1

[A] is greater than [a]

Table 3. Indicator species analysis of ground-dwelling spiders and carabid beetles, showing the habitat preference of each species. Habitat preference is according to Thiele (1977), Jukes *et al*. (2001), Harvey *et al.*, (2002), Luff (2007) and Nolan (2008), and includes: G = generalists, F = forest habitat specialists, O = open habitat specialists. Indicator value is presented as a percentage and significance level indicated by .<0.1, *<0.05, **<0.01.

Species	Habitat preference	Oak	Scots pine	Mix
Spiders				
Agyneta subtilis [b]	G	-	100**	-
Centromerus dilutus [b]	G	-	89.	-
Clubiona pallidula [b]	G	77.	-	-
Diplocephalus latrifrons [b]	F	91.	-	-
Diplocephalus picinus [bc]	F	85[b]* 94[c]*	-	94[bc]*
Dismodicus bifrons [c]	G	-	95*	-
Gongylidiellum vivum [b]	G	-	77.	-
Macrargus rufus [a]	F	81.	-	81.
Microneta viaria [bc]	F	95[b]** 98[c]*	-	95[bc]**
Ozyptila trux [a]	G	92.	-	-
Palliduphantes ericaeus [b]	G	-	89*	-
Palliduphantes pallidus [b]	G	-	87.	87.
Pardosa pullata [c]	O	-	87.	-
Pocadicnemis pumila [c]	G	-	93.	-
Scotina celans [a]	F		84.	84.
Tenuiphantes cristatus [b]	G	92*	92*	-
Walckenaeria cucullata [a]	F	-	88*	88*
Carabids				
Leistus fulvibarbis [b]	F	89*	-	-
Nebria brevicollis [b]	G	93*	-	93*

[a] New Forest
[b] Thetford Forest
[c] Ireland

Carabid beetles

Patterns in species abundance and richness

During the sampling period a total of 4,059, 16,015 and 3,314 adult carabid beetles were identified in the New Forest, Thetford Forest and Ireland, respectively. In the same region order, these comprised a total of 21, 37 and 28 species, respectively (Appendix 3). Two stands in Thetford Forest (Bridgham 3548a+b) contributed disproportionately high numbers of one species, *P. madidus*, a habitat generalist that is commonly found in the UK. These two stands are near a pheasant rearing station and it is possible that factors associated with the presence of the birds may be boosting the *P. madidus* population. *P. madidus* is a commonly found habitat generalist species in the UK. This particularly high abundance of a single species did not influence our species richness or indicator species analyses.

Forest specialist carabid beetle species comprised a high percentage of all carabids caught in the New Forest stands (55%). By contrast, forest specialist beetle species were notably scarce in Thetford Forest stands, occurring in a proportion of only 0.46% of all carabid beetles caught. This proportion changed little (increasing to 3%) when the disproportionately high numbers of the habitat generalist species *Pterostichus madidus* at two Thetford Forest stands (Bridgham 3548a+b) were removed as a component of the overall regional beetle species composition. Forest specialist carabid beetle species also comprised a high percentage of all carabids caught in the Irish forest stands (49%). Habitat generalist beetle species made up most of the remaining proportion of beetle species identified in all regions. Open habitat specialists were rare in all regions, occurring in proportions of 1%, 0.4% and 3% of all carabid beetles in the New Forest, Thetford Forest and Irish stands, respectively.

The only region in which stand type significantly affected carabid species richness was Thetford Forest. Here total carabid species richness was highest in oak monocultures; that is, 35% higher than in mixtures and 40% higher than in Scots pine monocultures. Kruskal-Wallis tests showed oak monocultures supported significantly higher richness of all species compared with Scots pine monocultures (X^2 (2) = 7.53, P = 0.02), although the factor level effect was marginal (P = 0.06) (Table 2). Richness of forest specialist carabids in oak monocultures was higher than in Scots pine monocultures or mixtures (X^2 (2) = 7.94, P = 0.02), although the factor level effect was again marginal (P = 0.08 (oak > Scots pine), P = 0.06 (oak > mixed).

Species composition

There was no effect of stand type on the species composition of carabid beetles in the New Forest ($F_{2,12}$ = 1.37, P = 0.18), Thetford Forest ($F_{2,12}$ = 1.78, P = 0.08) or in Ireland ($F_{2,7}$ = 0.87, P = 0.53). However, the carabid community composition of Thetford Forest showed a strong regional separation from the New Forest and Irish carabid communities which shared many of the most commonly occurring carabid beetle species. The most commonly recovered beetle species in the New Forest was the forest specialist species *A. parallelipipedus*. Then in the following order, the habitat generalists *P. madidus* > *Pterostichus niger* > *Oxypselaphus obscurus* > *Pterostichus strenuus*. These five most frequently captured species made up 97% of the region's catch total. In Thetford Forest, the most commonly trapped beetles across all stand types, in order of abundance, were *P. madidus*> *Calathus rotundicollis* > *Pterostichus melanarius* > *Carabus problematicus* > *Carabus violaceus*. All of these species are habitat generalists and were caught in all stand types. These species comprised 95% of the catch in Thetford. The five most common carabid beetle species, in order of occurrence across all forest stand types in Ireland, were *A. parallelipipedus, P. madidus, P. niger, P. melanarius,* and *N. brevicollis*. The species were caught in all stand types, and comprised 90% of the total catch in the Irish stands.

Indicator species analysis

Thetford Forest was the only region in which indicator species analysis showed any carabid beetle species to have an affinity for one stand type over another (Table 3). The analysis associated one forest specialist (*Leistus fulvibarbis)* with oak monocultures, and one habitat generalist (*Nebria brevicollis*) with both oak and mixed stands.

Environmental parameters

There were no significant differences in the measured environmental variables between the three forest types across the regions (Table 4).

Table 4. Median ± interquartile range of environmental variables measured in oak monoculture, Scots pine monoculture, and Scots pine and oak mixture in each region.

	New Forest			Thetford Forest			Ireland		
	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
pH	4.4 ± 0.3	4.2 ± 0.3	4.4 ± 0.3	5.3 ± 2.2	3.8 ± 0.1	5.2 ± 1.8	4.6 ± 1.2	4.0 ± 0.2	3.9 ± 0.1
Canopy openness	5.6 ± 2.5	6.3 ± 3.1	2.5 ± 0.8	0.8 ± 0.2	2.0 ± 3.0	4.3 ± 2.0	2.9 ± 1.3	7.0 ± 4.8	2.6 ± 0.8
Coarse woody debris (m^2)	29.3 ± 39.7	7.4 ± 2.8	17.6 ± 20.0	12.7 ± 22.4	31.2 ± 46.1	26.8 ± 44.9	19.3 ± 21.5	10.0 ± 3.2	36.1 ± 10.1
Understory	4.4 ± 6.5	5.0 ± 8.8	11.3 ± 11.9	7.5 ± 3.8	3.1 ± 13.8	3.1 ± 3.1	37.5 ± 19.1	3.9 ± 19.3	49.2 ± 33.3
Shrub cover (%)	6.6 ± 6.3	8.8 ± 11.4	11.9 ± 6.9	2.1 ± 6.9	6.9 ± 35.6	5.6 ± 4.4	51.7 ± 17.9	24.7 ± 29.0	21.3 ± 30.5
Herb cover (%)	52.8 ± 22.8	35.3 ± 43.9	81.3 ± 36.9	79.4 ± 28.8	60.6 ± 18.1	72.5 ± 18.8	13.0 ± 10.3	49.2 ± 34.1	56.3 ± 12.2
Litter cover (%)	44.6 ± 9.0	52.8 ± 46.3	29.8 ± 24.0	35.6 ± 11.4	36.3 ± 8.8	31.3 ± 18.9	95.0 ± 2.9	68.5 ± 11.7	92.4 ± 15.2
Bare soil	0.4 ± 2.1	0.3 ± 0.6	0.6 ± 1.6	0 ± 0.3	0 ± 0	0.1 ± 0.6	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.7

Discussion

The forest stand types considered in this study (oak monocultures, Scots pine monocultures and Scots pine and oak mixtures) exerted a limited comparative influence on the species composition and richness of both ground-dwelling spiders and carabid beetles and this was true in the three different regions of study. Where significant stand type effects were observed, monoculture stands supported higher richness than mixed stands, but the level of any effect was different in the three forest regions. For example, in Thetford Forest, Scots pine monocultures harboured highest richness of all spider species, habitat generalist species, and forest specialist species, but not open habitat specialists. In contrast, there was significantly higher species richness of spiders with preferences for open habitats in Scots pine monoculture stands compared with the other stand types in Ireland. However, in the New Forest spider species richness was not found to differ significantly between forest stand types. In terms of carabid beetle species richness, oak monoculture stands had significantly higher species richness of forest specialist species compared with Scots pine monocultures and Scots pine and oak mixtures in Thetford Forest, but there was no detectable effect of stand type on carabid beetle richness in either the Irish or New Forest stands. Therefore, our findings do not support the hypothesis that mixed tree species stands support higher species richness of ground-dwelling spiders and carabid beetles. Regional and individual tree species effects were more important influences on spider and carabid beetle assemblages.

The lack of any significant difference in the measured environmental variables (e.g. volume of CWD, composition and structure of ground vegetation, canopy openness) between the three forest stand types studied, is indicative of a potential high degree of overlap in the ecological resource provisioning of the three stands types. Limited responses by spiders and carabid beetle communities to stand type suggests that this is true for these taxa; i.e. the ecological value of mixed and monoculture stands of Scots pine and oak is highly comparable for these taxa, with the exception of only a small number of spider and carabid species that have stronger affiliations to one or other stand type as revealed by indicator species analysis. High levels of similarity in measured environmental parameters between mixed and monoculture stands were also found by Oxbrough *et al*. (2012) in Norway spruce (*Picea abies*)-Scots pine mixtures and Norway spruce-oak mixtures compared with Norway spruce monocultures. In that study, the question was raised as to whether the poor mixing

ratio of oak with Norway spruce (15-40%) was the reason for the limited differences found between stands for the environmental parameters measured. The mixing ratio of the broadleaf component in our study was comparatively high in all of the English stands (at least 40% oak in mixed stands), so if distinct environmental conditions were created by a Scots pine and oak mixture, these should have been evident.

Unlike the weak forest stand type effects observed, there were clear regional scale factors that could influence the species abundance, richness and composition of spider and beetle assemblages. Counts of spiders and carabid beetles, for example, were disproportionately high in Thetford Forest stands compared with the New Forest and Irish stands. The proportion of spider and beetle forest specialist species present in Thetford Forest was also much lower than the New Forest and Irish stands, while the proportion of generalist species was comparatively high. Additionally, Thetford Forest was the only region in which any beetle species was associated with a particular stand type; one forest specialist (*L. fulvibarbis*), which has a preference for woodlands with damp litter (Luff, 2007), was associated with oak monocultures, and one habitat generalist (*N. brevicollis*) was associated with both oak and mixed stands. Another species with a preference for damp conditions was entirely absent from our pitfall traps in Thetford Forest, but highly abundant in the New Forest and the Irish sites; this was *A. parallelipedus* which has been recovered previously in small numbers from Thetford Forest by Jukes *et al*. (2001), but, similarly to our study, in comparatively high numbers in the New Forest. Jukes *et al*. (2001) suggest that the limited numbers of *A. parallelipedus* in Thetford Forest could be related to the much drier conditions here, leading to a likely scarcity of the preferred prey; i.e. slugs and earthworms.

In addition to the drier conditions present in Thetford Forest that invariably influence the spider and carabid beetle species assemblages that are present there, our findings in the Thetford Forest region may also be related to the relatively 'young' status of this wooded area compared to greater periods of woodland continuity in the New Forest and Irish stands. Other influences on the spider and beetle composition in the Thetford Forest stands could be the former predominance of heathland in the region, but also the presence of a high proportion of non-native conifer woodland, including plantations of the Mediterranean tree species Corsican pine (*Pinus nigra*). These have previously been shown to influence the insect species that occur in the Thetford Forest region, many of which are common in heathland and ruderal habitats in Mediterranean regions but rare elsewhere in Britain (Dolman *et al*., 2010). Most of Thetford's significant indicator spider species were habitat

generalists that were significantly associated with Scots pine monocultures. One such species that appears to be supported by Thetford's Scots pine monocultures, *Agyneta subtilis*, is classed as vulnerable in Britain and is found in coastal and heathland habitats as well as woodland (Harvey *et al.*, 2002). This suggests that the Scots pine monocultures may act as a habitat reserve for some of the sandy heathland species that formerly inhabited the site, just as the deciduous woodland also supports a number of specialist deciduous beetle species. These results highlight the clear role of specific stand types for enhancing overall regional species richness and the importance of considering woodland continuity and historical context to help explain current species assemblages.

The spiders *M. viaria* and *D. picinus* were the only two species that emerged as consistent indicators of particular forest stand types in more than one region. These species are known to prefer deciduous woodland (Harvey *et al.*, 2002; Nolan, 2008) and as such were associated with Scots pine and oak mixtures and oak monocultures in Thetford Forest and Ireland. This low number of consistent indicator species across regions suggests that species selected as indicators of a forest type in one region may not be good indicators in other regions, and regional differences again seem to be more important drivers of habitat preferences than tree species composition. This is not unexpected as the distribution and number of spider and carabid species vary significantly across Britain and Ireland (Van Helsdingen, 1996; Harvey *et al.*, 2002; Ferriss *et al*., 2009). Overall, there were more spiders than carabid beetles associated with a particular stand type. The low number of carabid beetle indicator species significantly affiliated with specific forest stand types (4% of species) is consistent with other research (Oxbrough *et al.*, 2010). The higher percentage of significant spider indicator species showing associations with stand type, suggests that spiders may be more sensitive to the habitat variation attributable to these forest plantation stand types than carabids. The different levels of stand affiliation in carabids and spiders, along with their different responses to stand type, highlight the importance of choosing varied indicator taxa in biodiversity studies.

While this study, as others (e.g. Barbier *et al*., 2008; Oxbrough *et al*., 2012) does not lend support to current discussions around the potential biodiversity benefits of mixed stands over monocultures, other mixtures can be envisaged that may be beneficial. These include intimate mixtures with more main canopy tree species and/or different tree species to those studied here. Both oak and Scots pine are native to Britain, and as such innately support a high number of phytophagous insect and mite species (Kennedy & Southwood, 1984). In

contrast, admixing a native broadleaf to a non-native conifer plantation, where there are likely to be fewer associated insects, might substantially increase the abundance and diversity of, for example, herbivore canopy fall and associated predators as other authors have found (e.g. Butterfield & Malvido, 1992; Magura *et al*., 2002). Admixing a broadleaf to a conifer that casts a dense shade might also increase stand light levels with the consequence of increasing understory vegetation and, thus potentially increasing stand structural diversity (Humphrey *et al.*, 2003). In this study, canopy openness was not significantly different between stand types.

With regards to increasing the number of tree species, Schuldt *et al.,* (2008) have found that intermediate levels of tree species diversity significantly improved the richness and abundance of ground-living spiders compared with single species stands and a similar increase in canopy beetle species richness was observed by Sobek *et al*., (2009) across a tree diversity gradient. In our study, while spider and carabid beetles assemblages did not respond to Scots pine and oak mixtures, a number of species were strongly affiliated to the tree species present. Several carabid beetles, for example, favoured stands with oak over the Scots pine monocultures. Fuller *et al*. (2008) also found a significantly higher proportion of forest specialist carabid beetle species in mixed deciduous woodland comprised of oak, birch (*Betula* spp.) and sycamore (*Acer pseudoplatanus*) compared with Scots pine monocultures. Taboada *et al*. (2010) corroborate this finding with observations of significantly increased carabid beetle species richness in oak-dominated forest stands compared with Scots pine monocultures, although they found a higher proportion of forest specialists in Scots pine plantation stands compared to oak stands.

Conclusions and recommendations for forest management

It has been suggested that the inclusion of more than one dominant tree species to a forest stand, and particularly a native broadleaf species, could increase habitat heterogeneity and enhance forest biodiversity. However, our study found no significant consistent effect of mixed or monoculture tree species on ground-dwelling spider and carabid beetle diversity. At the levels of mixing considered within this study (10 - 50% broadleaf component), and considering the two tree species under study, Scots pine and oak, mixed stands showed no influence on spider or beetle diversity compared to monocultures of these species. This supports previous research suggesting that additional broadleaf canopy species confer no clear arthropod biodiversity benefits at levels of up to 40% of the mix (Oxbrough *et al*.,

2012; Barbier *et al*., 2008), although they may have an influence at greater broadleaf to conifer mixing ratios. European and UK forest management policies currently recommend much lower levels of mixing of broadleaved components in pine forests (such as 5% in the UK) (European Environment Agency, 2008; Forest Service, 2000; Forestry Commission, 2011); further research is needed to establish whether a greater broadleaf component in mixtures will improve their biodiversity value over stands of simpler species composition, but also, which specific species mixtures are most beneficial i.e. which tree species should be combined? How many different tree species should be combined in a mixture before benefits are derived?

There was no clear advantage or disadvantage of oak and Scots pine mixtures for spider and beetle diversity when compared to oak or Scots pine monocultures. Any benefit conferred by one monoculture stand type over the other was dependent on region and study taxa. Thus, for these arthropod species groups and forest stand types, at least, there does not appear to be any clear biodiversity management benefit to promoting a mixed tree species composition, or favouring one tree species for planting over another for biodiversity conservation with the exception possibly of regions with limited broadleaf components in the landscape, especially where the climate is drier; here a broadleaf component is likely to provide more significant benefits as in the case of oak in Thetford Forest which favours a number of specialist spider/carabid species. A combination of these stand types in a landscape matrix is more likely to satisfy any strong species-specific associations with either oak or Scots pine trees as was detected for a number of the spider and beetle species in this study in the two English regions.

Acknowledgements

We would like to thank: Jacqui Brunt, Mark Ferryman and Rob Deady for assistance with arthropod sample sorting and assistance with fieldwork, Steve Coventry, Paul Turner, John Lakey, Stephen Whall, Liz Richardson and Mark Oram for organisation of and help with fieldwork, David Williams for help with identification of the more cryptic carabid beetle species, Linda Coote and Mark Wilson for help with Irish site selection and Sandra Irwin, Tom Kelly, John O'Halloran and Daniel Kelly for initial discussions. Thank you also to Linda Coote for providing habitat data from Ireland. Many thanks to the anonymous reviewer for the detailed feedback provided. Funding for this research was provided by the Forestry Commission to Forest Research's Biodiversity Project and matched funding was provided by the European Union (European Regional Development Fund ERDF) within the framework of the European INTERREG IV A 2 Mers Seas Zeeën Cross-border Cooperation Programme 2007-2013 (Project 090316 016-FR MULTIFOR: Management of Multi-Functional Forests). Funding is also gratefully acknowledged from the Planforbio Research Programme which is funded by Ireland's the Department of Agriculture, Food and the Marine under the National Development Plan 2007-2013.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32-46.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved - A critical review for temperate and boreal forests. Forest Ecology and Management 254, 1-15.

Benton, T. G., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18, 182-188.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: Oxymoron or opportunity? Biodiversity and Conservation 17, 925–951.

Brown, A.H.F., 1992. Functioning of mixed-species stands at Gisburn, N.W. England. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific Publications, London, pp. 99-113.

Brown, N., Jennings, S. Wheeler, Nabe-Nielsen, J., 2000. An improved method for the rapid assessment of forest understorey light environments. Journal of Applied Ecology 37, 1044-1053.

Butterfield, J., Malvido, J.B., 1992. Effect of mixed-species tree planting on the distribution of soil invertebrates, in: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees, Spec. Publ. No. 11, British Ecological Society, Blackwell, Oxford, pp. 255–265.

Cameron, K. H., Leather, S.R., 2012. How good are carabid beetles (Coleoptera, Carabidae) as indicators of invertebrate abundance and order richness? Biodiversity and Conservation 21, 763-779.

Cavard, X., Macdonald, S. E., Bergeron, Y., Chen, H.Y.H., 2011. Importance of mixed woods for biodiversity conservation: Evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environmental Reviews 19, 142–161.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566-3574.

