UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

Centre for Biological Sciences

Evaluation of strategies for conserving biodiversity in temperate and boreal forests

by

Rebecca Spake

Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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EVALUATION OF STRATEGIES FOR CONSERVING BIODIVERSITY IN TEMPERATE AND BOREAL FORESTS

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Halting biodiversity loss and the associated decline of ecosystem functioning is one of the greatest challenges faced by mankind. The globally adopted Aichi Biodiversity Targets for 2011-2020, issuing from the 10th Conference of the Parties of the Convention on Biological Diversity, represent the strongest global commitment to this challenge. For forest ecosystems, biodiversity decline can be halted only with i) sustainable management of multifunctional production forests (Target 7), ii) formation of well-connected systems of protected areas (Target 11), and iii) forest restoration (Target 15). Reaching these targets for the world's forests requires a sound empirical understanding of the functioning and the relative importance of forests under different management regimes. Indeed, environmental policy should be informed by robust scientific evidence. This thesis addresses knowledge gaps that exist in the evidence-base for sustainable forest management and conservation in temperate and boreal forests.

Chapter 2 quantifies the recovery rates of different functional groups of beetles, lichens and fungi to forest restoration measures in temperate and boreal regions across the world. A systematic review and meta-analysis identifies functional-group-specific relationships in the response of species richness to stand age after forest disturbance, with some groups requiring around a century of stand continuity for recovery to old-growth levels. The slow recovery of these functional groups makes old-growth forest an effectively irreplaceable biodiversity resource that should be exempted from restoration offset initiatives.

Chapter 3 compares the biodiversity value of overmature even-aged planted and old-growth forest stands for ectomycorrhizal fungi in the New Forest National Park, UK. Overmature plantations are those beyond economic maturity, acquiring some of the structural characteristics of old-growth forests and there is increasing interest in their setting aside as a means of preserving species associated with old-growth forests. Analysis of 3 years of field data shows that setting aside of overmature planted forest is an effective means of conserving ectomycorrhizal communities associated with old-growth forests, given temporal continuity in the order of a century. This holds out particular promise for historically deforested regions such as the UK, where little old-growth forest remains and much planted forest exceeds a century in age.

Chapter 4 investigates the relative importance of abiotic and biotic drivers of carabid functional trait diversity and composition for coniferous production forests across the UK. Analysis of the dataset of the UK Forestry Commission's Biodiversity Assessment Project (BAP 1995-1999) contradicts previous studies in showing that ground vegetation diversity is not an important determinant of carabid functional diversity. This result suggests that restoration of plant communities, a major goal of forest restoration efforts, will not necessarily enhance carabid diversity in coniferous plantations. Canopy cover was the most important variable, tending to drive down carabid diversity.

Chapter 5 collates an evidence base that will inform forest biodiversity conservation and policy-making in Japan. Four management interventions, outlined in Japan's National Biodiversity Strategy, are assessed by systematic review and meta-analysis for their impacts on species richness, abundance and composition. The work provides general guidance for forest biodiversity conservation in Japan, and it highlights a major knowledge gap in a widely used contemporary intervention known as 'satoyama'.

Don’t it always seem to go, that you don’t know what you’ve got ‘til it’s gone… They paved paradise and put up a parking lot

(Joni Mitchell, *Big Yellow Taxi*, Siquomb Publishing Co. 1969).

Table of Contents

List of Tables

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

DECLARATION OF AUTHORSHIP

I, Rebecca Spake, declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

Evaluation of strategies for conserving biodiversity in temperate and boreal forests

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

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Signed: ....

Date:...

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Abbreviations

Abbreviation	Term
AIC	Akaike's Information Criterion
AICc	Akaike's Information Criterion corrected for small sample bias
ASNW	Ancient semi-natural woodland
BAP	Biodiversity Assessment Project
B-EF	Biodiversity for ecosystem functions
CBD	Convention on Biological Diversity
DNA	Deoxyribonucleic acid
EMF	Ectomycorrhizal fungi
FD	Functional diversity
FD_Q	Rao's quadratic entropy
ISA	Indicator species analysis
ITS	internal transcribed spacer region
IUCN	International Union for the Conservaiton of Nature
lnR	Log response ratio
ML	Maximum likelihood
NMDS	Non-metric multi-dimensional scaling
PCA	Principle components analysis
REML	Restricted maximum likelihood
SAC	Special Area of Conservation
SFM	Sustainable forest management

Chapter 1: General introduction to forest management and biodiversity conservation in temperate and boreal regions and thesis overview