Dannatt, N., 1996. Thetford Forest: its history and development. In: Ratcliffe, P., Claridge, J. (Eds.) Thetford Forest Park: The Ecology of a Pine Forest. Forestry Commission Technical Paper 13. Forestry Commission, Edinburgh.

Del Río, M., Sterba, H., 2009. Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. Annals of Forest Science 66, 502-512.

Dhôte, J., 2005. Implication of forest diversity in resistance to strong winds, in: Scherer-Lorenzen, M., Körner, C. (Eds.), Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin.

Dolman, P. M., Panter, C., Mossman, H. L., 2010. Securing Biodiversity in Breckland: Guidance for Conservation and Research. First Report of the Breckland Biodiversity Audit. University of East Anglia, Norwich.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67, 345-366.

European Environment Agency, 2008. European Forests – ecosystem conditions and sustainable use. EEA Report, Copenhagen.

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T.O., Fuller, R. J., Sirami, Siriwardena, G.M., Martin, J.-L., 2010. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14, 1-14.

Ferriss, S. E., Smith K. G., & Inskipp T. P. (eds.), 2009. Irish Biodiversity: a taxonomic inventory of fauna. Irish Wildlife Manuals, No. 38. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Forestry Commission, 2011. The UK Forestry Standard: The UK Government's Approach to Sustainable Forestry. The Forestry Commission, Edinburgh, UK.

Forest Service, 2000. Forest Biodiversity Guidelines. Forest Service, Department of the Marine and Natural Resources, Dublin.

Fuller, R. J., Oliver, T. H. & Leather, S. R., 2008. Forest management effects on Carabid beetle communities in coniferous and broadleaved forests: implications for conservation. Insect Conservation and Diversity 1, 242-252.

Grant, M.J., Edwards, M.E., 2008. Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). Vegetation History and Archaeobotany 17, 551-562.

Guest, C., Huss, J., 2012. Nursing of oak in Ireland. COFORD Connects. http://www.coford.ie/media/coford/content/publications/projectreports/cofordconnects/SM21-LR.PDF Last accessed: 09/03/2013.

Gunnarsson, B., 1983. Winter Mortality of Spruce-Living Spiders: Effect of Spider Interactions and Bird Predation. Oikos 40, 226-233.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2012. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 dataset. Submitted to International Journal of Climatology. Dataset last accessed January 2013 and retrieved from: http://badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae), Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Humphrey, J., Ferris, R., Quine, C., 2003. Biodiversity in Britain's planted forests. Forestry Commission, Edinburgh, 51-62.

Jukes, M.R., Peace, A.J., Ferris, R., 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. Forest Ecology and Management 148, 271–286.

Kennedy, C.E.J., Southwood, T.R.E., 1984. The Number of Species of Insects Associated with British Trees – a Re-Analysis. Journal of Animal Ecology 53, 455-478.

Kerr, G., Nixon, C.J. Matthews, R.W., 1992. Silviculture and yield of mixed-species stands: the UK experience. In: Cannell, M.G.R. Malcolm, D.C., Robertson, P.A. (Eds.). The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific Publications.

Koricheva, J., Vehvilainen, H., Riihimaki, J., Ruohomaki, K., Kaitaniemi, P., and Ranta, H., 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: Myth or reality? Canadian Journal of Forest Research 36, 324–336.

Kostylev, V. E., 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. Ecological Complexity 2, 272-282.

Lack, D., 1969. The numbers of bird species on islands. Bird Study 16, 193–209.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Luff, M., 2007. RES Handbook, Vol. 4, part 2: The Carabidae (Ground Beetles) of Britain and Ireland. Field Studies Council, Shropshire, UK.

Lust, N., Muys, B., Nachtergale, L., 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodiversity and Conservation 7, 249–260.

Magura, T., Tóthmérész, B., Elek, Z., 2002. Impacts of non-native spruce reforestation on ground beetles. European Journal of Soil Biology 38, 291–295.

Malaque, M.A., Maeto, K., Ishii, H.T., 2008. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Applied Entomology and Zoology 44, 1-11.

McGeoch, M. A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73, 181-190.

Morneau, F., Duprez, C., Hervé, J.C., 2008. Les forêts mélangées en France métropolotaine. Caractérisation à partir des résultats de l'Inventaire Forestier National. Revue Forestière Française LX, 107-120.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P., 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. Journal of Biogeography 19, 173–181.

Nolan, M., 2008. Database of Irish Spiders (Araneae), in Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171–183.

Oxbrough, A., Irwin, S., Kelly, T.C., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111– 2121.

Oxbrough, A., French, V., Irwin, S., Kelly, T. C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? Forest Ecolog and Management 270, 11-18.

Pearce, J. L., Venier, L.A., 2006. The use of beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. Ecological Indicators 6, 780–793.

Peterken, G.F., 1993. Woodland Conservation and Management, 2nd edn. Chapman & Hall, London.

Pérot, T., Picard, N., 2012. Mixture enhances productivity in a two-species forest: evidence from a modelling approach. Ecological Research 27, 83-94.

Platnick, N. I., 2012. The world spider catalog, version 13.0. American Museum of Natural History, online at: http://research.amnh.org/iz/spiders/catalog Last accessed: 09/03/2013.

R Core Team., 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Randall, R., Dymond, D., 1996. Why Thetford Forest? The human and natural history of Breckland before the early 20th century, in: Ratcliffe, P., Claridge, J. (Eds.), Thetford Forest

Park: The Ecology of a Pine Forest. Forestry Commission Technical Paper 13. Forestry Commission, Edinburgh.

Roberts, M.J., 1993. The spiders of Great Britain and Ireland. Harley Books, Colchester, UK.

Roche, J., Mitchell, F., Waldren, S., 2009. Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland. Biodiversity and Conservation 18, 2185-2203.

Schuldt, A., Fahrenholz, N., Brauns, M., Migge-Kleian, S., Platner, C., Schaefer, M. 2008. Communities of ground-living spiders in deciduous: Does tree species diversity matter? Biodiversity and Conservation 17, 1267-1284.

Simpson, E. H., 1949. Measurement of diversity. Nature 163, 688.

Sobek, S., Steffan-Dewenter, I., Scherber, C., Tscharntke, T. 2009. Spatiotemporal changes of beetle communities across a tree diversity gradient. Diversity and Distributions 15, 660-670.

Taboada, A., Tárrega, R., Calvo, L., Marcos, E., Marcos, J. A., Salgado, J.M., 2010. Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. European Journal of Forest Research 129, 31-45.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79–92.

Thiele, H., 1977. Carabid Beetles in their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour. Springer-Verlag, Berlin.

Uetz, G., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40, 29-42.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London.

Van Helsdingen, P. J., 1996. The county distribution of Irish spiders, incorporating a revised catalogue of the species. The Irish Naturalists' Journal 25, 1-92.

Walsh, S., 2012. A Summary of Climate Averages for Ireland 1981-2000. Climatological Note No. 14. Met Éireann, Glasnevin Hill, Dublin 9.

Winter, S., Möller, G. C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251–1261.

Wise, D.H., 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48, 181-188.

Chapter 6

The application of forest biodiversity indicators across forest stand types and regions



Pitfall trap in Scots pine plantation forest

Abstract

The goal of sustainable forest management is to manage forests for a range of ecological, economic and social functions, including the conservation and management of biological diversity in forest ecosystems. Environmental variables that are correlated with species richness are often referred to as biodiversity indicators and used to assess the habitat quality and biodiversity of forest ecosystems. Biodiversity indicators previously derived from Sitka spruce (*Picea sitchensis*) and ash (*Fraxinus excelsior*) plantation forests in Ireland were tested for bryophytes, vascular plants and active ground-dwelling spiders to determine their applicability across a broader geographical area. Fifteen Scots pine (*Pinus sylvestris*) monocultures, 14 oak (*Quercus petraea/robur*) monocultures and 14 intimately mixed Scots pine/oak stands were used in this study which was conducted in three regions: Ireland, the New Forest in southern England and Thetford Forest in eastern England. In each stand ground vegetation was sampled in 2m x 2m quadrats, the active ground-dwelling spider fauna was sampled by pitfall trapping, and the environmental variables used as biodiversity indicators were measured.

Litter cover was, in general, predicted to have a negative effect on total and open-associated species richness and a positive effect on forest-associated species. Field layer vegetation cover was predicted to have a positive effect on total spider species richness in England, but no effect in Ireland. Canopy openness was, in general, predicted to have a negative effect on total and forest-associated species richness of bryophytes and vascular plants and a positive effect on open-associated spider species richness. The majority of indicators had consistent relationships with species richness across all three stand types. However, these relationships were not consistent across the three regions investigated, possibly due to differences in land-use history and climate. This highlights the importance of rigorous testing of biodiversity indicators specific to each forest stand type and region to inform the selection of effective indicators. These results also emphasise the importance of individual site management for biodiversity and the consideration of local factors such as site history and geographical location in forest management plans.

Introduction

Forests represent some of the richest and most biologically diverse areas of the world (Lindenmayer *et al*., 2006) and are recognised as key ecosystems in need of protection by the Convention on Biological Diversity (Convention on Biological Diversity, 2012). Sustainable Forest Management (SFM) aims to strike a balance between the demand for forest products and services and the preservation of forest health and biodiversity (Forest Europe, 1998; MCPFE, 1993; United Nations Conference on Environment and Development, 1992). The importance of monitoring the effect of forest management on biodiversity is well recognised, however, compiling a full inventory of the species in a forest is not generally possible due to financial and time limitations (Gardner, 2010; Larsson, 2001; Lawton, 1998; Lindenmayer, 1999). Therefore methods which provide a surrogate measure of biodiversity, such as the use of indicators, are often advocated as a means of assessing the habitat quality and diversity of forest ecosystems (Noss, 1999). Indicators that are correlated with species richness are particularly useful since species richness is the most basic and universally accepted method of quantifying biodiversity (Magurran, 2004).

Three types of biodiversity indicators are commonly cited: structural indicators, functional indicators, and compositional indicators. Structural indicators of forest biodiversity indicate the physical organisation of a habitat, such as horizontal structural layers (Noss, 1990). A number of these have been identified that are correlated with species richness of a range of taxa including plants, invertebrates and birds (Humphrey *et al*., 1999; Oxbrough *et al*., 2005; Smith *et al*., 2008). Functional indicators are defined as those which indicate ecological and evolutionary processes, such as disturbance and nutrient cycling (Noss, 1990). Compositional indicators are species or species groups which can predict the response of other species (Noss, 1990). Successful compositional indicators can be more difficult to identify as they are often poor predictors of other species groups and require expert knowledge to identify (Gaspar *et al*., 2010; Jonsson and Jonsell, 1999; Kremen, 1992). Indicators should be repeatable, incur minimal observer bias, be ecologically meaningful, easy to identify and interpret by non-experts and data collection for the indicators should be inexpensive (Duelli and Obrist, 2003; Ferris and Humphrey, 1999; McGeogh, 1998). Furthermore, forest management operations are usually carried out at the Forest Management Unit (FMU) scale, therefore indicators should be developed for use at

this level in order to result in effective, targeted shifts in management practice to benefit biodiversity (Similä *et al*., 2006).

Both ground vegetation and spiders are sensitive to site characteristics, habitat quality and disturbance and are often used to infer information on other species groups due to the integral roles they play in ecosystem functioning. Furthermore, structural and functional biodiversity indicators for ground vegetation and spiders can also be indicators for other species groups (Ferris and Humphrey, 1999; Pearce and Venier, 2006). Ground vegetation communities are closely linked to the geographic, climatic and edaphic properties of a habitat (Ferris and Humphrey, 1999). However, in forest ecosystems, stand structure is also an influential determinant of species composition and richness (French *et al*., 2008). Ground vegetation performs many important functional roles in forest ecosystems both directly and indirectly by increasing site productivity (Ford, 1977), providing habitats for invertebrates, birds, and mammals (Humphrey *et al*., 1999) and influencing natural regeneration (Parker *et al*., 1997). Spiders are the dominant invertebrate predator in most terrestrial ecosystems and are generalist predators which regulate arthropod communities in all strata of the forest, from the litter to the canopy layer (Clarke and Grant, 1968; Halaj *et al*., 1998; Sanders *et al*., 2008). They are also a prey item for many birds and insectivorous mammals, providing a year-round food source (Churchfield *et al*., 1991; Gunnarsson, 1996). Spiders are primarily affected by vegetation and litter structure, factors which change with habitat and disturbance levels (Oxbrough *et al*., 2005; Robinson, 1981; Uetz, 1975) and show strong habitat specificity and so are appropriate for assessing changes over a small scale (Marc *et al*., 1999; Oxbrough *et al*., 2006b; Wise, 1993).

While many sets of functional, structural and compositional indicators have been proposed, much of this research remains to be validated to understand their applicability to different species groups, forest stand types and structural stages (Dale and Beyeler, 2001; Larsson, 2001; Lindenmayer *et al*., 2006; Noss, 1999). In the forestry sector, biodiversity indicators for a range of taxa and structural stages have been derived for Sitka spruce (*Picea sitchensis*) and ash (*Fraxinus excelsior*) plantation forests in Ireland (Oxbrough *et al*., 2005; Smith *et al*., 2008). These include five structural indicators (canopy openness, the area of old woodland within 1km radius of the forest stand, volume of coarse woody debris, litter percentage cover and field layer vegetation percentage cover) and one functional indicator (stand age), which were selected from a large set of potential indicators. These indicators were correlated with ground vegetation and ground-dwelling spiders. While these indicators

were tested and validated in a number of additional plantation forest stand types in Ireland, i.e. Sitka spruce, lodgepole pine (*Pinus contorta*), Scots pine (*Pinus sylvestris*), oak (*Quercus petraea/ robur*) and Scots pine/ oak mix (Coote *et al*., 2013), there is no evidence that these biodiversity indicators are applicable across a broader geographical area. A recent large-scale assessment of biodiversity indicators in agricultural habitats across Europe concluded that not all of the indicators consistently predicted species richness across regions (Billeter *et al*., 2008). This highlights the importance of first testing biodiversity indicators to determine if they are appropriate for the forest stand type and region before applying them to forest management plans.

The aim of this study was to determine the applicability of structural and functional forest biodiversity indicators identified by Oxbrough *et al*. (2005) and Smith *et al*. (2008) for predicting ground vegetation and ground-dwelling spider species richness across different plantation forest stand types and regions. This was achieved by testing comparable datasets collected using different sampling regimes in 1) monoculture conifer plantations, monoculture broadleaf plantations and conifer/ broadleaf intimate mix plantations, 2) three geographical regions: Ireland, the New Forest in southern England and Thetford Forest in eastern England.

Materials and methods

Study sites

Forty-three plantation forest stands of uniform species composition were selected for study from within larger forested areas across eastern and central Ireland, the New Forest in Hampshire in southern England and Thetford Forest in Norfolk in eastern England (Figure 1). Three stand types were selected for study: Scots pine (*Pinus sylvestris*) monoculture plantations, oak (*Quercus petraea/ robur*) monoculture plantations and intimately mixed Scots pine/ oak plantations. In Ireland five Scots pine monocultures, four oak monocultures and four intimately mixed Scots pine/ oak stands were sampled. These stands were greater than 5ha and were selected from larger forest blocks. In England five Scots pine monocultures, five oak monocultures and five intimately mixed Scots pine/ oak stands (hereafter referred to as mixed) were sampled in both the New Forest and Thetford Forest. These stands were greater than 1.5ha and were selected from larger forest blocks. Irish stands were all greater than 5ha and English stands were all greater than 1.5ha, selected

from larger forest blocks. All stands were even-aged mature and homogeneous and were planted on a range of soil types (Table 1).

Sampling was carried out in 10m x 10m plots placed at least 15m apart and at least 25m from the forest stand edge. Each plot additionally contained a nested 2m x 2m quadrat. In Ireland three plots were used per stand to sample ground vegetation, ground-dwelling spiders and environmental variables. In England eight plots were used per stand and were positioned around the perimeter of a 50m x 50m quadrat, four plots were used to sample ground vegetation and all eight plots were used to sample ground-dwelling spiders and environmental variables.

The data from the English stands were collected by Forest Research UK staff and were kindly provided for use in this study, except for the ground-dwelling spider species identification which I conducted.

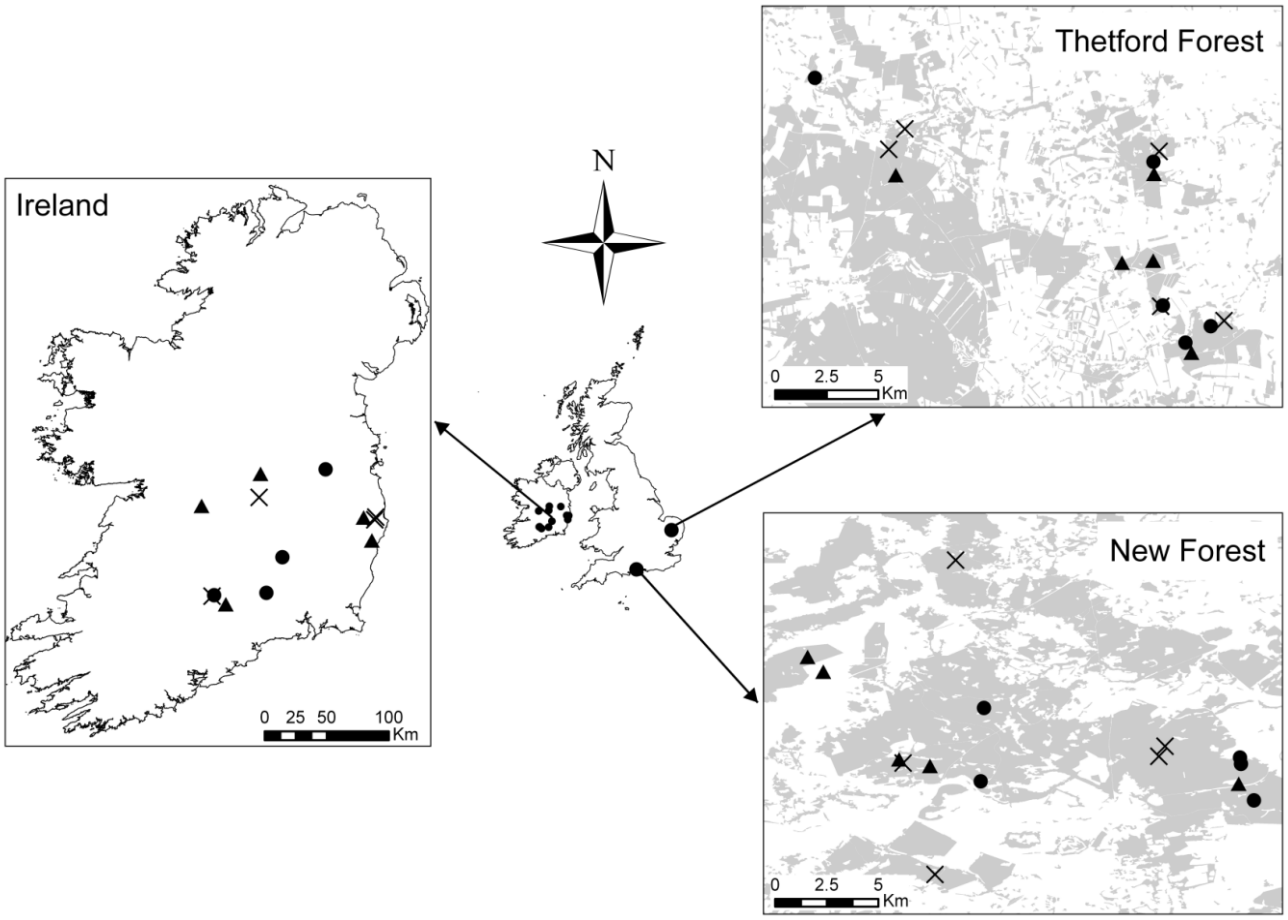


Figure 1. The 43 study sites located across Ireland and England. Scots pine (▲), Oak (●), Scots pine/ oak mix (**X**). Forested areas in the New Forest and Thetford Forest are coloured grey.

Table 1. Site characteristics of Scots pine, oak and mixed Scots pine/oak (oak %) stands in each region.

Region	Stand type	Mean stand size (range) (ha)	Mean stand age (range)	Soil types (number of stands)
Ireland	Scots pine	19.1 (12.5 – 29.1)	63 (60 – 65)	Brown earth (1), brown podzolic (1), gley (1), podzol (1)
	Oak	8.5 (6.2 – 12)	93 (72 – 151)	Brown earth (3), brown podzolic (1)
	Mixed (10-20%)	9.3 (5.5 – 13.3)	72 (65 – 79)	Brown earth (1), brown podzolic (1), podzol (2)
New Forest	Scots pine	5.2 (3.7 – 6.6)	66 (58 – 84)	Gley (5)
	Oak	3.0 (1.5 – 4.8)	84 (60 – 111)	Brown earth (2), gley (3)
	Mixed (40%)	6.4 (3.6 – 12.1)	72 (59 – 82)	Gley (5)
Thetford Forest	Scots pine	3.9 (1.6 – 7.1)	67 (44 – 81)	Brown earth (4), podzol (1)
	Oak	4.3 (2.4 – 6.8)	74 (57 – 79)	Brown earth (4), loam (1)
	Mixed (40%)	4.6 (3.4 – 5.2)	76 (70 – 79)	Brown earth (4), gley (1)

Ground vegetation sampling

Within each 2m x 2m quadrat the identity of each terrestrial species of vascular plant and bryophyte, including saxicolous and epixylic species, was recorded. Species nomenclature followed (Stace, 2010) and forest-associated species were determined based on information in Grime *et al*. (1988), Hill *et al*. (2004), Smith *et al*. (2005), Smith *et al*. (2006) and Hill *et al*. (2007).

Spider sampling

Pitfall traps were used to sample the active ground-dwelling spider fauna. In Ireland each 10m x 10m plot had five traps, set 2m apart in a linear arrangement, placed adjacent to the vegetation quadrat, resulting in a total of 15 traps per stand. Traps which were vulnerable to animal disturbance were covered with a 10cm x 10cm lid positioned 3cm above the ground. In England each 10m x 10m plot had a single pitfall trap placed within the 2m x 2m nested quadrat, resulting in a total of eight traps per stand. Each trap was covered by a 19cm x 19cm square steel lid that was positioned 3cm above the ground.

The contents of each pitfall trap were collected every 2-3 weeks from May to August 2011, totalling 84 trapping days in Ireland and the New Forest and 90 trapping days in Thetford Forest. The contents were stored in bottles filled with 70% ethanol. Spiders were sorted and identified to species level using Roberts (1993). Species nomenclature followed Platnick (2012) and species with forest or open habitat associations were classified based on information on spider species ecology in Nolan (2008) and Harvey (2002).

Environmental surveys

The age of each stand was determined from records of the planting year held by Coillte in Ireland and the Forestry Commission in England. Ordnance Survey maps c. 1900 were used to estimate the area of old woodland within a 1km radius of the centre of each forest stand. The percentage cover of litter (conifer and broadleaf combined) was measured inside the nested 2m x 2m quadrats. The total volume of coarse woody debris (CWD) including stumps, logs and snags ≥ 10cm in diameter and the percentage cover of herbaceous field layer vegetation, which included vascular herbs, graminoids and ferns but excluded climbing and woody species, were measured in the 10m x 10m plots. The canopy openness was estimated using a canopy scope (Brown *et al*., 2000), held 20cm above the eye;

measurements were taken from each corner and the centre of the 10m x 10m plot and the average value was calculated.

Data analysis

The relationship between a selection of the environmental variables and the species richness of vascular plants, bryophytes and ground-dwelling spiders was assessed to allow for comparisons with similar research, using the same environmental parameters as biodiversity indicators (Oxbrough *et al*., 2005; Smith *et al*., 2008) (Table 2). In these original studies the cover of deadwood was used as a biodiversity indicator for ground-dwelling spiders, however this information was not available here; therefore the volume of deadwood was used as a proxy. Additionally, litter cover was tested for bryophytes and vascular plants as it was recommended for further investigation as an indicator by Smith *et al*. (2005).

Prior to analyses individual-based rarefaction curves were calculated for the Irish ground-dwelling spider data to account for the effects of lost traps on species richness (Gotelli and Colwell, 2001). This was performed on unstandardised abundance data, then the number of individuals along the X axis was standardised and the species richness for each plot extracted. The number of individuals was standardised using the following formula: $ni / Ti * T$, where ni = the number of individuals at the *ith* plot, Ti = number of traps multiplied by the number of trapping day at the *ith* plot and T = lowest number of traps multiplied by the number of trapping days.

Table 2. Summary of the biodiversity indicators derived from Smith *et al*. (2008) and Oxbrough *et al*. (2005) in Sitka spruce and ash plantations for each species group. The species groups they were tested on in the present study (total species and forest-associated species of bryophytes, vascular plants and ground-dwelling spiders and open-associated ground-dwelling spiders), is indicated by X.

	Smith *et al.* (2008) and Oxbrough *et al*. (2005)	Bryophytes	Vascular plants	Ground-dwelling spiders
Stand age	+ Forest-associated bryophytes	X	X	X
	+ Forest-associated vascular plants			
	+ Forest-associated spiders			
Area of old woodland	+ Forest-associated vascular plants		X	
Litter cover	+ Forest-associated spiders	X	X	X
Coarse woody debris	+ Bryophytes	X		X
	+ Forest-associated bryophytes			
	+ Forest-associated spiders			
Field layer	+ Total spiders			X
	+ Forest-associated spiders			
Canopy openness	- Total bryophytes	X	X	X
	- Forest-associated bryophytes			
	+ Total vascular plant			
	- Forest-associated vascular plants			
	+ Open-associated spiders			

All analyses were carried out at the plot level to assess the effect of small-scale changes in the measured environmental variables on species richness. The ability of these environmental variables to indicate plant and spider species richness in each stand type within each country was tested using generalised linear mixed modelling (GLMM). This type of analysis is an extension of linear regression which allows the use of the Poisson distribution for species richness (count data) and random effects for nested data (Zuur *et al*., 2009). A separate model was run for each individual environmental variable and species group in each country, to test for significant relationships. Stand type was used as an explanatory variable to examine the interaction between each indicator and stand type. Additionally, analysis of the English data included region (Thetford Forest or New Forest) as an explanatory variable in the model to examine the interaction between region, stand type and each indicator. Where the interactions were not significant these terms were removed from the model. Plots were nested within stands in both the Irish and English analyses. Although species richness is the most widely used measure of biodiversity it does not represent functional trait diversity or species of conservation importance. In an effort to address a wider range of ecological roles filled by the species groups studied, these tests were also carried out on forest-associated bryophytes, vascular plants and spiders and open-associated spiders. Corrections for multiple tests were applied by calculating the number of significant p-values that could be attributed to chance occurrence with a 95% confidence. This was calculated from 1000 runs of randomly generated p-values based on the total number of tests conducted and the number of significant p-values found.

All analyses were completed using R (R Core Team, 2012). Rarefaction was carried out using the vegan package (Oksanen *et al*., 2012) and GLMM was conducted using the lme4 package (Bates *et al*., 2012).

Results

Stand age was either predicated to have a negative effect on species richness or no effect at all, and these effects differed according to stand type and region (Table 3). The area of old woodland within a 1km radius and the volume of CWD were not predicted to have a significant effect on the species richness of any of the groups they were tested on. Litter cover was the only indicator to consistently predict a negative effect on total vascular plant species richness across all stand types and regions (Table 3). In general it was also predicted to have a negative effect on total and open-associated species richness, and a positive effect

on forest-associated species, with the exception of a negative effect on forest-associated vascular plants in the New Forest. Field layer cover was predicted to positively affect total spider species richness in all stand types and regions in England, but again there was no detectable effect in Ireland (Table 3). Canopy openness was, in general, predicted to have a negative effect on total and forest-associated species richness of bryophytes and vascular plants, apart from a positive effect on total bryophyte species richness in the New Forest. Canopy openness was also predicted to have a positive effect on open associated spider species richness in all stand types in Ireland but no effect on spiders in any of the English stand types or regions. All other relationships between the tested biodiversity indicators and species groups which are not presented in Table 3 were non-significant ($P = > 0.05$). The mean and standard deviation of the environmental variables used as indicators in the analysis are presented in Table 4.

Table 3. Summary of the statistically significant positive (+) and negative (-) relationships from the GLMM analysis between the biodiversity indicators and bryophytes, vascular plants and ground-dwelling spider species richness and forest- and open-associated species richness in each region. Relationships hold for all stand types (Scots pine, oak and mixed) unless otherwise indicated. * < 0.05, ** < 0.01, *** < 0.001.

	Ireland	New Forest	Thetford Forest
Stand age	- Spiders ($z_{1,35}$ = -2.88**)		- Forest spiders (z1,229 = -2.24*)[5]
	- Forest vascular plants ($z_{1,38}$ = -2.21*)[4]		
Area of old woodland [1]	NA	NA	NA
Litter cover	- Bryophytes ($z_{1,38}$ = -2.99**)	- Vascular plants ($z_{1,111}$ = -3.95***)	- Vascular plants ($z_{1,111}$ = -3.95***)
	- Vascular plants ($z_{1,38}$ = -2.52*)	- Forest vascular plants ($z_{1,111}$ = -2.67**)	+ Forest vascular plants ($z_{1,111}$ =2.49*)
		+ Forest spiders ($z_{1,229}$ = 3.08**)	+ Forest spiders ($z_{1,229}$ = 3.08**)
		- Open spiders ($z_{1,229}$ = -2.22*)	- Open spiders ($z_{1,229}$ = -2.22*)
Coarse woody debris [2]	NA	NA	NA
Field layer [3]		+ Spiders ($z_{1,229}$ = 2.47*)	+ Spiders ($z_{1,229}$ = 2.47*)
Canopy openness	- Forest vascular plants ($z_{1,38}$ = -2.42*)	+ Bryophytes (z1,111 = 2.55*)	- Bryophytes ($z_{1,111}$= -2.84**)
	+ Open spiders ($z_{1,35}$ = 3.39***)		- Forest bryophytes ($z_{1,111}$ = -2.33*)

[1]Not tested on bryophytes or spiders, [2]not tested on vascular plants, [3]not tested on bryophytes or vascular plants, [4]in Scots pine stands only, [5]in mixed stands only

Table 4. Mean ± standard deviation of the structural environmental variables used as biodiversity indicators in each stand type and region.

	Ireland			New Forest			Thetford Forest		
	Scots pine	Oak	Mixed	Scots pine	Oak	Mixed	Scots pine	Oak	Mixed
Area of old woodland (km2)	0.62 ±0.26	0.58 ±0.49	1.31 ±0.84	1.83 ±0.72	1.91 ±0.29	2.28 ±0.51	0.33 ±0.26	0.45 ±0.26	0.58 ±0.30
Litter cover (%)	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4	64.1 ±28.4
Coarse woody debris (m3)	0.02 ±0.02	0.02 ±0.03	0.04 ±0.03	0.07 ±0.05	0.40 ±0.90	0.33 ±1.00	0.34 ±0.73	0.21 ±0.35	0.38 ±0.80
Field layer cover (%)	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9	42.7 ±26.9
Canopy openness	6.42 ±3.27	2.67 ±1.51	2.88 ±1.38	6.13 ±3.87	5.25 ±4.42	2.87 ±1.05	3.01 ±3.08	1.30 ±1.42	4.59 ±2.67

Discussion

Biodiversity indicators

Stand age was found to have a negative relationship with the species richness of vascular plants and spiders, however this relationship only held in some stand types and regions. The negative relationship with forest-associated vascular plants in Scots pine stands in Ireland is unexpected, considering the dispersal limitation of many vascular plant species and the likelihood that increased time is also correlated with increased species richness (Brunet and Goddert von, 1998; Dzwonko, 1993; Peterken and Game, 1984). Furthermore there is evidence that forest-associated vascular plant species richness increases over the forest cycle (Coote *et al*., 2013; Smith *et al*., 2008). The negative effect of stand age on total spider species richness in all stand types in Ireland and forest-associated spider species richness in mixed stands in Thetford Forest was also in contrast to findings by Coote *et al*. (2013) and Smith *et al*. (2008), who found a positive effect on total and forest-associated spider species richness in a range of broadleaf and conifer forest stand types. Spiders can exhibit a greater response to habitat structure than to forest age (Vehvilainen *et al*., 2008); however, these can be correlated, as the resulting changes in canopy cover, vegetation structure, litter cover, microclimate and prey availability over the forest cycle influences spider diversity (McIver *et al*., 1992b; Oxbrough *et al*., 2005). Before canopy closure light can penetrate to the forest floor, there is less litter cover, and higher abundance of prey that are associated with low-growing herbs and shrubs, which provides suitable habitat for many open-associated species (McIver *et al*., 1992a). At the time of canopy closure there is a reduction in the species richness of all spiders and open-associated spiders (Oxbrough *et al*., 2005). Often these changes favour forest-associated species as the forest matures (McIver *et al*., 1992a; Ziesche and Roth, 2008). In most stand types and regions tested here there was no effect of stand age on forest-associated spider species richness. Furthermore the evidence that forest-associated species richness increases over the forest cycle may mean that generally this relationship would not be expected. The age of the stands used in this analysis spanned a narrow range (Table 1), which may explain the lack of any strong effects, as well as the negative effects seen on forest-associated species. It is likely that stand age is a more successful predictor of species richness over the full range of the forest cycle, where associated changes in habitat also take place, compared to the limited range of stand ages used in this study.

Canopy openness was found to have both positive and negative relationships with species richness, which held across all stand types, however, these relationships differed across regions. In England, the negative relationship with total bryophyte and forest-associated bryophyte species richness in all stand types in Thetford Forest was similar to findings from ash plantation forests (Smith *et al*., 2008). However, in the New Forest the positive relationship with total bryophyte species richness was in contrast to findings from Smith *et al*. (2008) and from a broader range of conifer and broadleaf plantation forests (Coote *et al*., 2013). In Ireland, canopy openness had a negative effect on forest-associated vascular plant species richness, similar to the findings from ash plantation forests (Smith *et al*., 2008). Canopy cover can benefit bryophyte species richness in plantation forests as many species are shade-tolerant and require moist microclimates and can therefore be sensitive to desiccation in exposed habitats (Coote *et al*., 2013; Frisvoll and Prestø, 1997; Gates *et al*., 1965; Hill, 1979). The darker, moister conditions of spruce plantation forests generally lead to increased bryophyte richness compared to other more open stand types such as oak (French *et al*., 2008; Humphrey *et al*., 2002a), although extremely high canopy cover in conifer forests can lead to a decline in bryophyte species richness (Hill, 1979; Smith *et al*., 2008). Decreased light levels also lead to lower vascular plant diversity (Hill, 1979, 1986), which may benefit bryophytes by reducing competition for resources (Bergamini *et al*., 2001). Thetford forest is drier than the other regions studied meaning that canopy openness may leave bryophytes more open to desiccation here compared to the wetter climates of the New Forest and Ireland. Additionally, the levels of disturbance in the New Forest due to a long history of free-ranging cattle and ponies may mean that the species inhabiting these forests are more tolerant of, and may even benefit from, disturbance and the opening up of forest habitats (Mountford and Peterken, 2003). In terms of the effect on forest-associated vascular plants, these species require shaded conditions and benefit from more closed canopy conditions (Hannerz and Hånell, 1997; Hermy *et al*., 1999).

Open-associated spider species richness was also positively affected by canopy openness in all stand types in Ireland, similar to the findings from Sitka spruce plantation forests (Oxbrough *et al*., 2005), possibly due to the provision of more suitable microclimatic and habitat conditions for these species (McIver *et al*., 1992a). Canopy openness also affects understory vegetation which can influence invertebrate species richness. Field layer cover positively affected total spider species richness in all stand types in the New Forest and Thetford Forest, similar to the findings from Sitka spruce plantation forests (Oxbrough *et al*., 2005) and a broader range of conifer and broadleaf forest types (Coote *et al*., 2013),

however there was no detectable effect in Ireland. It has been noted that in ash plantation forests the deciduous nature and greater light penetration through the leaves may contribute to the lack of an effect of field layer vegetation in this forest type (Smith *et al*., 2008). Generally, increased structural complexity of the vegetation benefits spider diversity as it supports various hunting strategies exhibited by spiders, providing web-attachment points for web-spinning spiders and shelter for sit-and-wait spiders (Greenstone, 1984; Hore and Uniya, 2008; Wise, 1993). Additionally, increased cover of vegetation provides refuge areas from both inter and intra-specific predators (Gunnarsson, 1983, 1985; Gunnarsson, 1996). In England the stands were subject to higher levels of grazing than those in Ireland, particularly in the New Forest which has free-ranging cattle and ponies (Grant and Edwards, 2008), meaning the cover of field layer vegetation could have a greater influence on spider diversity. It is possible that the differences in spider sampling procedures used here could also impact on the results. Although there were fewer pitfall traps used in the English stands there were a greater number of plots overall per stand, which could mean that any effect of field layer cover on spiders may be more detectable. The well documented effect of field layer cover on spider diversity in other stand types, and from previous research in Ireland (Dennis *et al*., 1998; Oxbrough *et al*., 2006b; Uetz, 1991), means it may still be a useful biodiversity indicator, but is perhaps more effective in conifer plantation forests.

Litter cover was the only indicator which consistently predicted a negative effect on vascular plant species richness across all stand types and regions, similar to findings by Smith *et al*. (2005). Litter cover also predicted a negative effect on total bryophyte in all stand types in Ireland and a negative effect on forest-associated vascular plant species richness in all stand types in the New Forest. However, in Thetford Forest litter cover had a positive effect on forest-associated vascular plant species richness in all stand types. Litter can suppress vegetation diversity (Xiong and Nilsson, 1999) and there may also be a combined effect of litter and resource competition on vegetation diversity in productive environments (Foster and Gross, 1998). In terms of spider diversity, litter cover positively affected forest-associated spider species richness and negatively affected open-associated spider species richness in all stand types in the New Forest and Thetford Forest. These results have also been found in previous studies in Sitka spruce and ash plantation forests (Oxbrough *et al*., 2005), although were not replicated here. Again this may be due to the higher number of plots in the English stands, making any effects on species richness more detectable. Increased cover and depth of the litter layer results in greater structural complexity of the habitat. This is known to benefit forest-associated spider diversity by

increasing habitat quality, including available niches, refuge from predators and the abundance of prey (Bultman T.L. and Uetz, 1982; Stevenson and Dindal, 1982; Uetz, 1979, 1991; Uetz, 1975).

CWD volume was not found to indicate bryophyte or ground-dwelling spider species richness in these stand types and regions, despite evidence to suggest that it can be a useful indicator (Botting and DeLong, 2009; Coote *et al*., 2013; Rambo and Muir, 1998; Smith *et al*., 2008). The range of values of coarse woody debris were low among the stands (Table 4), therefore the levels at which an effect is detectable may be higher than those used in this analysis. CWD provides important habitat for many plant and invertebrate species as well as other groups such as lichens, fungi and small mammals and should be retained and promoted in plantation forests (Ecke *et al*., 2001; Humphrey *et al*., 2002a; Kruys and Jonsson, 1999; Norden *et al*., 2004; Stokland, 2001). The area of old woodland within 1km radius of the forest stand was also found to have no effect on vascular plant species richness, in contrast to findings in Sitka spruce and ash forests (Smith *et al*., 2008) but similar to findings from a broader range of conifer and broadleaf forest stand types (Coote *et al*., 2013), which again may be due to the low values present among the majority of the stands used in this study (Table 4). There is evidence to suggest that including this factor in landscape management will increase forest-associated vascular plant diversity. Seed dispersal ability of forest-associated vascular plant species is often limited as many species rely on wind dispersal and proximity to old woodland facilitates the spread of seeds to other forested areas (Dzwonko, 1993; Peterken and Game, 1984; Whitney and Foster, 1988). Therefore proximity, rather than the area of old woodland, may be a crucial factor for vegetation diversity, particularly in countries where forests are isolated patches planted within a predominantly agricultural landscape (Coote *et al*., 2013; Petit *et al*., 2004).