1.1 Forests are species-rich ecosystems that deliver crucial ecosystem services

1.1.1 Forest biodiversity and ecosystem function

Biodiversity is the sum of all biotic variation, from the genetic diversity between individuals of the same population, to the diversity of landscapes and ecosystems (CBD, 1992). In an era where human actions have become the main driver of global environmental change, the ‘Anthropocene’ (Steffen et al., 2011), biodiversity is being lost at a rate one thousand times faster than the highest rates estimated from the fossil record (MA, 2005). Land-use changes are cumulatively a major driver of the biodiversity crisis via habitat loss and fragmentation (Sala et al., 2000, Foley et al., 2005), primarily incurred through agricultural expansion (Foley et al., 2011). Worldwide, agriculture has already cleared or converted 70% of the grassland, 50% of the savanna, 45% of the temperate deciduous forest, and 27% of the tropical forest biome (Foley et al., 2011). Other major drivers of terrestrial biodiversity loss result from the degradation of ecosystems through climate change, nitrogen deposition, the establishment of exotic species, and elevated carbon dioxide concentrations (Sala et al., 2000). According to the International Union for Conservation of Nature (IUCN) Red List of threatened and endangered species, one-quarter of mammal species, one-eighth of bird species, and over 40% of amphibian species are threatened; although much less is known about invertebrates, fungi and plants, thousands of these species are also at risk (Monastersky, 2014, McGill et al., 2015).

Evidence that extinctions are altering key processes important to the productivity and sustainability of ecosystems that humans rely on is mounting (Hooper et al., 2012). The realisation of these links has incited international agreements to stop the ongoing decline of biodiversity. The Aichi Biodiversity Targets for 2011 to 2020, which were adopted by the 196 national parties to the 2010 Conference of the Convention on Biological Diversity

(CBD) in Nagoya, Japan, represent the strongest of such commitments. Aichi Target 11 is particularly noteworthy, stating that by 2020, at least 17% of terrestrial areas of particular importance for biodiversity and ecosystem services are to be conserved through “ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures”. The fulfilment of this and other Aichi Targets therefore demands a sound understanding of the relationships between environmental change, biodiversity and ecosystem services. This need has motivated the development of frameworks that conceptualise, classify and quantify biodiversity and ecosystem service relationships. Mace et al. (2012) distinguish three roles for biodiversity in ecosystem service delivery. Biodiversity can be: (i) a good, with educational, religious or recreational values; (ii) a regulator of ecosystem processes that deliver ecosystem services; or (iii) an ecosystem service itself, for example as a source of new medicines. Over the last decade, research effort has increased manifold into the regulatory role of biodiversity, which attempts to establish causative links between species diversity and the magnitude and stability of ecosystem functions (‘biodiversity for ecosystem functions’, henceforth: B-EF) . Although many controversies still exist, and mechanisms remain to be understood, accumulated knowledge generally supports the hypothesis that some services are reduced by loss of biodiversity (Hooper et al., 2005, Cardinale, 2012).

Forests cover nearly one third of global land area (FAO, 2010), contain over 80% of global terrestrial biodiversity (Aerts and Honnay, 2011), and contribute crucial ecosystem services including carbon storage and protection of watersheds, fisheries and soils (MA, 2005). The extent and quality of forest as a habitat is decreasing at an alarming rate; around 40 million ha of primary forest was lost or degraded due to selective logging and other human interventions between 2000 and 2010 (FAO, 2010), raising concerns for ecosystem service delivery and human well-being (Balvanera et al., 2006). Agricultural expansion is estimated to be the proximate driver for around 80% of deforestation worldwide (Kissinger et al. 2012), and currently occurs mainly in the tropics, where around 80% of new croplands are replacing forests (Gibbs et al., 2010). The loss and degradation of the world’s forests is a global concern, given that their clearance is a major source of greenhouse gas emissions, and that forests are rich reservoirs of biodiversity and key ecosystem services (MA, 2005).