Broad applicability of biodiversity indicators

Fewer biodiversity indicators had significant relationships with species richness across regions in this study compared with studies in other plantation stand types tested in a single region (Oxbrough *et al*., 2005; Smith *et al*., 2008). Scots pine and oak forests exhibit a more open canopy structure, drier microclimate and greater vegetation structure compared to other tree species such as Sitka spruce and lodgepole pine, which are commonly used in plantation forestry (Docherty and Leather, 1997; Humphrey *et al*., 1999). Furthermore, the level of light penetration through broadleaf canopies such as oak is higher than conifer

canopies, leading to further differences in understory conditions (Canham *et al*., 1994; Coote *et al*., 2013). Often forest management for biodiversity is aimed at creating naturalness in exotic conifer plantations to imitate conditions of native woodlands (Angelstam and Dönz-Breuss, 2004). Scots pine is regarded as a semi-native species in Ireland and a native species in England, and oak is a native species to both Ireland and England (Bennett, 1984; Godwin, 1975; Mitchell, 2006; Roche *et al*., 2009) and so these forests may already provide closer conditions to natural woodlands than the conifer plantations these indicators were derived from. Smith *et al*. (2005) and Smith *et al*. (2008) noted that ash plantation forests exhibited fewer relationships with ground vegetation species richness and that the deciduous nature of this forest type may have affected the responses of both ground vegetation and spider species richness to biodiversity indicators. Therefore, these particular indicators may be better at predicting species richness in plantation forests of non-native conifers than in semi-native Scots pine and native oak tree species.

Although the biodiversity indicators predicted species richness across stand types within regions, they have a limited ability to predict species richness across different geographical regions. Differences in climate and land-use history of the three regions may also contribute to the variation observed in species responses to the biodiversity indicators tested. All three regions of study have a temperate oceanic climate ranging between 13.4°C to 14.3°C average maximum temperature and 5.9°C to 7.3°C average minimum temperature over a 30 year period from 1981 – 2010 (Met Office, 2013; Walsh, 2012). However these regions experience different levels of precipitation relative to one another. Over the same 30 year period the mean annual precipitation was lowest in the most easterly forest region in Thetford Forest (653mm), intermediate in the New Forest (777mm) and highest in the stands located in Ireland (823mm) (Met Office, 2013; Walsh, 2012). The moisture and temperature in forest environments affects both plants and animals and can shape the species assemblage and therefore the response of species groups to environmental variables (Chen *et al*., 1999; Uetz, 1979).

The land-use histories of each region also differ with much of Thetford Forest planted on areas of former heathland where there was previously no forest planted. Thetford is an important area for Mediterranean species that do not occur elsewhere in Britain or Ireland and many species in this region require open and ruderal heathland habitat and are not associated with the stand types that have been newly planted (Dolman *et al*., 2010).

Therefore, Thetford Forest may benefit from alternative methods of management for biodiversity conservation, tailored to the unique species in this area. Similarly, many of the stands in Ireland were planted where there was previously no forest planted and Ireland has had a long history of deforestation, which may have resulted in a generalist fauna (Anon, 2008; Whitehouse, 2006). The New Forest is situated in ancient woodland pasture which is still used for grazing by cattle and ponies and may have a more well-developed forest species assemblage compared to Thetford Forest and Ireland (Grant and Edwards, 2008). There are also differences in species distribution and abundance across geographical areas even within countries (Harvey *et al*., 2002; Preston *et al*., 2002), furthermore many species present in Britain are not found in Ireland (Ferriss *et al*., 2009).

Application of biodiversity indicators in forest management

The biodiversity indicators tested here can be modified through forest management to enhance biodiversity, although this should be carried out in conjunction with more detailed management, which is specific to the forest stand in terms of other important factors such as site conditions and land-use history. Management to increase gaps in forest canopies to create a mosaic of open well-vegetated areas and shaded areas with lower vegetation will support the highest biodiversity in plantation forests by providing for a range of species' ecological requirements. Thinning is recommended as the best method for altering canopy openness, which is particularly important in conifer plantations and into successive rotations which can have increased canopy cover compared to first rotations (Coote *et al*., 2013; Oxbrough *et al*., 2010). However, small gaps in the canopy may only promote the diversity of species already present, with gaps larger than 12m having the greatest effect on plant species richness (Corney *et al*., 2006). Unplanted glades in plantation forests promote the greatest invertebrate and plant species diversity (Gittings *et al*., 2006; Oxbrough *et al*., 2006b; Smith *et al*., 2007) and should be considered for inclusion in the forest at the planning stage. The selection of canopy tree species can also be used to control below-canopy light levels, broadleaf trees which allow greater light penetration through the leaves than conifer species (Gates *et al*., 1965; Hill, 1979) could be included in the canopy matrix as an alternative means of enhancing below-canopy structural diversity (Coote *et al*., 2013).

Despite the negative effects of litter cover on ground vegetation species richness, it should not be removed as it can benefit forest-associated plants, which are adapted to penetrate leaf litter, compared to other competitively dominant plants which cannot (Sydes and Grime,

1981a; Sydes and Grime, 1981b). Furthermore, broadleaf litter is important in coniferous plantation forests where it can help to mitigate the acidifying effect of needle litter, which may reduce the number of forest-associated plant species (Petit *et al*., 2004). Litter cover also provides vital habitat for many organisms, including litter-dwelling arthropods which play an important role in nutrient cycling and provide prey for ground-dwelling spiders and other predatory species groups of the forest floor (Clarke and Grant, 1968; Lawrence and Wise, 2000; Wise, 2004).

Although the volume of CWD was not found to affect the species richness of the species groups studied here it is still an important component of the ecological processes in forest ecosystems. Leaving wind-thrown trees and tree snags, as well as logs and branches from thinning will increase the volume of CWD (Humphrey *et al*., 2002b). However, there is a growing demand by stakeholders for deadwood removal from forests due to biofuel demands, which may present a conflict with the goals of biodiversity conservation in sustainable forest management plans (Deuffic and Lyser, 2012; Rudolphi and Gustafsson, 2005). Similarly the area of old woodland within 1km may be an important factor in forest management, despite the lack of effects detected here. In particular, where forests occur in small patches it is important to manage them for high habitat quality by creating a mosaic of old and new forests within the landscape which will increase the connectivity and biodiversity of fragmented landscapes (Fahrig, 2001; Grashof-Bokdam and Geertsema, 1998; Honnay *et al*., 1999).

Conclusions

Canopy openness, litter cover and field layer vegetation cover predicted species richness across a range of different stand types, but not across regions. These biodiversity indicators can be modified through forest management to enhance biodiversity in a range of broadleaf and conifer plantation forest stand types, and can be easily and quickly assessed by non-experts. However, the use of biodiversity indicators cannot be relied upon to ensure biodiversity conservation and enhancement in plantation forests and this method should be incorporated into forest management plans which also take into consideration other important local factors such as site conditions and history (Larsson, 2001). The use of biodiversity indicators has been criticised due to the difficulties of encompassing the full complexity of ecological systems and processes, the lack of specific goals and lack of scientific testing (Dale and Beyeler, 2001; Lindenmayer *et al*., 2006). This study

demonstrates the importance of rigorous testing of structural and functional indicators specific to each forest type and region in the indicator selection process and demonstrates the requirement for local scientific knowledge to inform the selection of effective indicators.

References

Angelstam, P., Dönz-Breuss, M., 2004. Measuring Forest Biodiversity at the Stand Scale: An Evaluation of Indicators in European Forest History Gradients. Ecological Bulletins 51, 305-332.

Anon, 2008. Irish Forests - A Brief History. Department of Agriculture, Fisheries and Food. Government of Ireland.

Bates, D., Maechler, M., Bolker, B., 2012. Package 'lme4'. Linear mixed-effects models using S4 classes. R version 0.999999-2.

Bennett, K.D., 1984. The post-glacial history of Pinus sylvestris in the British Isles. Quaternary Science Reviews 3, 133-155.

Bergamini, A., Pauli, D., Peintinger, M., Schmid, B., 2001. Relationships between productivity, number of shoots and number of species in bryophytes and vascular plants. Journal of Ecology 89, 920-929.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M., Edwards, P.J., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. Journal of Applied Ecology 45, 141-150.

Botting, R.S., DeLong, C., 2009. Macrolichen and bryophyte responses to coarse woody debris characteristics in sub-boreal spruce forest. Forest Ecology and Management. 258, Supplement, S85-S94.

Brown, N., Jennings, S., Wheeler, P., Nabe-Nielsen, J., 2000. An improved method for the rapid assessment of forest understorey light environments. Journal of Applied Ecology 37, 1044–1053.

Brunet, J., Goddert von, O., 1998. Migration of Vascular Plants to Secondary Woodlands in Southern Sweden. Journal of Ecology 86, 429-438.

Bultman T.L., Uetz, G., 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55, 34-41.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 24, 337-349.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in Forest Ecosystem and Landscape Ecology. BioScience 49, 288-297.

Churchfield, S., Hollier, J., Brown, V.K., 1991. The Effects of Small Mammal Predators on Grassland Invertebrates, Investigated by Field Exclosure Experiment. Oikos 60, 283-290.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

Convention on Biological Diversity, 2012. Forest Biodiversity. Secretariat of the Convention on Biological Diversity.

Coote, L., Dietzsch, A.C., Wilson, M.W., Graham, C.T., Fuller, L., Walsh, A.T., Irwin, S., Kelly, D.L., Mitchell, F., Kelly, T.C., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. Ecological Indicators 32, 107-115.

Corney, P.M., Duc, M.G.L., Smart, S.M., Kirby, K.J., Bunce, R.G.H., Marrs, R.H., 2006. Relationships between the species composition of forest field-layer vegetation and environmental drivers, assessed using a national scale survey. Journal of Ecology 94, 383-401.

Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecological Indicators 1, 3-10.

Dennis, P., Young, M., Gordon, I., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23, 253–264.

Deuffic, P., Lyser, S., 2012. Biodiversity or bioenergy: is deadwood conservation an environmental issue for French forest owners?11 This article is one of a selection of papers

from the International Symposium on Dynamics and Ecological Services of Deadwood in Forest Ecosystems. Canadian Journal of Forest Research 42, 1491-1502.

Docherty, M., Leather, S., 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. Forest Ecology and Management 95, 197-207.

Dolman, P., Panter, C., Mossman, H.L., 2010. Securing biodiversity in Breckland: guidance and recommendations for conservation and research, First report of the Breckland Biodiversity Audit. University of East Anglia, Norwich.

Duelli, P., Obrist, M.K., 2003. Biodiversity indicators: the choice of values and measures. Agriculture, Ecosystems & Environment 98, 87-98.

Dzwonko, Z., 1993. Relations between the Floristic Composition of Isolated Young Woods and Their Proximity toAncient Woodland. Journal of Vegetation Science 4, 693-698.

Ecke, F., Löfgren, O., Hörnfeldt, B., Eklund, U., Ericsson, P., Sörlin, D., 2001. Abundance and Diversity of Small Mammals in Relation to Structural Habitat FactorsAuthor. Ecological Bulletins 49, 165-171.

Fahrig, L., 2001. How much habitat is enough? Biological Conservation 100, 65-74.

Ferris, R., Humphrey, J.W., 1999. A review of potential biodiversity indicators for application in British forests, pp. 313-328.

Ferriss, S.E., Smith, K.G., Inksipp, T.P., 2009. Irish Biodiversity: a taxonomic inventory of fauna. Irish Wildlife Manuals, No. 38. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Ford, E.D., Newbould, P.J., 1977. The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. Journal of Ecology 65, 201-212.

Forest Europe, 1998. Pan-European Operational Level Guidelines for Sustainable Forest Management, Third Ministerial Conference on the Protection of Forests in Europe.

Foster, B.L., Gross, K.L., 1998. Species Richness in a Successional Grassland: Effects of Nitrogen Enrichment and Plant Litter. Ecology 79, 2593-2602.

French, L.J., Smith, G.F., Kelly, D.L., Mitchell, F.J.G., O'Donoghue, S., Iremonger, S.F., McKee, A.-M., 2008. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. Forest Ecology and Management 255, 476-494.

Frisvoll, A.A., Prestø, T., 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. Ecography 20, 3-18.

Gardner, T., 2010. Monitoring Forest Biodiversity: Improving Conservation through Ecologically-Responsible Management. Earthscan, UK.

Gaspar, C., Gaston, K.J., Borges, P.A.V., 2010. Arthropods as surrogates of diversity at different spatial scales. Biological Conservation 143, 1287-1294.

Gates, D.M., Keegan, H.J., Schleter, J.C., Weidner, V.R., 1965. Spectral Properties of Plants. Applied Optics 4, 11-20.

Gittings, T., O'Halloran, J., Kelly, T., Giller, P., 2006. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management 237, 290–300.

Godwin, H., 1975. History of the Natural Forests of Britain: Establishment, Dominance and Destruction. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 271, 47-67.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379-391.

Grant, M.J., Edwards, M.E., 2008. Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). Vegetation History and Archaeobotany 17, 551-562.

Grashof-Bokdam, C.J., Geertsema, W., 1998. The Effect of Isolation and History on Colonization Patterns of Plant Species in Secondary Woodland. Journal of Biogeography 25, 837-846.

Greenstone, M.H., 1984. Determinants of web spider species diversity: Vegetation structural diversity vs. prey availability. Oecologia 62, 299-304.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative Plant Ecology. Unwin Hyman Ltd, London.

Gunnarsson, B., 1983. Winter Mortality of Spruce-Living Spiders: Effect of Spider Interactions and Bird Predation. Oikos 40, 226-233.

Gunnarsson, B., 1985. Interspecific Predation as a Mortality Factor among Overwintering Spiders. Oecologia 65, 498-502.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Halaj, J., Ross, D., Moldenke, A., 1998. Habitat Structure and Prey Availability as Predictors of the Abundance and Community Organization of Spiders in Western Oregon Forest Canopies. Journal of Arachnology 26, 203-220.

Hannerz, M., Hånell, B., 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. Forest Ecology and Management 90, 29-49.

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdamc, C., Lawessond, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biological Conservation 91, 9-22.

Hill, M.O., 1979. The development of a flora in even-aged plantations, in: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.), The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, pp. 175-192.

Hill, M.O., 1986. Ground flora and succession in commercial forests, in: Jenkins, D. (Ed.), Trees and wildlife in the Scottish uplands. Institute of Terrestrial Ecology, Cambridge, pp. 71–78.

Hill, M.O., Preston, C.D., Bosanquet, S.D.S., Roy, D.B., 2007. BRYOATT. Attributes of British and Irish Mosses, Liverworts and Hornworts, NERC Centre for Ecology and Hydrology and Countryside Council for Wales.

Hill, M.O., Preston, C.D., Roy, D.B., 2004. PLANTATT. Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats, Biological Records Centre and NERC Centre for Ecology and Hydrology.

Honnay, O., Hermy, M., Coppin, P., 1999. Effects of area, age and diversity of forest patches in Belgium on plant species richness, and implications for conservation and reforestation. Biological Conservation 87, 73-84.

Hore, U., Uniya, V.-P., 2008. Influence of space, vegetation structure, and microclimate on spider (Araneae) species composition in Terai Conservation Area, India, in: Nentwig, W., Entling, M., Kropf, C. (Eds.), Proceedings of the 24th European Congress of Arachnology, Natural History Museum, Bern, pp. 71-77.

Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002a. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biological Conservation 107, 165–180.

Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R., Jukes, M.R., 1999. Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecology and Management 113, 11-21.

Humphrey, J.W., Stevenson, A., Whitfield, P., Swailes, J., 2002b. Life in the deadwood: a guide to managing deadwood in Forestry Commission forests. Forestry Commission, Edinburgh.

Jonsson, B.G., Jonsell, M., 1999. Exploring potential biodiversity indicators in boreal forests. Biodiversity and Conservation 8, 1417-1433.

Kremen, C., 1992. Assessing the Indicator Properties of Species Assemblages for Natural Areas Monitoring. Ecological Applications 2, 203-217.

Kruys, N., Jonsson, B.G., 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29, 1295-1299.

Larsson, T.B., 2001. Biodiversity evaluation tools for European forests, Ecological Bulletins, Blackwell, Oxford.

Lawrence, K.L., Wise, D.H., 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44, 33-39.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.H., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification on tropical forests. Nature 391, 72-76.

Lindenmayer, D.B., 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. Forest Ecology and Management 115, 277-287.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433-445.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell Publishing, Oxford.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems & Environment 74, 229-273.

McGeogh, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73, 181-201.

McIver, J.D., Parsons, G.L., Moldenke, A.R., 1992a. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22, 984-992.

McIver, J.D., Parsons, G.L., Moldenke, A.R., 1992b. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22, 984-992.

MCPFE, 1993. Second Ministerial Conference on the Protection of Forests in Europe, Helsinki, Finland.

Met Office, 2013. 1981–2010 averages. Met Office.

Mitchell, F., 2006. Where Did Ireland's Trees Come From? Biology & Environment: Proceedings of the Royal Irish Academy 106, 251-259.

Mountford, E.P., Peterken, G.F., 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. Forestry 76, 19-43.

Nolan, M., 2008. Database of Irish Spiders (Araneae), Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin.

Norden, B., Ryberga, M., Gotmark, F., Olaussona, B., 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117, 1-10.

Noss, R.F., 1990. Indicators for Monitoring Biodiversity: A Hierarchical Approach. Conservation Biology 4, 355-364.

Noss, R.F., 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. Forest Ecology and Management 115, 135-146.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Hendry, M., Stevens, H., Wagner, H., 2012. Vegan: Community Ecology Package. R version 2.0-7.

Oxbrough, A., Irwin, S., Kelly, T., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111–2121.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006b. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Parker, W.C., Watson, S.R., Cairns, D.W., 1997. The role of hair-cap mosses (Polytrichum spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management 92, 19-28.

Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6, 780-793.

Peterken, G.F., Game, M., 1984. Historical Factors Affecting the Number and Distribution of Vascular Plant Species in the Woodlands of Central Lincolnshire. Journal of Ecology 72, 155-182.

Petit, S., Griffiths, L., Smart, S., Smith, G.M., Stuart, R.C., Wright, S.M., 2004. Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. Landscape Ecology 19, 463-471.

Platnick, N.I., 2012. The World Spider Catalog, Version 13.0. The American Museum of Natural History.

Preston, C.D., Pearman, D.A., Dines, T.D., 2002. New atlas of the British and Irish flora. An atlas of the vascular plants of Britain, Ireland, the Isle of Man and the Channel Islands. Oxford University Press, Oxford, UK.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rambo, T.R., Muir, P.S., 1998. Bryophyte Species Associations with Coarse Woody Debris and Stand Ages in Oregon. The Bryologist 101, 366-376.

Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK.

Robinson, J., 1981. The Effect of Architectural Variation in Habitat on a Spider Community: An Experimental Field Study. Ecology 62, 73-80.

Roche, J., Mitchell, F.G., Waldren, S., 2009. Plant community ecology of Pinus sylvestris, an extirpated species reintroduced to Ireland. Biodiversity and Conservation 18, 2185-2203.

Rudolphi, J., Gustafsson, L., 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. Scandinavian Journal of Forest Research 20, 235-242.

Sanders, D., Nickel, H., Grützner, T., Platner, C., 2008. Habitat structure mediates top-down effects of spiders and ants on herbivores. Basic and Applied Ecology 9, 152-160.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L., Huhta, E., 2006. Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? Ecological Indicators 6, 686-700.

Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Kelly, T., Iremonger, S., McKee, A.-M., Giller, P., 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodiversity and Conservation 17, 991-1015.

Smith, G.F., Gittings, T., Wilson, M., French, L.J., Oxbrough, A., O'Donoghue, S., Pithon, J., O'Donnell, V., McKee, A.-M., Iremonger, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Giller, P., Kelly, T., 2005. Assessment of Biodiversity at Different Stages of the Forest Cycle, Bioforest Final Report, Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Smith, G.F., Gittings, T., Wilson, M., Oxbrough, A., Iremonger, S., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D.L., Pithon, J., O'Sullivan, A., Neville, P., Mitchell, F.J.G.,, Giller, P., O'Donnell, V., Kelly, T., 2006. Biodiversity Assessment of Afforestation Sites, Bioforest Final Report. Environmental Protection Agency (EPA) and the Council for Forest Research and Development (COFORD).

Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S., Mitchell, F.J.G., 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. Biological Conservation 136, 283-294.

Stace, C., 2010. New flora of the British Isles, 3rd Edition ed. Cambridge University Press, Cambridge.

Stevenson, B.G., Dindal, D.L., 1982. Effect of Leaf Shape on Forest Litter Spiders: Community Organization and Microhabitat Selection of Immature Enoplognatha Ovata (Clerck) (Theridiidae). Journal of Arachnology 10, 165-178.

Stokland, J.N., 2001. The Coarse Woody Debris Profile: An Archive of Recent Forest History and an Important Biodiversity Indicator. Ecological Bulletins, 71-83.

Sydes, C., Grime, J.P., 1981a. Effects of Tree Leaf Litter on Herbaceous Vegetation in Deciduous Woodland: I. Field Investigations. Journal of Ecology 69, 237-248.

Sydes, C., Grime, J.P., 1981b. Effects of Tree Leaf Litter on Herbaceous Vegetation in Deciduous Woodland: II. An Experimental Investigation. Journal of Ecology 69, 249-262.

Uetz, G., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40, 29-42.

Uetz, G., 1991. Habitat structure and spider foraging, in: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

Uetz, G.W., 1975. Temporal and Spatial Variation in Species Diversity of Wandering Spiders (Araneae) in Deciduous Forest Litter. Environmental Entomology 4, 719-724.

United Nations Conference on Environment and Development, 1992. Agenda 21, the Rio Declaration on Environment and Development, the Statement of Forest Principles, the United Nations Framework Convention on Climate Change and the United Nations Convention on Biological Diversity, Rio de Janeiro.

Vehvilainen, H., Koricheva, J., Ruohomaki, K., 2008. Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117, 935-943.

Walsh, S., 2012. A summary of climate averages for Ireland 1981-2010. Met Eireann, Dublin.

Whitehouse, N., 2006. The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. Quaternary Science Reviews 25, 15–16.

Whitney, G.G., Foster, D.R., 1988. Overstorey Composition and Age as Determinants of the Understorey Flora of Woods of Central New England. Journal of Ecology 76, 867-876.

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press.

Wise, D.H., 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48, 181-188.

Xiong, S., Nilsson, C., 1999. The Effects of Plant Litter on Vegetation: A Meta-Analysis. Journal of Ecology 87, 984-994.

Ziesche, T.M., Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? Forest Ecology and Management 255, 738-752.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, LLC, New York, USA.

Chapter 7

Ground-dwelling spider diversity in rare European oak and yew woodlands and the impact of grazing



Pitfall traps in grazed control area of oak woodland (left) and ungrazed deer exclosure in oak woodland (right), Killarney National Park

A manuscript based on this chapter has been accepted for publication in *Biodiversity and Conservation*.

Abstract

In Ireland, only 1% of the total land area is semi-natural woodland, which tends to be small and fragmented. Killarney National Park in south-west Ireland contains the most extensive semi-natural woodland in the country, and includes oak (*Quercus petraea*) and yew (*Taxus baccata*) woodlands which are internationally protected. Here, over-grazing by large populations of red deer (*Cervus elaphus*) and Asian sika deer (*Cervus nippon*) have lead to changes in overstory and understory vegetation species composition and structure. This study presents the first description of ground-dwelling spider fauna in the rare woodlands of Killarney National Park and the effect of grazing on their diversity. Active ground-dwelling spiders were sampled in the oak and yew woodlands by pitfall trapping within deer-proof exclosures and adjacent grazed controls.

The ground-dwelling spider fauna was typical of other forest types in Ireland, including plantation forests. However, Killarney National Park may be important for five species, not typically found in plantation forests, which rely on nationally scarce habitats. Deer grazing caused decreased abundance and species richness in the oak woodland by reducing structural diversity of the habitat. Abundance was higher in grazed plots in the yew woodland, although no effect on species richness was detected. Results provide evidence that controlling deer grazing is important for woodland biodiversity, although further research is required to understand the long-term effects of deer grazing exclosures on spider diversity.

Introduction

Currently the forest cover of Europe stands at 45% of the total land area and 70% of this is classified as semi-natural woodland (Forest Europe *et al.*, 2011). In contrast, the forest cover of Ireland, which has historically undergone vast deforestation and modification of its natural environment, is just 11% (737,000 ha) of the total land area (Forest Europe *et al.*, 2011). The majority of this is comprised of exotic conifer plantations (513,000 ha) and only 11% of the total forest cover is semi-natural woodland (82,000 ha) (Forest Europe *et al.*, 2011). These remnants of semi-natural woodland tend to be small and fragmented, with approximately 68% less than 10 hectares in area (Perrin *et al.*, 2008).

Killarney National Park in south-west Ireland has been a designated UNESCO biosphere reserve since 1982 (UNESCO, 2001) and contains the most extensive areas of semi-natural woodland in Ireland (1,400 ha) (NPWS, 2005). Several areas of internationally important woodland are found here, including yew (*Taxus baccata*) and acidophilus sessile oak (*Quercus petraea*). These two woodland types have a very limited distribution across Europe and yew woodland in particular is one of the rarest European woodland types (Perrin *et al.*, 2006). In Ireland, yew covers just 40 hectares and sessile oak 7,300 hectares of the land surface (Anon, 2007). The yew woodland of Killarney National Park is the largest of its kind in Ireland (25 hectares) and is a priority habitat under Annex I of the EU Habitats Directive (National Parks and Wildlife Service, 2008). Furthermore, it is in an area of karst limestone pavement, making it even more unique. The acidophilus sessile oak woodlands are also included in Annex I of the EU Habitats Directive (National Parks and Wildlife Service, 2008) and are considered to be the most natural sessile oak woodlands in Ireland (National Parks and Wildlife Service, 2006).

These woodlands are known to have a large population of red deer (*Cervus elaphus*), which may have been present in County Kerry since the Neolithic period (Carden *et al.*, 2011; Carden *et al.*, 2012). There is also a population of the more recently introduced Asian sika deer (*Cervus Nippon*) (Carden *et al.*, 2011; Carden *et al.*, 2012). Little information is available on deer densities in Ireland, although the estimated density in Killarney National Park is 5 – 25 deer per km^2 (Purser, 2009). Grazing pressure from large ungulates, such as deer, can have far reaching ecological impacts by reducing the cover and diversity of field layer vegetation and decreasing the survival of tree saplings. This not only changes the species composition of the overstory but also has a cascading effect on biodiversity,

including invertebrates, birds and mammals (Côté *et al.*, 2004). In Killarney, it has already been noted that grazing pressure from these large herbivores has significantly altered the woodlands by reducing the diversity of field layer vegetation and inhibiting woodland regeneration (Perrin *et al.*, 2006).

Fencing to exclude large grazers is often used in areas where grazing intensity is a problem (Hester *et al.*, 2000; Spooner *et al.*, 2002) and large areas of woodland in Killarney National Park have had fences erected to exclude deer. Several long-term studies have been conducted in these exclosures to determine the impact of grazing on vegetation and tree regeneration in these woodlands (Kelly, 2002; Perrin *et al.*, 2006; Perrin *et al.*, 2011). Other research in the park has investigated the diversity of ground vegetation, birds and small mammals in these rare woodland habitats (Batten, 1976; Kelly, 1981; Smal and Fairley, 1982; Lynch and McCann, 2007). However less attention has been given to other elements of their biodiversity, such as arthropods and other invertebrates.

Ground-dwelling spiders are sensitive to changes in structural heterogeneity of their habitat (Uetz, 1991; Oxbrough *et al.*, 2005), making them a useful group for studying changes in diversity as a result of habitat disturbance. Consequently, they have been used to determine the effects of grazing on invertebrate communities in grasslands and forests (Brown *et al.*, 1992; Gibson *et al.*, 1992; Miyashita *et al.*, 2004). Spiders play an important role in the functioning of all ecosystems and form an integral part of food webs as both predators of other arthropods and prey for insectivorous birds and small mammals (Clarke and Grant, 1968; Gunnarsson, 1983; Wise, 1993). Additionally, they are ubiquitous in the ground layer of woodlands, easily caught by pitfall trapping and taxonomically well-known.

This study provides the first investigation into the ground-dwelling spider diversity of nationally and internationally rare oak and yew woodlands in Killarney National Park. This research aimed to 1) examine the ground-dwelling spider diversity, 2) present the first investigation into the effect of deer grazing on ground-dwelling spider diversity in these woodlands.

Materials and methods

Study sites

One oak woodland and one yew woodland were sampled in the summer of 2011 in Killarney National Park (longitude 9˚34′, latitude 52˚1′) (Figure 1). Derrycunihy wood to the south of the National Park is acidophilus Atlantic sessile oak woodland and had 11 deer exclosures erected in 2005, with corridors left between the exclosures to allow movement of deer through the area. Three of these exclosures and an adjacent control area next to each exclosure were sampled. Reenadinna wood on the Muckross peninsula is Yew woodland on a karst limestone pavement and had one exclosure erected in 2002. This exclosure and an adjacent control area were sampled. A total of four sites were sampled across the two woodlands and each site consisted of two treatments: an ungrazed exclosure and an adjacent paired grazed control.

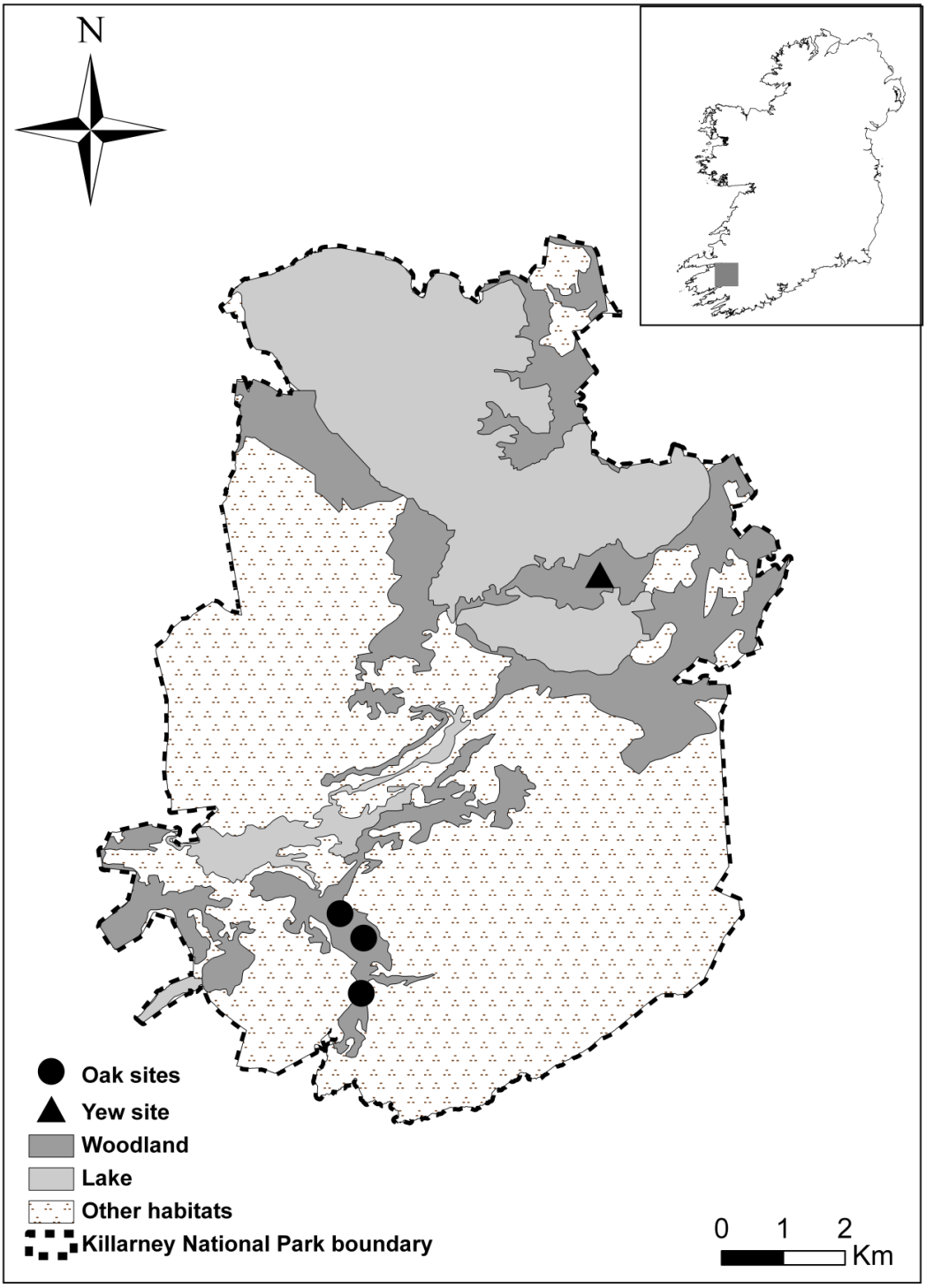


Figure 1. Location of Killarney National Park in Ireland and the distribution of sampling sites within the Park. Three paired exclosure and control sites in sessile oak woodland (●) and one paired exclosure and control site in yew woodland (▲).

Spider sampling

The active ground-dwelling spider fauna were sampled using a standardised sampling method (O'Halloran *et al*., 2011). Pitfall traps were dug into the ground so that the rim of the trap sat just below the ground surface. The traps were plastic cups of approximately 7cm diameter and 9cm high, which had drainage slits cut 1cm from the top of the cup. Traps were filled to 3cm with ethylene glycol (anti-freeze) used as a killing agent. Each trap had a steel mesh cage placed over the top to prevent animal disturbance. Each cage was 10cm x 10cm x 10cm and the mesh was 1cm x 1cm to allow invertebrates to move freely through the cage.

In each site x treatment combination three plots were placed in areas that were representative of the woodland in terms of ground vegetation, topography and canopy cover. Plots were placed a minimum of 50m apart and a minimum of 50m from the edge of the woodland. Each plot consisted of five pitfall traps set 2m apart in a linear arrangement. The contents of each pitfall trap were collected every three weeks from May to August in 2011, resulting in a total of four collections and 84 trapping days. After each collection the plastic cup was placed back in the ground and filled with fresh anti-freeze. The contents of the traps were transferred to labelled sample bottles and stored in 70% ethanol used as a preservative.

Spiders were identified to species using Roberts (1993) and nomenclature follows Platnick (2012). Forest and open specialists were determined based on Nolan (2008) and families were assigned to feeding guilds using Uetz *et al.* (1999). Information from Britain by Dawson *et al.* (2008) was used to designate conservation status, as comparable data for a majority of spider species in Ireland is not currently available.

Environmental surveys

Habitat was surveyed within a $1m^2$ quadrat placed over each pitfall trap. The percentage cover of the following variables was measured: bare ground, leaf/ needle litter, fine woody debris (<10cm diameter), coarse woody debris (>10cm diameter), ground layer vegetation (0 – 10cm), lower field layer vegetation (10 – 50cm) and upper field layer vegetation (50 – 200cm). The depth of the leaf/needle litter was also measured and percentage canopy cover was calculated using GLA 2.0 (Frazer *et al.*, 1999) from a hemispherical photograph taken at the centre of the pitfall plot, at a height of 1.3m.

Data analysis

The traps and collections were pooled for each plot and plot level data was used as the sample unit in all analyses. The dominance of each species, expressed as a percentage of the total species, in each woodland type was calculated. This was based on each species overall abundance weighted by its overall frequency of occurrence among plots, using the method developed by Pinzón and Spence (2010). Total abundance and species richness were compared between treatments using generalised linear mixed modelling (GLMM). This type of analysis is an extension of linear modelling which controls for the effects plots nested within sites (Zuur *et al.*, 2009). The abundance and species richness of forest specialist species and the three most abundant feeding guilds (ground runners, wandering sheet/ tangle weavers and space web-spinners) were also compared in this way.

Non-metric multi-dimensional scaling (NMDS) was used to examine spider species composition among plots. This is a type of unconstrained ordination which allows the entire variation in the data to be represented by the axes (McCune and Grace, 2002). The Bray-Curtis dissimilarity measure was used, singletons were removed, and the data were Hellinger transformed (Legendre and Gallagher, 2001). Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to test the effect of grazing within the oak and yew woodlands on species composition. This analysis was performed on Hellinger transformed species abundance data, using a blocking variable for site and using 4999 permutations.

The environmental variables measured within the $1m^2$ quadrat were averaged across the five quadrats per plot and plot level data was used in all analyses. The variables were compared between treatments with GLMM. Percentage cover values of variables were arcsine transformed before testing.

NMDS was conducted in PC-ORD (McCune and Mefford, 2011). All other analyses were conducted in R (R Core Team, 2012). GLMM used the lme4 package (Bates *et al.*, 2012) and the nlme package (Pinheiro *et al.*, 2013). Hellinger transformations and PERMANOVA were carried out using the vegan package (Oksanen *et al.*, 2012).

Results

Over the sampling period 1,133 adult spiders were collected belonging to 66 species and 14 families (Appendix 4). Thirty of these species were classified as forest specialists, six were classified as open specialists and the remaining 30 species were habitat generalists. The most abundant family was Linyphiidae (83%) and the dominant species was *Tenuiphantes zimmermanni* (Table 1) in both the yew and oak woodlands.

Spider fauna of oak and yew woodlands

A total of 59 species were captured in the oak woodland and the ten dominant species are presented in Table 1. One specimen of *Coelotes terrestris* was caught; this species is associated with coarse woody debris in semi-natural woodland and is restricted to the south of England (Harvey *et al.*, 2002). Three of the Linyphiid species caught here, *Saaristoa firma*, *Tapinocyba insecta* and *Walckenaeria dysderoides*, are classed as vulnerable in Great Britain.

A total of 20 species were caught in the yew woodland and the ten dominant species are presented in Table 1. Dominance was heavily weighted in favour of *Tenuiphantes zimmermanni*, with other species making up lesser proportions of the assemblage. No rare species were caught in this woodland, although one specimen of *Philodromus albidus* was found. This species is widespread in western and central Europe, but is confined to the south of England and its presence in Ireland was only recently discovered (Harvey *et al.*, 2002; Cawley, 2008).

NMDS ordination resulted in a final stress of 16.88 for a two-dimensional solution and explained 83% of the variation in species composition. The ordination revealed that species composition among plots was clustered according to forest type along Axis 1 (Figure 2).

Table 1. The ten dominant species in each of the oak and yew woodlands.