The majority of B-EF research studies have been performed under experimental conditions in relatively simple grassland communities (e.g. Tilman et al. (2001)), in which the number and identity of species has been highly controlled, leading to criticisms of their practical relevance for management and conservation (Mori et al., 2013). Nevertheless, increasing attention is being paid to more complex forest ecosystems through observational study. Most B-EF research in forest ecosystems has focussed on trees (review in Nadrowski et al. (2010)). Specifically, relationships have been explored between tree richness and productivity and carbon storage. The ability to draw general quantitative conclusions from these studies through meta-analysis has been hampered by inherent differences amongst studies including methodological, spatial extent and spatial grain (sample unit size) differences (Chisholm et al., 2013). Chisholm et al. (2013) investigated species richness relationships with productivity and biomass across 25 study sites spanning temperate and tropical regions across five continents. At small spatial grains (0.04 ha) species richness was generally positively related to productivity and biomass within plots, with a doubling of species richness corresponding to an average 48% increase in productivity and 53% increase in biomass. At larger spatial grains (0.25 ha, 1 ha) however, results were mixed, with negative relationships becoming more common. Similarly, Poorter et al. (2015) investigated environmental variables determining above-ground biomass in neotropical forests and found that it was strongly driven up by tree species richness at small spatial scales, but was less important at larger scales. The results of these studies highlight the fundamental role of scale in determining the observed relationship between species richness and ecosystem function in forests; at small spatial scales, where an additional species can still make a difference in terms of niche complementarity, species richness has strong effects on ecosystem functioning (Poorter et al. 2015).

Ecosystem functions and services other than productivity and carbon storage have also been investigated. At a regional scale, Gamfeldt et al. (2013) showed positive relationships between tree species richness within production forests and multiple ecosystem services including berry production and game production potential. Furthermore, the characterisation of forest B-EF relationships for taxa other than plants is becoming an active area of research (Dirzo et al., 2014). For example, Slade et al. (2007) used exclusion experiments to study the effects of dung beetle functional group richness and composition on two interlinked ecosystem functions, dung removal and secondary seed dispersal, in tropical forest in Sabah, Malaysia. They found that both dung and seed removal increased with dung beetle functional group richness, but that these effects were dependent on the identity of the functional groups present, indicating an important role for functional group composition.

1.1.2 Forest biodiversity and ecosystem resilience

Ecosystems can differ greatly in how they respond to disturbance, both in terms of their resistance (i.e., the degree to which they remain unchanged by disturbance) and resilience (i.e., their capacity to return to a reference state over time following a perturbation; Holling (1973); Wardle and Jonsson (2014)). Differences in how ecosystems respond are driven by a multitude of biotic and abiotic factors (Wardle and Jonsson, 2014), of which species diversity and composition have been shown to be important (Thompson et al., 2011), in addition to the functional traits possessed by plant communities (Cardenas et al., 2014).

Resistance is of particular concern with regards to invasive species. A considerable body of literature on the relationship between biodiversity and resistance to invasion exists, with several studies suggesting that diversity enhances resistance (Cardinale, 2012). In a study of forestlands in the southern U.S, Wang and Grant (2012) found that the probability of invasion by invasive shrubs (Ligustrum sp.) is determined by, among other factors, the species diversity of plants.

1.1.3 Forest harvest impacts on biodiversity

Globally, there was a net loss of some 129 million ha of forest (natural and planted) from 1990 to 2015, representing an annual rate of –0.13 percent and a total area about the size of South Africa (FRA, 2015). The rate of deforestation is currently the greatest in the tropics, with the biggest loss of forest having occurred in South America and Africa over the past decade, although per capita forest area decline is occurring in every climatic domain (except in the temperate domain) as the human population increases and forest land is converted to agriculture and other land uses (FRA, 2015). In addition to this massive annual loss in forest area, existiting forests are continually being degraded, principally by timber extraction and logging activities (Kissinger et al., 2012). The intensity of forest management for timber varies across and within regions (Levers et al., 2014), and range from intensive systems based on clear-cutting and artificial regeneration to the fostering of irregular stand structures based on natural regeneration (Duncker et al., 2012).

A vast literature exists quantifying forest harvest impacts of a range of intensities on biodiversity. To determine such impacts, comparison with a reference is required, whereby the reference typically has attributes of an undegraded ecosystem (Bullock et al., 2011). Accordingly, empirical research studies have compared biodiversity values of managed, harvested forest stands with relatively undisturbed old-growth, or primary controls.

Numerous quantitative syntheses analysing these biodiversity differences have been done for tropical, temperate and boreal regions (Paillet et al., 2010, Gibson et al., 2011, Clark and Covey, 2012, Duguid and Ashton, 2013, Johansson, 2008, chapter 2, chapter 5), and have demonstrated that the ecological responses following forest harvesting vary markedly according to taxonomic group, harvest intensity (e.g. whether selectively or clear-cut), the ecological metric used and geographic region (Gibson et al., 2011).

1.1.3.1 Selective logging

Selective logging, the removal of specific timber trees from a forest stand, is the principal forestry technique in the tropics, produces approximately one eighth of global timber (Blaser et al., 2011), and is an important contributor to many local and national economies (Martin et al. 2015). Empirical studies of selective logging impacts on biodiversity have yielded extremely mixed results, with similar numbers of studies reporting increases as decreases in biodiversity (Burivalova et al., 2014). An understanding the causes of this variation is vital to inform forest management. An early quantitative review of selective logging studies by Gibson et al. (2011) reported an overall relatively benign effect of logging on biodiversity, but they treated selective logging as a uniform land use. More recent meta-analyses have quantified the relationship between biodiversity responses to logging and logging intensity, which varies widely across the tropics (Burivalova et al., 2014, Bicknell et al., 2015, Martin et al., 2015). Burivalova et al. (2014) reported overall linear declines in species richness of most vertebrate groups with increasing logging intensity, but observed a slight increase in bird species richness at low logging intensities. Similarly, Martin et al. (2015) demonstrated linear declines in tree species richness with increasing intensity, but noted an initial increase in species richness in logged forests at low intensities, likely due to an influx of shade intolerant species (Connell, 1978). These studies provide thresholds of logging intensity for different taxonomic groups that could help inform evidence-based sustainable logging practices for biodiversity conservation.

As well as negatively impacting on biodiversity, selective logging can result in increased carbon emissions (Bryan et al., 2010), primarily through the felling of large trees. The crushing and death of non-target trees during removal of logs can also be a major contributor of carbon emissions (Putz et al., 2008). The death of non-target trees can also limit forest recovery and above-ground carbon accumulation. These negative effects on carbon emissions could potentially be minimised by reducing large tree mortality, reducing residual damage to trees that are not felled, or increasing the recruitment of priority species (Martin et al., 2015)

1.1.3.2 Clear-cut logging

Whilst selective logging is the principal forestry technique in the tropics, clear-cut logging predominates in temperate and boreal regions, notably in North America and northern Europe (Rosenvald and Lohmus, 2008, Lindenmayer and Laurance, 2012). It is a cost-effective method of harvesting trees and facilitates the rapid growth of a new stand, either through re-planting or natural regeneration. The impact of clear-cutting on forest biodiversity depends on a range of factors including taxonomic group and the time since cutting (Chapter 2). Open-habitat specialists including certain small mammal species tend to increase in abundance in clear-cuts (Bogdziewicz and Zwolak, 2014), suggesting that that the colonisation of clear-felled sites is a key process maintaining the diversity of open-habitat species in afforested areas (Brockerhoff et al., 2008). Taxa that depend on old forest conditions, such as lichens that only colonise the bark of old trees, will disappear in clear-cuts (Johansson, 2008). A meta-analysis of European forests by Paillet et al. (2010) found that clear-cutting followed by plantation/regeneration with different tree species generally had a more negative effect on species richness than clear-cutting without tree species change and selective cutting, and that results varied among taxonomic group.

1.1.4 Sustainable forest management

Increasing recognition of B-EF relationships within forest ecosystems, for example by the UN Convention on Biodiversity (CBD) and the Ministerial Conference on the Protection of Forests in Europe (MCPFE), has broadened the scope of forest management towards ecosystem-based approaches which aim to conserve biodiversity and sustain the capacity of forest ecosystems to deliver a range of goods and services (Eriksson and Hammer, 2006). Resource managers seeking to conserve forest biodiversity while still meeting production targets are presented with two alternative strategies. Firstly, they could intensively harvest within plantations and leave the remaining forest unharvested within reserves. Alternatively, they could harvest timber at low intensity across the whole concession (Gustafsson et al., 2012, Edwards et al., 2014). These competing solutions are analogous to the land-sharing vs. land-sparing debate often applied to land-use management in agricultural landscapes (Lindenmayer et al., 2012, Edwards et al., 2014).

Currently just 12% of global forest area has biodiversity conservation designated as its primary function (FAO, 2010). Whilst the sparing of such reserves is essential to national and international strategies to counter biodiversity loss, alone they are insufficient to adequately support viable and well-distributed populations of many forest-dependent species (Lindenmayer et al., 2006, Fischer et al., 2006, Mascia and Pailler, 2011). Although the proportion of forest reserves is likely to increase, the majority global forest estate will continue to play a multifunctional role in balancing timber provision with the production of other goods and services that human society needs (Thompson et al., 2011, Gustafsson et al., 2012). Indeed, around 55% of global forest area is managed as production forests or used to extract multiple values (FAO, 2010). Developing ways to sustain these forests is imperative given their large extent and potential for goods and service delivery (Lindenmayer et al., 2012). New ‘paradigms’ of management of these multi-functional forests are emerging under the general label of sustainable forest management (McDonald and Lane, 2004). A central tenet to sustainable forest management (henceforth: SFM) is the integration of biodiversity conservation within productive forest landscapes, a practice being increasingly implemented in northern Europe, Australia and North America (Rosenvald and Lohmus, 2008, Gustafsson et al., 2010, Lindenmayer and Franklin, 2002).