	Family	Habitat association	Dominance %
Oak			
Tenuiphantes zimmermanni	Linyphiidae	Forest specialist	22
Robertus lividus	Theridiidae	Habitat generalist	12
Monocephalus fuscipes	Linyphiidae	Forest specialist	11
Diplocephalus latifrons	Linyphiidae	Forest specialist	10
Tenuiphantes alacris	Linyphiidae	Forest specialist	8
Pirata hygrophilus	Lycosidae	Habitat generalist	7
Agyneta subtilis	Linyphiidae	Habitat generalist	6
Saaristoa abnormis	Linyphiidae	Habitat generalist	5
Microneta viaria	Linyphiidae	Forest specialist	5
Agyneta ramose	Linyphiidae	Forest specialist	4
Yew			
Tenuiphantes zimmermanni	Linyphiidae	Forest specialist	75
Agyneta subtilis	Linyphiidae	Habitat generalist	11
Tenuiphantes alacris	Linyphiidae	Forest specialist	3
Saaristoa abnormis	Linyphiidae	Habitat generalist	3
Metellina mengei	Tetragnathidae	Habitat generalist	2
Neriene peltata	Linyphiidae	Forest specialist	2
Linyphia hortensis	Linyphiidae	Forest specialist	1
Diplostyla concolor	Linyphiidae	Habitat generalist	1
Harpactea hombergi	Dysderidae	Forest specialist	0.4
Cyclosa conica	Araneidae	Forest specialist	0.2

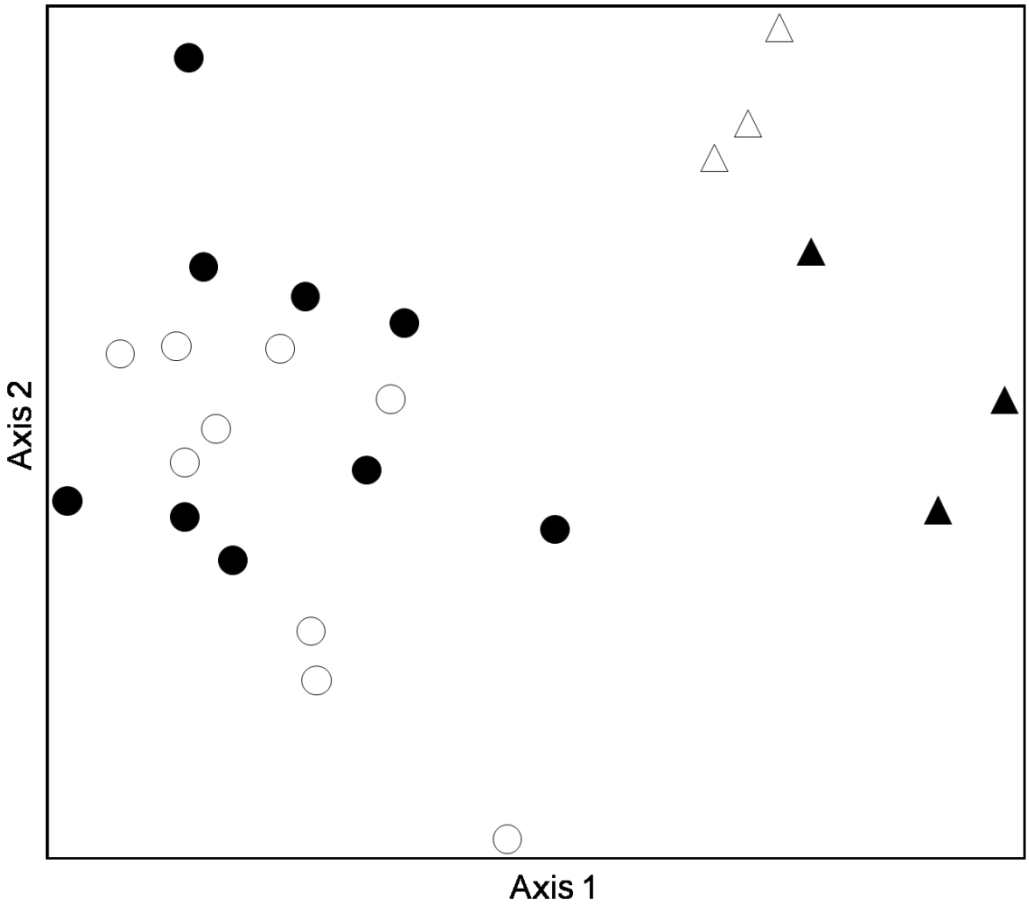


Figure 2. NMDS ordination of species assemblages at each treatment x woodland type plot. Oak (●), yew (▲). Unfilled = ungrazed plots, filled = grazed plots. Axis 1 = 66%, P = 0.02. Axis 2 = 18%, P = 0.02.

Effects of grazing in oak and yew woodlands

In the oak woodland, the structural diversity of ground layer habitats was higher in the ungrazed plots, which had significantly greater cover of litter and lower field layer vegetation compared to the grazed plots, whereas the grazed plots had significantly greater cover of bare ground (Table 2). There was also a positive effect of the ungrazed plots compared to grazed plots on the abundance of all species, forest specialist species, ground runner species, space web-weaving species and wandering sheet/ tangle weaver species (Table 3). Total species richness was also significantly higher in the ungrazed plots compared with grazed plots, which was driven by higher species richness of wandering sheet/ tangle weaver spiders. In terms of species composition NMDS did not show any clustering of ungrazed and grazed plots (Figure 2) and PERMANOVA did not identify treatment as a significant factor affecting species composition ($F_{1,17}$ = 1.39, P = 0.17).

In the yew woodland, ungrazed plots had significantly higher cover of upper field vegetation compared with grazed plots; however there was no effect on any of the other habitat variables (Table 2). Total species and forest specialist species abundance was significantly higher in grazed plots compared to ungrazed plots, which was driven by a greater abundance of wandering sheet/ tangle weaver spiders, and in particular the species *Tenuiphantes zimmermanni*, which was three times more abundant in the grazed plots (n = 92) compared to ungrazed plots (n=30). However, there was no effect of treatment on species richness (Table 3). NMDS showed separation of species composition among ungrazed and grazed plots by treatment along Axis 2 (Figure 2), however, PERMANOVA did not identify a significant effect of treatment on species composition ($F_{1,5}$ = 4.01, P = 0.10).

Table 2. Mean ± SE for habitat variables from plots (n) each woodland type x treatment combination. Differences between ungrazed and grazed plots tested with GLMM: * < 0.05, ** < 0.01.

	Oak			Yew		
	Ungrazed (n = 9)	Grazed (n = 9)	GLMM	Ungrazed (n = 3)	Grazed (n = 3)	GLMM
Bare ground	28.33 ± 7.11[a]	45.28 ± 4.52[A]	$t_{1,17}$ = -2.11*	46.39 ± 7.24	54.72 ± 1.21	$t_{1,5}$ = -1.09
Litter cover	79.35 ± 3.49[A]	65.93 ± 5.11[a]	$t_{1,17}$ = 3.30**	54.17 ± 17.22	55.83 ± 16.07	$t_{1,5}$ = -0.02
Litter depth	1.78 ± 0.21	1.53 ± 0.18	$t_{1,17}$ = 0.82	0.50 ± 0	0.92 ± 0.21	$t_{1,5}$ = -2.62
Fine woody debris cover	21.87 ± 4.62	29.98 ± 5.36	$t_{1,17}$ = -1.26	43.67 ± 12.61	42.56 ± 16.50	$t_{1,5}$ = 0.03
Coarse woody debris m^3	1.48 ± 1.42	1.38 ± 0.48	$t_{1,17}$ = 0.10	4.17 ± 3.37	2.22 ± 1.11	$t_{1,5}$ = 0.55
Ground vegetation cover	76.48 ± 5.23	62.69 ± 4.66	$t_{1,17}$ = 1.91	92.22 ± 6.19	81.39 ± 9.82	$t_{1,5}$ = 0.65
Lower field cover	56.48 ± 10.74[A]	21.48 ± 10.72[a]	$t_{1,17}$ = 2.54*	1.67 ± 0.96	3.33 ± 3.33	$t_{1,5}$ = -0.48
Upper field cover	6.85 ± 3.82	0 ± 0	$t_{1,17}$ = 1.78	5.28 ± 1.55[A]	0 ± 0[a]	$t_{1,5}$ = 3.41*
Canopy cover	83.33 ± 1.44	84.00 ± 1.00	$t_{1,17}$ = 0	80.00 ± 5.77	88.33 ± 1.67	$t_{1,5}$ = 0

[A] is greater than [a]

Table 3. Mean ± SE for species metrics from plots (n) in each woodland type x treatment combination. Differences between ungrazed and grazed plots tested with GLMM: ** < 0.01, *** < 0.001.

	Oak			Yew		
	Ungrazed (n = 9)	Grazed (n = 9)	GLMM	Ungrazed (n = 3)	Grazed (n = 3)	GLMM
Abundance						
All species	66.33 ± 6.65^{A}	37.11 ± 3.92^{a}	$t_{1,17}$ = 8.50***	25.33 ± 3.84^{a}	42.00 ± 4.93^{A}	$t_{1,5}$ = -3.48***
Forest specialists	39.22 ± 5.43^{A}	22.11 ± 2.42^{a}	$t_{1,17}$ = 6.47***	13.33 ± 3.38^{a}	32.33 ± 4.91^{A}	$t_{1,5}$ = -4.71***
Ground runners	6.22 ± 2.97^{A}	3.00 ± 0.75^{a}	$t_{1,17}$ = 3.11**	0.33 ± 0.33	0.67 ± 0.33	$t_{1,5}$ = -0.57
Space web-builders	8.00 ± 1.59^{A}	2.00 ± 0.53^{a}	$t_{1,17}$ = 5.25***	0.33 ± 0.33	0.33 ± 0.33	$t_{1,5}$ = 0
Wandering sheet/tangle weavers	50.44 ± 6.97^{A}	30.67 ± 3.35^{a}	$t_{1,17}$ = 6.52***	22.00 ± 4.36^{a}	40.00 ± 4.62^{A}	$t_{1,5}$ = -3.90***
Species richness						
All species	17.44 ± 1.48^{A}	13.67 ± 1.53^{a}	$t_{1,17}$ = 2.03*	7.00 ± 0.58	7.00 ± 1.00	$t_{1,5}$ = 0
Forest specialists	8.44 ± 0.65	7.11 ± 0.63	$t_{1,17}$ = 1.01	3.00 ± 0	2.33 ± 0.67	$t_{1,5}$ = 0.50
Ground runners	1.78 ± 0.28	2.11 ± 0.45	$t_{1,17}$ = -0.51	0.33 ± 0.33	0.67 ± 0.33	$t_{1,5}$ = -0.56
Space web-builders	1.11 ± 0.11	0.78 ± 0.15	$t_{1,17}$ = 0.72	0.33 ± 0.33	0.33 ± 0.33	$t_{1,5}$ = 0
Wandering sheet/ tangle weavers	13.44 ± 1.22^{A}	9.56 ± 0.94^{a}	$t_{1,17}$ = 2.42*	4.67 ± 0.33	5.33 ± 0.88	$t_{1,5}$ = -0.37

^{A} is greater than ^{a}

Discussion

To the authors knowledge these results provide the first description of the ground-dwelling spider fauna of Killarney National Park and the first insight into ground-dwelling spider diversity in yew woodland in Ireland. Furthermore Killarney National Park provides a unique opportunity to assess the effects of grazing in extremely rare habitat types. However, it must be noted that results from the yew woodland should be interpreted with caution as only one deer grazing exclosure was available for study and a lack of replication may be a limitation on the findings (Hurlbert, 1984).

Spider fauna of oak and yew woodlands

Killarney National Park is one of the few areas in Ireland which has had continuous woodland cover since the last glacial period (Mitchell, 1988). Rare and ancient woodlands often support specialised species groups, particularly for vascular plants (Peterken and Game, 1984; Hermy *et al.*, 1999). Therefore, it might be expected that these woodlands could also support a distinct spider species assemblage. However, both the oak and yew woodlands supported a typical forest spider assemblage and the majority of species were associated with many types of broad-leaved and coniferous woodland (Oxbrough *et al.*, 2006; Nolan, 2008; Oxbrough *et al.*, 2010). In particular, *Tenuiphantes zimmermanni*, the most dominant species caught, is frequently found in Irish conifer plantations and could be thought of as a ubiquitous forest species (Oxbrough *et al.*, 2010; Oxbrough *et al.*, 2012).

Species richness of the oak woodland was similar to the species richness reported from Sitka spruce plantations in Ireland and shared many of the same species, providing further evidence that plantation forests are able to support a diverse spider species assemblage (Oxbrough *et al.*, 2005; Oxbrough *et al.*, 2010; Oxbrough *et al.*, 2012). The yew woodland supported very low species richness compared to the oak woodland and to reports from other forest types in Ireland (Oxbrough *et al.*, 2005; Nolan, 2008; Oxbrough *et al.*, 2010), therefore this could potentially be a naturally species poor habitat. The dense canopy cover, leading to little light penetration, and the lack of vegetation and litter structure in the yew woodland could explain this, as forest spider diversity is associated with these factors (Oxbrough *et al.*, 2005). There is no published research on the diversity of spiders in yew woodlands, but the findings reported here indicate that although this is a rare habitat it does not support rare spider species.

The migratory ability of spiders to colonise new areas of suitable habitat and their response to habitat structure (Wise, 1993), which can vary regardless of the cover tree species (Ziesche and Roth, 2008), is the most likely reason for the majority of species caught in these woodlands occurring in both native and exotic forest types. It is also possible that the long history of deforestation in Ireland has resulted in a forest generalist spider fauna, where species have adapted to the conditions of exotic plantation forests, with few species retaining a strong preference for native woodlands (Whitehouse, 2006).

Despite the similarities between these woodlands and other more common forest types in Ireland, a number of species were discovered which are of interest from a conservation perspective. *Coelotes terrestris* is range-restricted in Great Britain and is known to be threatened by the removal of coarse woody debris and the loss of semi-natural woodland (Harvey *et al.*, 2002). These threats are also present in Ireland, which has an intensively managed landscape, where exotic conifers dominate the forested area and there is very little coarse woody debris (Sweeney *et al.*, 2010; Forest Europe *et al.*, 2011). Furthermore the interest in removing deadwood for biofuel has increased throughout Europe in recent years (Rudolphi and Gustafsson, 2005; Deuffic and Lyser, 2012).

Philodromus albidus, recently discovered in Ireland (Cawley, 2008), is a canopy species associated with clearings in mature broad-leaved woodland and old hedgerows (Jones, 1992; Harvey *et al.*, 2002). Interestingly, this species was caught in the yew woodland, although there have been a few instances of *P. albidus* recorded on yew trees (Russell-Smith, 1991). Whilst *P.albidus* is not listed as threatened, its range is restricted in Great Britain and undetermined in Ireland. The closure of woodland and loss of old hedgerows will be detrimental to this species and management to prevent woodland closure can utilise light grazing by large mammals such as deer (Harvey *et al.*, 2002).

Three other species of conservation importance were found in these woodlands which are classed as vulnerable in Britain (Dawson *et al.*, 2008). *Saaristoa firma* uses a variety of wet habitats in Britain and is thought to have undergone a decline due to the drainage of wetlands, however, in Ireland this species is known to prefer damp, deciduous woodlands. The area of Killarney experiences relatively high rainfall and humidity and the oak woodland sampled here is poorly drained in places making conditions ideal for this species. *Tapinocyba insecta* is thought to have undergone long-term decline in Britain and occurs in flushes and leaf litter in ancient semi-natural broadleaved woodland in both Britain and

Ireland. This habitat type is scarce in both countries and it is likely that it has also undergone long-term decline in Ireland, due to the loss of ancient woodlands. *Walckenaeria dysderoides* is known from a variety of habitats in Britain and reasons for its decline here are unclear. In Ireland, this species occurs in mosses and litter in both broadleaved and coniferous woodlands and plantation forests.

S. firma and W. dysderoides are able to utilise a variety of habitats present in Ireland and their presence in Killarney National Park is probably of less significance than that of *C. terrestris, P. albidus* and *T. insecta*. The latter three species are more specialised in their ecological requirements and the lack of ancient semi-natural woodland in Ireland suggests Killarney National Park may provide an important and nationally scarce habitat for these species.

Effects of grazing

Ungrazed plots in the oak woodland supported greater abundance of ground-dwelling spiders, including forest specialist species and ground runner, space web-weaver and wandering sheet/ tangle weaver feeding guilds. However, only total species richness and wandering sheet/ tangle weaver species richness was significantly higher in the ungrazed plots compared with the grazed plots. The Linyphiidae were the most abundant family and form part of the wandering sheet/ tangle weaver guild. Species from this spider family are particularly sensitive to the effects of grazing, due to their dependence on vegetation structure (Dennis *et al*., 1998). Conversely, in the yew woodland, spider abundance was higher in the grazed plots compared to ungrazed plots, although no effect on species richness was observed. The majority of species caught in these woodlands are adapted to hunt in the litter and low vegetation layers (Nolan, 2008), meaning that the greater cover of litter and lower field layer vegetation in the ungrazed plots in the oak woodland is likely to influence abundance and species richness here, by increasing the available habitat area, associated prey, web-attachment points, and shelter from predators (Uetz, 1979; Stevenson and Dindal, 1982; Uetz, 1991; Gunnarsson, 1996). The higher abundance of spiders observed in grazed plots compared to ungrazed plots in the yew woodland was driven mainly by one species, *T. zimmermanni*, which often occurs in high numbers in the moss and needle litter layer in conifer forests with little ground vegetation (Docherty and Leather, 1997; Nolan, 2008). However, the lack of a difference in species richness indicates that overall ground-dwelling spider diversity did not differ between the two treatments.

Despite these differences in abundance and richness there was no effect of treatment on species composition in the oak or yew woodlands. These results are surprising given the known influence of habitat structure on ground-dwelling spiders and the documented impact of deer grazing on biodiversity (Mitchell and Kirby, 1990; Perrin *et al.*, 2011). However, it must be noted that these exclosures have only been in place for five years and effects on spider species composition may not be apparent until the exclosures have been in place for a longer period of time. Additionally, invertebrate communities which utilise higher layers of the vegetation, such as field layer and arboreal spiders, may be more susceptible to the effects of deer browsing. Invertebrate herbivore species or feeding guilds which have strong plant species associations could also be useful indicators when investigating the effect of grazing (Brousseau *et al.*, 2013). The current methodology did not sample these species groups and suction sampling or sweep netting which sample higher strata of the vegetation could provide more significant results and information on species which may be useful indicators of over-grazing.

Although there was an initial increase in lower field vegetation cover as a result of deer exclusion, this may not last. Previous research within deer exclosures at Killarney National Park has shown that as the understory vegetation increased in cover the ground flora diversity declined due to competitive plant species such as bramble (*Rubus fruticosus*) and ivy (*Hedera helix*) outcompeting woodland specialist species (Perrin *et al.*, 2011). Therefore, using long-term deer exclosures in the oak woodlands may lead to a decline in vegetation diversity and a decline in spider diversity. Recommendations have been made for maintaining a low level of grazing, as this could benefit woodland specialist ground vegetation (Perrin *et al.*, 2011). Furthermore, light grazing is recommended to prevent woodland closure, which will benefit species such as *P. albidus*. Therefore, if the conservation objective is to increase biodiversity in these woodlands permanent deer grazing exclosures may not be necessary. A more appropriate system could include deer as part of a management plan for biodiversity rather than using exclusion zones. Deer are an integral part of many natural woodland ecosystems and studies on deer grazing in Britain have concluded that if they are managed appropriately they could be a useful tool in woodland management (Mitchell and Kirby, 1990; Kirby *et al.*, 1994; Hester *et al.*, 2000; Stewart, 2001). However, as these exclosures have only been in place for five years the temporal and spatial effects of grazing requires further investigation to determine the long-term effects on spider diversity.

These findings not only have implications for the remaining areas of semi-natural woodland, but also for sustainable forest management as the increase in plantation forestry has been associated with the recent range expansion of deer across Ireland (Purser, 2009). Therefore monitoring of grazing levels may need to be incorporated in forest management plans in both semi-natural woodlands and plantation forests.

Conclusions

These rare oak and yew woodlands supported a spider species assemblage typical of Irish forests. However, in the context of Ireland's highly modified landscape, Killarney National Park may provide important habitat for a number of vulnerable and range-restricted species, which are threatened by the decline of semi-natural woodland in Ireland and Britain.

This research has also shown that deer grazing reduces the overall abundance and species richness of ground-dwelling spiders in the oak woodlands of Killarney National Park, however, spider species composition remains unaffected. Further research is required to understand the long-term effects of deer grazing exclosures on spider diversity. Additionally, research into the effect of grazing on arthropod species groups which utilise higher layers of the vegetation is recommended, as these taxa may prove to be useful as indicators of over-grazing.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32-46.

Anon, 2007. National Forest Inventory: Republic of Ireland Results. Department of Agriculture, Food and the Marine, Government of Ireland.

Bates, D., Maechler, M., Bolker, B., 2012. Package 'lme4'. Linear mixed-effects models using S4 classes. R version 0.999999-2.

Batten, L.A., 1976. Bird Communities of Some Killarney Woodlands. Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science 76, 285-313.

Brousseau, P.-M., Hébert, C., Cloutier, C., Côté, S., 2013. Short-term effects of reduced white-tailed deer density on insect communities in a strongly overbrowsed boreal forest ecosystem. Biodiversity & Conservation 22, 77-92.

Brown, V.K., Gibson, C.W.D., McGavin, G.C., Losito, L., 1992. The response of invertebrate assemblies to grazing. Ecography 15, 166-176.

Carden, R.F., Carlin, C.M., Marnell, F., McElholm, D., Hetherington, J., Gammell, M.P., 2011. Distribution and range expansion of deer in Ireland. Mammal Review 41, 313–325.

Carden, R.F., McDevitt, A.D., Zachos, F.E., Woodman, P.C., O'Toole, P., Rose, H., Monaghan, N.T., Campana, M.G., Bradley, D.G., Edwards, C.J., 2012. Phylogeographic, ancient DNA, fossil and morphometric analyses reveal ancient and modern introductions of a large mammal: the complex case of red deer (*Cervus elaphus*) in Ireland. Quaternary Science Reviews 42, 74-84.

Cawley, M., 2008. More records for uncommon spiders (Araneae), including four species new to Ireland. Bulletin of the Irish Biogeographical Society 32, 69-83.

Clarke, R.D., Grant, P.R., 1968. An Experimental Study of the Role of Spiders as Predators in a Forest Litter Community. Part 1. Ecology 49, 1152-1154.

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological Impacts of Deer Overabundance. Annual Review of Ecology, Evolution, and Systematics 35, 113-147.

Dawson, I., Harvey, P., Russell-Smith, T., 2008. A national Status Review - the draft results. Spider Recording Scheme News 112, 18-24.

Dennis, P., Young, M., Gordon, I., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. Ecological Entomology 23, 253–264.

Deuffic, P., Lyser, S., 2012. Biodiversity or bioenergy: is deadwood conservation an environmental issue for French forest owners? Canadian Journal of Forest Research 42, 1491-1502.

Docherty, M., Leather, S., 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. Forest Ecology and Management 95, 197-207.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Frazer, G., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University and the Institute of Ecosystem Studies, Millbrook, New York.

Gibson, C.W.D., Hambler, C., Brown, V.K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. Journal of Applied Ecology 29, 132-142.

Gunnarsson, B., 1983. Winter Mortality of Spruce-Living Spiders: Effect of Spider Interactions and Bird Predation. Oikos 40, 226-233.

Gunnarsson, B., 1996. Bird Predation and Vegetation Structure Affecting Spruce-Living Arthropods in a Temperate Forest. Journal of Animal Ecology 65, 389-397.

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdamc, C., Lawessond, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biological Conservation 91, 9-22.

Hester, A.J., Edenius, L., Buttenschøn, R.M., Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73, 381-391.

Hurlbert, S.H., 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs 54, 187-211.

Jones, D., 1992. *Philodromus albidus* Kulczynski in Hampshire. Newsletter of the British Arachnological Society 64, 7.

Kelly, D.L., 1981. The Native Forest Vegetation of Killarney, South-West Ireland: An Ecological Account. Journal of Ecology 69, 437-472.

Kelly, D.L., 2002. The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: a 25-year experimental study. Forest Ecology and Management 166, 207-226.

Kirby, K.J., Mitchell, F.J.G., Hester, A.J., 1994. A role for large herbivores (deer and domestic stock) in nature conservation management in British semi-natural woods. Arboricultural Journal 18, 381-399.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Lynch, Á., McCann, Y., 2007. The diet of the pine marten (*Martes martes*) in Killarney National Park. Biology & Environment: Proceedings of the Royal Irish Academy 107, 67-76.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities, MjM Software Design, Oregon, USA.

McCune, B., Mefford, M.J., 2011. PC ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.

Mitchell, F.J.G., 1988. The Vegetational History of the Killarney Oakwoods, SW Ireland: Evidence from Fine Spatial Resolution Pollen Analysis. Journal of Ecology 76, 415-436.

Mitchell, F.J.G., Kirby, K.J., 1990. The Impact of Large Herbivores on the Conservation of Semi-natural Woods in the British Uplands. Forestry 63, 333-353.

Miyashita, T., Takada, M., Shimazaki, A., 2004. Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. Ecoscience 11, 74-79.

National Parks and Wildlife Service, 2006. Site synopsis: Killarney National Park, Macgillycuddy's Reeks and Caragh River Catchment. Department of the Environment, Heritage and Local Government, Ireland.

National Parks and Wildlife Service, 2008. The Status of EU Protected Habitats and Species in Ireland. Department of the Environment, Heritage and Local Government, Ireland.

Nolan, M., 2008. Database of Irish Spiders (Araneae). Irish Wildlife Manuals. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin.

NPWS, 2005. Management Plan for Killarney National Park 2005-2009. Government of Ireland.

O'Halloran, J., Irwin, S., Kelly, D. L., Kelly, T. C., Mitchell, F. J. G., Coote, L., Oxbrough, A., Wilson, M. W., Martin, R. D., Moore, K., Sweeney, O., Dietzsch, A. C., Walsh, A., Keady, S., French, V., Fox, H., Kopke, K., Butler, F. and Neville, P. 2011 Management of biodiversity in a range of Irish forest types. Report prepared for the Department of Agriculture, Fisheries and Food, Government of Ireland.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Hendry, M., Stevens, H., Wagner, H., 2012. Vegan: Community Ecology Package. R version 2.0-7.

Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? Forest Ecology and Management 270, 11-18.

Oxbrough, A., Irwin, S., Kelly, T., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111–2121.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management 212, 171-183.

Perrin, P., Martin, J., Barron, S., O'Neill, F., McNutt, K., Delaney, A., 2008. National Survey of Native Woodlands 2003-2008. National Parks and Wildlife Service, Ireland.

Perrin, P.M., Kelly, D.L., Mitchell, F.J.G., 2006. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Natural regeneration and stand dynamics. Forest Ecology and Management 236, 356-367.

Perrin, P.M., Mitchell, F.J.G., Kelly, D.L., 2011. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Changes in ground flora and species diversity. Forest Ecology and Management 262, 2328-2337.

Peterken, G.F., Game, M., 1984. Historical Factors Affecting the Number and Distribution of Vascular Plant Species in the Woodlands of Central Lincolnshire. Journal of Ecology 72, 155-182.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2013. Package 'nlme'. R version 3.1-109.

Pinzón, J., Spence, J., 2010. Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. Journal of Insect Conservation 14, 439-458.

Platnick, N.I., 2012. The World Spider Catalog, Version 13.0. The American Museum of Natural History.

Purser, P., Wilson, F., & Carden, R. , 2009. Deer and forestry in Ireland: A review of current status and management requirements. Woodlands of Ireland.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK.

Rudolphi, J., Gustafsson, L., 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. Scandinavian Journal of Forest Research 20, 235-242.

Russell-Smith, A., 1991. *Philodromus albidus* Kulczynski from East Anglia. Newsletter of the British Arachnological Society 61, 3.

Smal, C.M., Fairley, J.S., 1982. The dynamics and regulation of small rodent populations in the woodland ecosystems of Killarney, Ireland. Journal of Zoology 196, 1-30.

Spooner, P., Lunt, I., Robinson, W., 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management & Restoration 3, 117-126.

Stevenson, B.G., Dindal, D.L., 1982. Effect of Leaf Shape on Forest Litter Spiders: Community Organization and Microhabitat Selection of Immature *Enoplognatha Ovata* (Clerck) (Theridiidae). Journal of Arachnology 10, 165-178.

Stewart, A.J.A., 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry 74, 259-270.

Sweeney, O.F.M., Martin, R.D., Irwin, S., Kelly, T.C., O'Halloran, J., Wilson, M.W., McEvoy, P.M., 2010. A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. Forest Ecology and Management 259, 2056-2064.

Uetz, G., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40, 29-42.

Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Ed.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, London, UK.

Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild Structure of Spiders in Major Crops. Journal of Arachnology 27, 270-280.

UNESCO, 2001. Biosphere Reserve Information. Ireland. Killarney. UNESCO.

Whitehouse, N., 2006. The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. Quaternary Science Reviews 25, 15–16.

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press.

Ziesche, T.M., Roth, M., 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? Forest Ecology and Management 255, 738-752.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science + Business Media, LLC, New York, USA.

Chapter 8

Concluding synthesis



Eupeodes latifasciatus from afforested agricultural grassland

Main conclusions

The forest areas of Ireland and, to a lesser extent, Britain are unique compared to much of mainland Europe, where extensive forest cover is common (Forest Europe *et al.*, 2011). The majority of afforestation in Ireland is carried out in agricultural grasslands and this has important implications for ecosystem services, including biodiversity, biological control and pollination. Chapter 2 presents the first within site assessment of the effects of afforestation in agricultural grasslands on invertebrate species groups in Ireland. The results of this research indicate that planting forests in agricultural land provides a greater number of habitats and microhabitats, therefore increasing landscape heterogeneity and site-level habitat heterogeneity. This positively influences the species richness of ground-dwelling spider species and benefits the species composition of ground-dwelling spiders and hoverflies. Wooded areas, including hedgerows, support high abundance and diversity of predatory species, such as spiders and hoverflies, which can contribute towards the biological control of crop pests (Peng *et al.*, 1993; Kajak, 2007; Bennewicz, 2011). Additionally, hoverflies are an important contributor to pollination services for both wildflowers and crops (Larson *et al.*, 2001; Fontaine *et al.*, 2006; Albrecht *et al.*, 2012; Jauker *et al.*, 2012). Hedgerows are also important for landscape connectivity, provide important supplementary habitat in newly afforested sites, and may be the only semi-natural habitat occurring in agricultural land and non-native plantation forests (Le Coeur *et al.*, 2002; Marshall and Moonen, 2002; Benton *et al.*, 2003).

The planting of new forests and subsequent rotations of existing plantation forests provide an important opportunity to plan and manage for biodiversity conservation from the time of establishment. One of the fundamental influences on species composition and diversity in forests is the amount of light which can penetrate to the forest floor (Sparks and Greatorex-Davies, 1992; Watkins *et al.*, 2003; Oxbrough *et al.*, 2006; Avon *et al.*, 2010). Chapter 3 investigated the importance of open forest road habitat for ground-dwelling spider diversity and presents the first study to explicitly test the effect of manipulating forest road-widths. The presence of vulnerable and endangered species, particularly those which require herbaceous vegetation and damp habitats, in young open plantation forest habitat and forest road-verges indicates the importance of open habitat within forests for species of conservation priority. The present study found no difference in ground-dwelling spider species richness or composition between the road-verges and forest interior, or standard (15m) and wide (30m) roads in young plantation forests. However, the influence of canopy

cover in later stages in the forest cycle is likely to have an effect on ground-dwelling spider diversity and species composition (Oxbrough *et al.*, 2006). These results provide important baseline data and repeat surveys are recommended for all stages of the forest cycle in order to determine how spider diversity is affected by changes in canopy cover and habitat succession in plantation forest road-verges. Research into methods of maximising biodiversity in young plantation forests is particularly relevant in countries undertaking large-scale afforestation, to inform policy development and forest management.

Forest management to manipulate influential features such as open spaces is important for biodiversity conservation throughout the forest cycle (Warren and Fuller, 1993; Lindenmayer *et al.*, 2006). However, the selection of tree species can also have a profound effect on the biodiversity supported by plantation forests and provide an alternative means of enhancing below canopy conditions (Palik and Engstrom, 1999; Horgan *et al.*, 2003). Although fast growing non-native species dominate the Irish forestry sector, there is the potential to use conifer species which provide habitat that naturally supports higher biodiversity. Chapter 4 presents the first investigation into the value of four commonly used conifer tree species in plantation forests in Ireland for ground-dwelling spider diversity. The findings of this research indicate that Scots pine, a semi-native tree species, and Norway spruce, a species of European provenance, support higher ground-dwelling spider species richness compared to the two most commonly planted North American species, Sitka spruce and lodgepole pine. Additionally, Scots pine forests are associated with a greater diversity of species and functional groups and have a more open canopy structure which increases light penetration and results in a greater cover of upper field vegetation, and more native fauna (Speight, 1985; Roche *et al.*, 2009), compared with the three other conifer types. Forest policy advocates using a mixed tree species composition in plantation forests to increase habitat heterogeneity and enhance forest biodiversity (European Environment Agency, 2008; Forest Service, 2000; Forestry Commission, 2011). However, the study conducted with Forest Research UK, which is presented in Chapter 5, indicates that there are few consistent effects of mixed or monoculture tree species on ground-dwelling spider and carabid beetle diversity, and no benefit to species richness when the secondary tree species is used at levels of up to 40% in an intimate mix.

Biodiversity assessments of species groups in forests require extensive sampling and identification to gain a representative picture of the species inhabiting the forest. This is rarely possible for forest managers to undertake, due to constraints on time, money, and

expertise (Lawton, 1998; Lindenmayer, 1999). Chapter 6 presents the first study to examine the reliability of biodiversity indicators for predicting species richness in different forest types across Ireland and England. The results indicate that the use of easily measured site characteristics such as stand age, canopy openness, litter cover, and field layer cover, which affect a number of species groups, including ground vegetation and ground-dwelling spiders, can support forest management plans by providing a quick indication of the species richness in a plantation forest stand. These indicators are easy and inexpensive to assess by non-experts, can be controlled through forest management to enhance biodiversity, and most are applicable in both conifer and broadleaf plantation forests. However, this study also emphasises the need for rigorous scientific testing of biodiversity indicators to determine those which are effective in specific forest types and regions. Additional factors such as climate and land use history also determine the management required for biodiversity conservation in a plantation forest stand.

Chapter 7 presents the first investigation into ground-dwelling spider diversity in an important area of ancient semi-natural woodland in Ireland. The findings indicate that these remnant areas of ancient semi-natural woodland may provide important habitat for a number of vulnerable and range-restricted ground-dwelling spider species, which are threatened by the decline of semi-natural woodland. Deer grazing was an important determinant of ground-dwelling spider species richness in the oak woodlands, through its effects on herbaceous vegetation, although the effects in the yew woodland were less clear. However, as these exclosures have only been in place for five years the temporal and spatial effects of grazing requires further investigation, to determine the long-term effects on spider species richness and composition.

The results of this research are relevant for many countries with a similar situation to Ireland and Britain, such as Hungary, Denmark and parts of Australia and New Zealand, where there has been vast deforestation, replacement with agricultural and urban development, and a recent increase in plantation forestry (Mather, 1992).

Forest management recommendations

Hedgerows provide supplementary habitats, which are an important contributor to biodiversity in landscapes and plantation forests (Marshall and Moonen, 2002; Gittings *et al.*, 2006; Oxbrough *et al.*, 2007). These should be protected from forestry related activities through the use of buffer zones to prevent shading and competition from the dominant tree

species. Increasing light penetration through the canopy to create a mosaic of open well-vegetated areas and shaded areas with lower vegetation will support the highest biodiversity, and potentially also species of conservation priority, in plantation forests. Methods for achieving this include thinning, which is particularly important in conifer plantations and into successive rotations, which can have increased canopy cover compared to first rotations (Oxbrough *et al.*, 2010; Coote *et al.*, 2013). Open glades can also promote high species diversity (Gittings *et al.*, 2006; Oxbrough *et al.*, 2006; Smith *et al.*, 2007), and forest roads may be an important contributor to open spaces for biodiversity conservation. These areas should be planned and managed from the time of establishing a plantation forest. The selection of tree species can also be used to manage below-canopy light levels. Broadleaf species or species such as Scots pine, which allow greater light penetration through the leaves, compared with other conifer species, should be considered for use and, after further testing to determine levels at which biodiversity is enhanced, could be included as a secondary species in a mix, to increase below-canopy structural diversity (Gates *et al.*, 1965; Hill, 1979; Lust *et al.*, 1998; Coote *et al.*, 2013). The structural diversity of below canopy layers is subject to alteration through grazing activity by wild animals, such as deer, which in turn affects the biodiversity of many trophic levels, including plants and invertebrates. Therefore, monitoring of the impact of grazing is an important consideration in forest management plans for biodiversity enhancement in native woodlands, but also potentially in plantation forests.

Further research

This research has important findings and implications for many of the topics relating to sustainable forest management in the contemporary forests of Ireland and Britain. However, there are a number of forest management issues addressed here which require further research to determine their effects on biodiversity and usefulness in management plans. The effects of afforestation in agricultural land, the value of open space provided by forest roads and the benefit of deer grazing exclosures have only been investigated in their initial stages of implementation. Many changes occur during the forest cycle and the effects of these on biodiversity should be monitored throughout each stage to thoroughly understand and effectively manage them for biodiversity conservation. Additionally, the ratios and planting patterns at which a mixed tree species composition has an effect on invertebrate diversity requires further investigation to inform forest policy for biodiversity enhancement. Further to these findings, another area of research which should be considered is the prey species

consumed by predatory invertebrate species, such as spiders and carabid beetles. The species data used in many studies of biodiversity assumes a ready and continuous supply of prey, however, there is evidence to suggest that predatory invertebrate species are affected by prey abundance and distribution (McIver *et al.*,1992; Halaj *et al*., 1998). Analysis of prey data may reveal more information about the species composition and diversity of spider and carabid beetle species in forest ecosystems.

References

Albrecht, M., Schmid, T., Hautier, Y., Müller, C., 2012. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences 7, 4845-4852.

Avon, C., Bergès, L., Dumas, Y., Dupouey, J.-L., 2010. Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecology and Management 259, 1546-1555.

Bennewicz, J., 2011. Aphidivorous hoverflies (Diptera: Syrphidae) at field boundaries and woodland edges in an agricultural landscape. Polish Journal of Ecology 80, 129-149.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182-188.

Coote, L., Dietzsch, A.C., Wilson, M.W., Graham, C.T., Fuller, L., Walsh, A.T., Irwin, S., Kelly, D.L., Mitchell, F., Kelly, T.C., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. Ecological Indicators 32, 107-115.

European Environment Agency, 2008. European Forests – ecosystem conditions and sustainable use. EEA Report, Copenhagen.

Fontaine, C., Dajoz, I., Meriguet, J., Loreau, M., 2006. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLoS Biology 4, e1.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Forest Service, 2000. Forest Biodiversity Guidelines. Forest Service, Department of the Marine and Natural Resources, Dublin.

Forestry Commission, 2011. The UK Forestry Standard: The UK Government's Approach to Sustainable Forestry. The Forestry Commission, Edinburgh, UK.

Gates, D.M., Keegan, H.J., Schleter, J.C., Weidner, V.R., 1965. Spectral Properties of Plants. Applied Optics 4, 11-20.

Gittings, T., O'Halloran, J., Kelly, T., Giller, P., 2006. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management 237, 290–300.

Halaj, J., Ross, D., Moldenke, A., 1998. Habitat Structure and Prey Availability as Predictors of the Abundance and Community Organization of Spiders in Western Oregon Forest Canopies. Journal of Arachnology 26, 203-220.

Hester, A.J., Edenius, L., Buttenschøn, R.M., Kuiters, A.T., 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73, 381-391.

Hill, M.O., 1979. The development of a flora in even-aged plantations. In: Ford, E.D., Malcolm, D.C., Atterson, J. (Eds.), The ecology of even-aged forest plantations. Institute of Terrestrial Ecology, Cambridge, pp. 175-192.

Horgan, T., Keane, M., McCarthy, R., Lally, M., Thompson, D., 2003. A Guide to Forest Tree Species Selection and Silviculture in Ireland. COFORD, Dublin.

Jauker, F., Bondarenko, B., Becker, H.C., Steffan-Dewenter, I., 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology 14, 81-87.

Kajak, A., 2007. Effects of forested strips on spider assemblages in adjacent cereal fields: dispersal activity of spiders. Polish Journal of Ecology 55, 691-704.

Kirby, K.J., Mitchell, F.J.G., Hester, A.J., 1994. A role for large herbivores (deer and domestic stock) in nature conservation management in British semi-natural woods. Arboricultural Journal 18, 381-399.

Larson, B.M.H., Kevan, P.G., Inouye, D.W., 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. The Canadian Entomologist 133, 439-465.

Larsson, T.B., 2001. Biodiversity evaluation tools for European forests. Ecological Bulletins, Blackwell, Oxford.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.H., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt,

A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification on tropical forests. Nature 391, 72-76.

Le Coeur, D., Baudry, J., Burel, F., Thenail, C., 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. Agriculture, Ecosystems & Environment 89, 23-40.

Lindenmayer, D.B., 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. Forest Ecology and Management 115, 277-287.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433-445.

Lust, N., Muys, B., Nachtergale, L., 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodiversity & Conservation 7, 249-260.