Lindenmayer et al. (2012) outline three approaches central to SFM: i) the protection of sensitive areas within productive landscapes such as riparian zones and cultural sites; ii) the restoration of appropriate forest conditions at the stand-scale such as old-growth conditions, and at the landscape-scale, such as maintaining heterogeneity of forest age classes at the landscape scale; and iii) the maintenance of key ecological processes. It is essential that the management and conservation actions that aim to achieve these goals are informed by robust scientific evidence (Pullin and Knight, 2003). Despite this now universial recognition, this is not always the case (Russell-Smith et al. 2015). The objective of thesis thesis is to address knowledge gaps that exist in the forest management and conservation evidence base through a series of case-studies evaluating impacts of forest management on biodiversity in temperate and boreal regions (Figure 1.1). Several management interventions representative of Lindenmayer et al.’s (2012) approaches are addressed in this thesis: biodiversity recovery with stand age following forest restoration actions (chapters 2 and 5), the biodiversity value of planted forest set aside to acquire old-growth characteristics (chapters 3 and 5), and the assessment of biodiversity in forest stands that vary in abiotic and biotic factors as imposed through management practices (chapters 4 and 5; Figure 1.1).

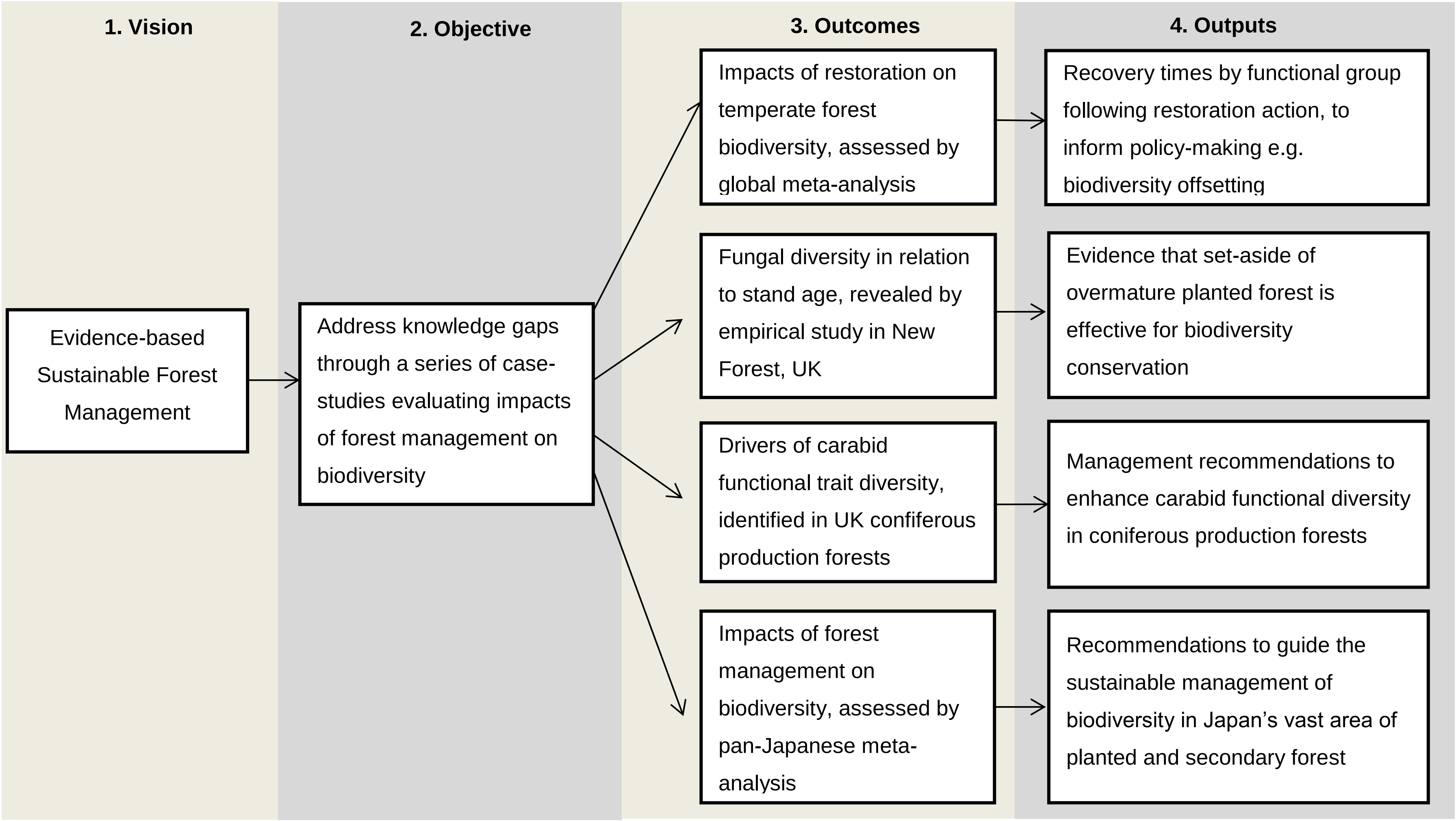

Figure 1.1 Hierarchical framework of thesis evaluating strategies for biodiversity conservation in temperate and boreal regions.

1.2 Thesis overview and objectives

1.2.1 Chapter 2 – A meta-analysis of functional group responses to forest recovery outside of the tropics

Chapter 2 quantifies the recovery rates of different functional groups of beetles, lichens and fungi to forest restoration measures in temperate and boreal regions across the world. This is achieved through the use of standard systematic review methodologies (Pullin and Stewart, 2006) and meta-analysis (Koricheva et al., 2013; Figure 1.1).

1.2.1.1 The use of systematic review and meta-analysis in ecology

Systematic review methodology is now widespread in use and has become a recognised standard for accessing, appraising and collating robust scientific data (Pullin and Stewart, 2006). The synthesis of data collated using systematic review can be done narratively, or quantitatively using meta-analysis. Meta-analysis provides a powerful unbiased set of tools for summarising the results of multiple studies on the same topic (Koricheva et al., 2013). It offers many advantages over traditional narrative reviews, which provided all research synthesis in ecology prior to the early 1990s, whence meta-analytical techniques were adapted from the medical and social sciences for use in ecology (Gurevitch et al., 2001, Koricheva et al., 2013). While narrative syntheses can serve important functions, for example conveying historical development of ideas, they are inherently subjective and cannot quantify objectively the variation in results amongst studies, or evaluate whether hypotheses are supported by the assemblage of existing studies (Koricheva et al. (2013); table 1.1).

Table 1.1 Comparison of narrative and meta-analytical research syntheses. From Koricheva et al. (2013).

Characteristic of review type	Narrative review	Meta-analysis
Imposes restrictions on the type of studies that can be used in a review	N	Y
Interprets study outcome based on its statistical significance	Y	N
Accounts for sample size and statistical power of primary studies	N	Y
Asses statistical significance of the mean overall effect (i.e. whether an effect size is significantly greater than 0).	N	Y
Quantify the magnitude of a mean effect	N	Y
Allows analysis of sources of variation amongst studies	N	Y

Meta-analysis expresses the outcome of multiple studies on a common scale, through the calculation of an ‘effect size’ for each study, which represents the magnitude of a difference or the strength of a relationship (Koricheva et al., 2013). Meta-analysis allows the estimation of the magnitude of an overall effect size (and the corresponding variance) characterising a population of studies; and the identification of factors that moderate the effect size (Koricheva et al., 2013).

1.2.1.2 Chapter 2 context and overview

Forest restoration measures including planting and natural regeneration are taking an increasingly central role in global commitments to impede biodiversity loss. For example, the Convention on Biological Diversity’s Strategic Plan for Biodiversity and Aichi Biodiversity Targets (http://www.cbd.int/sp/) aim for the restoration of 15% of degraded ecosystems by 2020 (Bullock et al., 2011). Furthermore, forest restoration is also used as a biodiversity offsetting mechanism to permit the loss of natural habitat incurred by development. The primary goal of biodiversity offsetting is to achieve no change to species composition and habitat structure as well as no loss in ecosystem function or perceived cultural values associated with biodiversity (Bull et al., 2013). Despite the perceived importance of restoring forest for biodiversity conservation, information is lacking on the timescales and recovery patterns of different taxa following restoration action (Martin et al., 2013), particularly for temperate and boreal regions. This information is urgently needed to guide policy and sustainable forest management practices.

Stand age has been suggested as a potential indicator of biodiversity that is easily controlled by forest management (Moning and Müller, 2009, Smith et al., 2008, Ferris and Humphrey, 1999), yet it remains unclear what exactly it may indicate about biodiversity. Syntheses of stand age-diversity relationships have been produced for several taxonomic groups in secondary tropical forests, including trees, epiphytes, birds, amphibians, mammals, ants and other invertebrates (Martin et al., 2013, Dunn, 2004, Dent and Wright, 2009, Chazdon et al., 2009). These tropical syntheses show that different taxonomic groups exhibit contrasting patterns and rates of recovery with stand age and that these must be acknowledged by forest management strategies (Martin et al., 2013), as different taxa make different contributions to ecosystem functioning (Hooper et al., 2002).