Marshall, E.J.P., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems & Environment 89, 5-21.

Mather, A.S., 1992. The Forest Transition. Area 24, 367-379.

McIver, J.D., Parsons, G.L., Moldenke, A.R., 1992. Litter spider succession after clear-cutting in a western coniferous forest. Canadian Journal of Forest Research 22, 984-992.

Mitchell, F.J.G., Kirby, K.J., 1990. The Impact of Large Herbivores on the Conservation of Semi-natural Woods in the British Uplands. Forestry 63, 333-353.

Oxbrough, A., Irwin, S., Kelly, T., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management 259, 2111–2121.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2006. The influence of open space on ground-dwelling spider assemblages within plantation forests. Forest Ecology and Management 237, 404-417.

Oxbrough, A.G., Gittings, T., O'Halloran, J., Giller, P.S., Kelly, T.C., 2007. Biodiversity of the ground-dwelling spider fauna of afforestation habitats. Agriculture, Ecosystems & Environment 120, 433-441.

Palik, B., Engstrom, R.T., 1999. Species composition. In: Hunter, M.J. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, pp. 65-94.

Peng, R.K., Incoll, L.D., Sutton, S.L., Wright, C., Chadwick, A., 1993. Diversity of Airborne Arthropods in a Silvoarable Agroforestry System. Journal of Applied Ecology 30, 551-562.

Perrin, P.M., Mitchell, F.J.G., Kelly, D.L., 2011. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Changes in ground flora and species diversity. Forest Ecology and Management 262, 2328-2337.

Peterken, G.F., Ausherman, D., Buchenau, M., Forman, R.T.T., 1992. Old-growth Conservation within British Upland Conifer Plantations. Forestry 65, 127-144.

Purser, P., Wilson, F., & Carden, R. , 2009. Deer and forestry in Ireland: A review of current status and management requirements. Woodlands of Ireland.

Quine, C.P., Humphrey, J., 2003. The future management of plantation forests for biodiversity. In: Humphrey, J.W., Ferris, F., Quine, C.P. (Eds.), Biodiversity in Britain's Planted Forests. Forestry Commission, Edinburgh, pp. 1-118.

Roche, J., Mitchell, F.G., Waldren, S., 2009. Plant community ecology of Pinus sylvestris, an extirpated species reintroduced to Ireland. Biodiversity & Conservation 18, 2185-2203.

Smith, G.F., Iremonger, S., Kelly, D.L., O'Donoghue, S., Mitchell, F.J.G., 2007. Enhancing vegetation diversity in glades, rides and roads in plantation forests. Biological Conservation 136, 283-294.

Sparks, T., Greatorex-Davies, J.N., 1992. The effect of shade in plantation woodland on invertebrate abundance and biodiversity. Aspects of Applied Biology 29, 89-96.

Speight, M.C.D., 1985. The Extinction of Indigenous Pinus sylvestris in Ireland: Relevant Faunal Data. The Irish Naturalists' Journal 21, 449-453.

Stewart, A.J.A., 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry 74, 259-270.

Warren, M.S., Fuller, R.J., 1993. Woodland Rides and Glades: Their Management for Wildlife. Nature Conservancy Council, Peterborough, UK.

Watkins, R.Z., Chen, J., Pickens, J., Brosofske, K.D., 2003. Effects of Forest Roads on Understory Plants in a Managed Hardwood Landscape. Conservation Biology 17, 411-419.

Acknowledgements

This research was carried out as part of the PLANFORBIO Research Programme, which is funded by the Department of Agriculture, Food and the Marine, under the National Development Plan 2007-2013. Thank you to the staff at Coillte, Killarney National Park, and the landowners for allowing access to the study sites and providing site information, and to the staff at Forest Research UK for facilitating the research in British forests, which was funded by the Forestry Commission and the European Regional Development Fund. Thank you also to the members of the PLANFORBIO Advisory Group who provided scientific steering.

Special thanks to my supervisors, John O'Halloran and Tom Kelly, who have been a great source of support, guidance and encouragement during my PhD. Thank you to my colleagues, Mark Wilson, Conor Graham, and Scott Pedley at University College Cork, and Linda Coote, Anke Dietzsch, and Miles Newman at Trinity College Dublin, for their help. I am also incredibly grateful to Tom Gittings for his work on the hoverfly sampling and identification. A massive thank you goes to Sandra Irwin and Anne Oxbrough for being an inspiration and for providing a huge amount of support and advice and always taking a great deal of time to comments on drafts, and to Rob Deady, who provided a tremendous amount of help throughout the good times and the bad with fieldwork and sample sorting. Thank you also to Rebecca Martin, Eimear Egan, Tom Drinan, Luke Harman, Meabh Boylan, Alice D'Arcy, Elaine Brown, and Jose Avila who helped with fieldwork and labwork, and to the BEES postgrad community who brought a lot of fun and laughter to my time in Ireland.

And last but not least, thank you to my amazing parents, Diane and Ken Fuller, my inspirational Grandpa, Edward Lederer, and my wonderful Nanny, Ursula Lederer, for making my education possible; the Fuller, Williamson and Attree clan, for being a wonderful, supportive, hilarious and loving family; my fantastic friends back home, particularly my sister "Bug", my cousin Fiona Williamson, and my best friends Katie Chisholm and Jess Worsley.

Appendix 1

Locations and number of individuals (n) of spider species of conservation importance caught in the baseline and repeat survey from Chapter 3. Standard treatment (S), wide treatment (W), Open 1 plot (O1), Open 2 plot (O2), Forest plot (F).

Species	Conservation status	Site	Grid ref	County	Baseline (n)	Plot – baseline	Repeat (n)	Plot – repeat
Agyneta subtilis	Vulnerable	Ballingate	S977605	Wicklow	31	SO1, SO2, SF, WO1, WO2, WF	3	SO1, SF
		Bawnoge	O016032	Wicklow	94	SO1, SO2, SF, WO1, WO2, WF	28	SO1, SO2, SF, WO1, WO2, WF
		Cardtown	S277995	Laois	7	SO2, WO1, WO2	18	SO1, SO2, SF, WO2, WF
		Carrigagulla	W373836	Cork	10	SO1, SF, WO1, WO2, WF	11	SO1, SO2, SF, WO1, WO2
		Cloontycarthy	W208707	Cork	14	SO1, SO2, SF, WO1, WO2, WF	9	SO1, SO2, SF, WO1, WO2, WF
		Fossy Hill	S550891	Laois	11	SO1, SO2, WO1, WO2, WF	13	SF, WO1, WO2, WF
		Lismore	S027063	Waterford	60	SO1, SO2, SF, WO1, WO2, WF	29	SO1, SO2, SF, WO1, WO2, WF
		Tooranaraheen	S128059	Waterford	37	SO1, SO2, SF, WO1, WO2, WF	35	SO1, SO2, SF, WO1, WO2, WF

Species	Conservation status	Site	Grid ref	County	Baseline (n)	Plot - baseline	Repeat (n)	Plot - repeat
Erigonella ignobilis	Vulnerable	Cloontycarthy	W208707	Cork	*0*	*NA*	1	SO1
		Lismore	S027063	Waterford	1	SF	*0*	*NA*
Hypselistes jacksoni	Vulnerable	Bawnoge	O016032	Wicklow	5	SO2, SF	*0*	*NA*
Jacksonella falconeri	Endangered	Bawnoge	O016032	Wicklow	0	NA	1	SO1
Maro minutus	Vulnerable	Ballingate	S977605	Wicklow	9	SO2, SF, WF	1	SO1
		Bawnoge	O016032	Wicklow	5	WO1, WF	9	WO1, WO2, WF
		Cardtown	S277995	Laois	34	SO1, SO2, SF, WO1, WO2, WF	4	SO1, SO2, SF
		Carrigagulla	W373836	Cork	5	SO1, WO1, WO2, WF	*0*	NA
		Fossy hill	S550891	Laois	4	WO1, WO2, WF	1	WF

Species	Conservation status	Site	Grid ref	County	Baseline (n)	Plot - baseline	Repeat (n)	Plot - repeat
Meioneta mollis	Endangered	Lismore	S027063	Waterford	*0*	*NA*	1	WO2
Saaristoa firma	Vulnerable	Cardtown	S277995	Laois	*0*	*NA*	1	WO2
		Carrigagulla	W373836	Cork	1	SO2	*0*	*NA*
		Cloontycarthy	W208707	Cork	2	SF, WF	2	SO1, WF
		Lismore	S027063	Waterford	*0*	*NA*	1	SF
		Tooranaraheen	S128059	Waterford	3	WO1, WO2, WF	2	SO2, WO2
Taranucnus setosus	Vulnerable	Ballingate	S977605	Wicklow	*0*	*NA*	3	SO1, SO2, WF
		Bawnoge	O016032	Wicklow	*0*	*NA*	2	SO2, SF
		Cardtown	S277995	Laois	*0*	*NA*	1	WO2
		Carrigagulla	W373836	Cork	*0*	*NA*	3	SO1, SO2, WO1
		Cloontycarthy	W208707	Cork	1	SF	4	SF, WF
		Fossy Hill	S550891	Laois	1	SO1	8	SO1, SF, WO1, WO2, WF
		Lismore	S027063	Waterford	*0*	*NA*	2	SO1, WF

Species	Conservation status	Site	Grid ref	County	Baseline (n)	Plot – baseline	Repeat (n)	Plot – repeat
Trochosa spinipalpis	Vulnerable	Ballingate	S977605	Wicklow	2	SO1, WF	*0*	*NA*
		Lismore	S027063	Waterford	1	WO2	*0*	*NA*
Walckenaeria dysderoides	Vulnerable	Ballingate	S977605	Wicklow	5	SO2, WO1, WF	*NA*	*NA*
		Cardtown	S277995	Laois	*0*	*NA*	2	WO1, WO2
		Carrigagulla	W373836	Cork	3	WO1, WO2	2	SO2, WO2
		Cloontycarthy	W208707	Cork	28	SO1, SO2, SF, WO1, WO2, WF	10	SO1, SF, WO1, WO2, WF
		Lismore	S027063	Waterford	1	WO1	*0*	*NA*

Appendix 2

Presence/ absence of the ground-dwelling spider species caught in the three study regions.

	Ireland	New Forest	Thetford Forest
Agyneta ramosa	X	X	X
Agyneta subtilis	X	X	X
Centromerus dilutus	X	X	X
Ceratinella brevis	X	X	X
Clubiona comta	X	X	X
Dicymbium tibiale	X	X	X
Diplocephalus latifrons	X	X	X
Diplostyla concolor	X	X	X
Gongylidiellum vivum	X	X	X
Hahnia helveola	X	X	X
Linyphia hortensis	X	X	X
Metellina mengei	X	X	X
Micrargus herbigradus	X	X	X
Microneta viaria	X	X	X
Monocephalus fuscipes	X	X	X
Neon reticulatus	X	X	X
Neriene clathrata	X	X	X
Neriene peltata	X	X	X
Ozyptila trux	X	X	X
Pachygnatha clercki	X	X	X
Pachygnatha listeri	X	X	X
Palliduphantes ericaeus	X	X	X
Palliduphantes pallidus	X	X	X
Pardosa lugubris	X	X	X
Pirata hygrophilus	X	X	X
Robertus lividus	X	X	X
Saaristoa abnormis	X	X	X
Tenuiphantes flavipes	X	X	X
Tenuiphantes tenebricola	X	X	X
Tenuiphantes zimmermanni	X	X	X
Trochosa terricola	X	X	X

Walckenaeria acuminata	X	X	X
Walckenaeria cucullata	X	X	X
Walckenaeria nudipalpis	X	X	X
Zora spinimana	X	X	X
Gongylidiellum latebricola	X	X	
Pardosa pullata	X	X	
Pocadicnemis pumila	X	X	
Walckenaeria cuspidata	X	X	
Walckenaeria vigilax	X	X	
Agyneta conigera	X		X
Bathyphantes gracilis	X		X
Bathyphantes nigrinus	X		X
Ceratinella scabrosa	X		X
Diplocephalus picinus	X		X
Enoplognatha ovata	X		X
Gonatium rubellum	X		X
Gongylidium rufipes	X		X
Maso sundevalli	X		X
Tenuiphantes alacris	X		X
Walckenaeria atrotibialis	X		X
Walckenaeria dysderoides	X		X
Agroeca brunnea		X	X
Amourobius fenestralis		X	X
Centromerus sylvaticus		X	X
Clubiona corticalis		X	X
Clubiona terrestris		X	X
Episinus angulatus		X	X
Euophrys frontalis		X	X
Harpactea hombergi		X	X
Macrargus rufus		X	X
Pachygnatha degeeri		X	X
Phrurolithus festivus		X	X
Pirata latitans		X	X
Robertus neglectus		X	X

Tenuiphantes cristatus		X	X
Tenuiphantes mengei		X	X
Walckenaeria obtuse		X	X
Xysticus cristatus		X	X
Zelotes pedestris		X	X
Agroeca proxima	X		
Asthenargus paganus	X		
Centromerus arcanus	X		
Ceratinella brevipes	X		
Clubiona recluse	X		
Cryphoeca silvicola	X		
Dismodicus bifrons	X		
Erigone atra	X		
Erigone dentipalpis	X		
Ero furcata	X		
Leptorhoptrum robustum	X		
Linyphia triangularis	X		
Metellina merianae	X		
Metellina segmentata	X		
Metopobactrus prominulus	X		
Monocephalus castaneipes	X		
Neriene Montana	X		
Obscuriphantes obscures	X		
Oedothorax fuscus	X		
Oedothorax gibbosus	X		
Paidiscura pallens	X		
Pardosa amentata	X		
Pardosa nigriceps	X		
Pardosa prativaga	X		
Pocadicnemis juncea	X		
Rugathodes instabilis	X		
Saaristoa firma	X		
Tapinocyba pallens	X		
Tenuiphantes tenuis	X		

Clubiona brevipes	X	
Coelotes terrestris	X	
Dipoena tristis	X	
Drassodes cupreus	X	
Euryopis flavomaculata	X	
Gonatium rubens	X	
Haplodrassus silvestris	X	
Hilaira excisa	X	
Micaria pulicaria	X	
Minyriolus pusillus	X	
Pirata uliginosus	X	
Porrhomma campbelli	X	
Porrhomma egeria	X	
Porrhomma montanum	X	
Porrhomma pallidum	X	
Scotina celans	X	
Tiso vagans	X	
Trochosa robusta	X	
Trochosa spinipalpis	X	
Walckenaeria antica	X	
Walckenaeria furcillata	X	
Xysticus luctator	X	
Zelotes apricorum	X	
Anyphaena accentuata		X
Bathyphantes parvulus		X
Clubiona lutescens		X
Clubiona pallidula		X
Enoplognatha thoracica		X
Erigonella hiemalis		X
Gongylidiellum murcidum		X
Hahnia montana		X
Lepthyphantes minutus		X
Maro minutus		X
Meioneta saxatilis		X

Moebelia penicillata	X
Ozyptila atomaria	X
Ozyptila praticola	X
Philodromus dispar	X
Philodromus fallax	X
Porrhomma pygmaeum	X
Savigyna frontata	X
Segestria senoculata	X
Tapinocyba insecta	X
Tibellus oblongus	X

Appendix 3

Presence/ absence of the carabid beetle species caught in the three study regions.

	Ireland	New Forest	Thetford Forest
Calathus rotundicollis	X	X	X
Carabus problematicus	X	X	X
Clivia fossor	X	X	X
Cychrus caraboides	X	X	X
Harpalus latus	X	X	X
Nebria brevicollis	X	X	X
Pterostichus madidus	X	X	X
Pterostichus melanarius	X	X	X
Pterostichus niger	X	X	X
Pterostichus strenuous	X	X	X
Abax parallelipipedus	X	X	
Amara convexior	X		X
Calathus micropterus	X		X
Carabus nemoralis	X		X
Loricera pilicornis	X		X
Notiophilus substriatus	X		X
Trechus obtusus	X		X
Carabus violaceus		X	X
Notiophilus biguttatus		X	X
Notiophilus rufipes		X	X
Oxypselaphus obscures		X	X
Agonum fuliginosom	X		
Amara plebeja	X		
Badister sodalist	X		
Carabus granulates	X		
Curtonotus aulicus	X		
Elaphrus cupreus	X		
Leistus terminates	X		
Pterostichus anthracinus	X		
Pterostichus nigrita/rhaeticus	X		
Pterostichus vernalis	X		

Synchus vivalis	X		
Bembidion guttula		X	
Bembidion lampros		X	
Bembidion mannerheimi		X	
Platynus assimilis		X	
Pterostichus minor		X	
Trechus secalis		X	
Amara eurynota			X
Amara similata			X
Badister bullatus			X
Bradycellus harpalinus			X
Chlaenius nigricornis			X
Harpalus rufipes			X
Harpalus tardus			X
Laemostenus terricola			X
Leistus fulvibarbis			X
Leistus rufomarginatus			X
Leistus spinibarbis			X
Nothiophilus palustris			X
Ophonus laticollis			X
Platyderus depressus			X
Pterostichus cristatus			X
Stomis pumicatus			X
Trechus quadristriatus			X

Appendix 4

Species list of ground-dwelling spiders caught in the oak and yew woodlands of Killarney National Park from Chapter 6, including the number of individuals caught in each woodland type.

Family	Species	Oak	Yew
Amaurobiidae	*Amourobius fenestralis*	2	0
	Coelotes terrestris	1	0
Anyphaenidae	*Anyphaena accentuata*	2	0
Araneidae	*Cyclosa conica*	1	2
Dictynidae	*Cryphoeca silvicola*	1	0
Dysderidae	*Harpactea hombergi*	2	2
Hahniidae	*Hahnia helveola*	1	0
Linyphiidae	*Agyneta cauta*	12	0
	Agyneta ramosa	37	1
	Agyneta subtilis	55	26
	Asthenargus paganus	1	0
	Bathyphantes nigrinus	2	0
	Centromerus dilutus	1	0
	Centromerus prudens	2	0
	Dicymbium tibiale	10	0
	Diplocephalus latifrons	74	0
	Diplocephalus picinus	10	0
	Diplostyla concolor	5	5
	Hypomma cornutum	1	0
	Leptorhoptrum robustum	0	1
	Linyphia hortensis	26	6
	Maso sundevalli	1	0
	Meioneta saxatilis	1	0
	Micrargus herbigradus	0	1
	Microneta viaria	34	0
	Minyriolus pusillus	4	0
	Monocephalus fuscipes	77	0
	Neriene clathrata	5	1
	Neriene peltata	2	5
	Obscuriphantes obscurus	1	0
	Palliduphantes pallidus	7	0
	Pocadicnemis pumila	3	0
	Porrhomma campbelli	0	1
	Porrhomma montanum	2	0
	Saaristoa abnormis	42	9

	Saaristoa firma	1	0
	Tapinocyba insecta	1	0
	Tapinocyba pallens	1	0
	Tenuiphantes alacris	59	8
	Tenuiphantes cristatus	2	0
	Tenuiphantes flavipes	77	0
	Tenuiphantes zimmermanni	139	122
	Tiso vagans	3	0
	Walckenaeria acuminata	17	0
	Walckenaeria atrotibialis	5	0
	Walckenaeria cuspidata	3	0
	Walckenaeria dysderoides	3	0
	Walckenaeria nudipalpis	4	0
Lycosidae	*Pardosa amentata*	1	0
	Pardosa lugubris	7	0
	Pardosa nigriceps	2	0
	Pirata hygrophilus	60	0
	Pirata piraticus	1	0
	Trochosa terricola	4	0
Mimetidae	*Ero furcata*	0	2
Philodromidae	*Philodromus albidus*	0	1
Segestriidae	*Segestria senoculata*	6	1
Tetragnathidae	*Metellina mengei*	4	6
	Pachygnatha clercki	2	0
	Pachygnatha degeeri	4	0
	Pachygnatha listeri	3	0
Theridiidae	*Anelosimus vittatus*	0	1
	Pholcomma gibbum	0	1
	Robertus lividus	89	0
Thomisidae	*Diaea dorsata*	1	0
	Ozyptila trux	7	0
Total abundance		**931**	**202**
Total species richness		**59**	**20**