Chapter 2 uses systematic review methodology (Pullin and Stewart, 2006), to collate publications that assessed species richness differences between ‘treatment’ stands of planted and naturally regenerating forest following major disturbance, and ‘control’ stands of relatively undisturbed old-growth, in temperate and boreal regions. Sufficient information was obtained to investigate six frequently studied functional groups deemed important for forest ecosystem function: epiphytic lichens, deadwood fungi, litter fungi, mycorrhizal fungi, saproxylic beetles and non-saproxylic beetles. It is useful to determine the diversity (typically measured as species richness) of organisms within different trophic levels, because it is thought that this information provides an indirect measure of ecosystem resilience (Peterson et al., 1998, Ruiz-Jaen and Aide, 2005)

The systematic review retrieved 78 separate species richness comparisons (‘studies’) from 30 individual publications. Meta-analysis was used to synthesise data quantitatively from these studies, and to identify causal factors explaining species richness differences between control and treatment stands. The effect size used to assess recovery was the log response ratio, lnR, which represents the proportional difference in species richness between control and treatment groups (Hedges et al., 1999). An informatic evaluation approach (Burnham and Anderson, 2002) applied to generalised linear mixed models was used to assess the influence on lnR of stand age, functional group, and other environmental variables consistently reported in the literature (latitude, stand origin). Model selection suggested that the most parsimonious model explaining variation in lnR across all studies included stand age, functional group, their interaction and latitude. Coefficients derived from this model were used to construct graphs of lnR vs. stand age, in order to predict the recovery times of different functional groups.

Functional groups showed varying directions and rates of recovery following disturbance. For example, species richness of ectomycorrhizal fungi was predicted to require 83 years to recover to undisturbed old-growth levels, whereas lichens required 140 years. Saproxylic beetle richness reached old-growth values after 60 years, whilst non-saproxylic beetles benefitted from early successional forest, and exhibited twice the species richness of old-growth forest in 5-year old forest. Given such large differences, use of stand age as a biodiversity indicator for setting management and conservation priorities must consider functional group-specific responses. This research shows that biodiversity does not recover to old-growth levels within a reasonable length of time, deeming old-growth forest as vulnerable biodiversity resource that simply cannot be replaced by offsetting initiatives.

1.2.2 Chapter 3 – The value of overmature planted forest for ectomycorrhizal fungal conservation

The objective of chapter 3 is to investigate the diversity and community composition of ectomycorrhizal fungi in planted overmature and ancient old-growth semi-natural forest stands. Ancient forest is forest that has been originated before 1600 A.D., likely or natural origin. This is achieved through the analysis of 3 years of field data from the New Forest National Park in southern England (Figure 1.1).

1.2.2.1 Ectomycorrhizal fungi

Ectomycorrhizal fungi (EMF) are ubiquitous in temperate and boreal forest soils, contributing up to 39% of microbial biomass and 10–35% of respiration (Tedersoo et al., 2010). Through a symbiotic exchange of soil-derived nutrients for carbohydrates from host plant roots, EMF are the main pathway through which most economically and ecologically important tree species acquire mineral nutrients (Kernaghan, 2005, Smith and Read, 2008, Tedersoo et al., 2012).

Over 7,750 species of EMF from 236 genera have been identified worldwide (Comandini et al. 2012), the majority from temperate forest soils (Allen et al., 1995). These include species from multiple families in the Basidiomycota and Ascomycota and some species of Endogone from the Zygomycota (Bruns et al. 2002). EMF form symbiotic relationships primarily with the finest roots of angiosperm and coniferous trees, including oaks (Quercus), beeches (Fagus), birches (Betula), poplars (Populus), pines (Pinus), spruces (Picea), firs (Abies) and larches (Larix) (Lang and Polle, 2011, O'Hanlon, 2011). Wide taxonomic distributions of EMF and plants in all continents except Antarctica suggests ancient origins of the EMF symbiosis (Tedersoo et al., 2006). Tedersoo et al. (2010) propose that EMF have evolved (and persisted) 66 times independently from non-EMF ancestors.

1.2.2.2 Importance of EMF biodiversity

EMF form highly diverse communities in forest ecosystems comprising tens to hundreds of species (Tedersoo et al., 2006). High diversity is important to both individual host vigour and to the functioning of forest ecosystems. With different EMF species delivering species-specific benefits to host plants (Tedersoo et al., 2006), and differing in their capacities to mobilise nutrients from soil organic matter, a high diversity provides insurance to host-trees facing environmental stresses (Courty et al., 2010). At the ecosystem level, high EMF diversity is likely to contribute to resilience, stability, net primary productivity, biogeochemical cycling and soil carbon storage (Smith and Read, 2008), through a range of mechanisms including increased resistance to disease and extreme environmental conditions such as drought (Kernaghan, 2005).

1.2.2.3 Describing forest EMF communities

Until recently, studies of EMF communities have been almost exclusively based on the incidence of sporocarps (Smith et al., 2002, Richard et al., 2004); the reproductive structure of the fungus. The method is cost-effective, it allows researchers to study extensive areas with minimal interference, and most sporocarps can be identified to species level (Dahlberg et al. 1996). However, sporocarp production is sensitive to a host of environmental factors (Dahlberg et al., 1997), and consequently sporadic annual fruiting patterns necessitate long term monitoring (Dahlberg et al., 2001, O'Hanlon, 2011). In mesic temperate climates, 3-8 years is considered the minimum sampling period necessary to have a reasonable representation of fungal community structure according to the size of the site (Gardes and Bruns, 1996). Moreover, it has been found that the sporocarps of some species are inconspicuous and often overlooked (e.g. Sebacinaceae, hypogeous species, or non-existent e.g. Cenococcum geophilum (Peter et al., 2001, Richard et al., 2004)), leading to underestimates of diversity. Furthermore, it is well established that sporocarp production is not a good indicator of the abundance of EMF belowground (Taylor, 2002). Despite their limitations, sporocarp surveys are still a cost-effective and useful method to assess the diversity of EMF communities. Surveys are essential for detecting those rare species that form conspicuous sporocarps (Smith et al., 2002), and for detecting species that are ecologically active in the community (O’Hanlon, pers. comm.). Furthermore, performing simultaneous surveys across replicate sites of interest increases the validity of comparisons drawn between communities (Humphrey et al., 2003).

Recent approaches to sampling EMF communities involve the analysis of the fungi present on the tips of tree roots after taking bulk samples of soil (Taylor, 2002). Root tip identification of EMF may be done using morphological characters, so-called morphotyping, or molecular methods. Morphological features of EMF structures are conserved at the species and genus level (Agerer, 2006). Distinguishing species using diagnostic features such as the shape of emanating hyphae relies on the training and experience of the investigator and can offer a low resolution; distinct morphological characters are often insufficient and morphology may change with EMF age (Taylor, 2002). Molecular methods can identify EMF to species level (Peter et al., 2001). A well-established technique is the polymerase chain reaction – restriction fragment length polymorphism (PCR–RFLP) analysis of the internal transcribed spacer (ITS) region of the nuclear small rRNA. Species identification is possible following extraction of DNA from a single mycorrhizal tip, PCR-amplifying, sequencing and comparing it with the sequences of databases (NCBI: http://www.ncbi.nlm.nih.gov/; UNITE: http://unite.zbi.ee; Koljalg et al. (2005)). Although identifications are fully reproducible, molecular methods are expensive and time-consuming resulting in less root tips being screened than by morphotyping (Peter et al., 2001).

A host of biotic and abiotic factors interact to govern the distribution and structure of EMF communities (see review in Koide et al. (2011)). The resulting non-random distribution of many species necessitates careful thought being given to sampling strategies in order to acquire an accurate representation of the EMF community (O'Hanlon, 2012). Chapter 3 describes the sampling strategy used for this study. I sampled both above- and below-ground to acquire an unbiased representation of the whole EMF community, as studies employing both above- and below-ground sampling methods often report a poor correspondence between them in terms of species richness and community composition (O'Hanlon, 2012, Dahlberg et al., 1997). For below-ground sampling, I followed the widely agreed principle that extensive sampling (few roots from many samples) is better than intensive sampling (many roots from few samples) to accurately describe EMF richness and structure of a forest stand (O'Hanlon, 2012).

1.2.2.4 The New Forest National Park

Located in central southern England, the New Forest is widely recognised as one of the most important areas for wildlife in the UK. Particular importance is given to the large-scale representation of three habitat formations: lowland heath (13,633 ha); valley mire (1,450 ha); and ancient semi-natural woodland (3,692 ha; Figure 1.3) (FC, 2008). The combination of these habitats on such a large scale justifies its inclusion amongst the most valuable areas for biodiversity conservation in lowland western Europe (Newton, 2010).

A number of conservation designations apply to the Forest at different scales, from national to global. Granted National Park status in 2005, and designated as a Site of Special Scientific Interest (SSSI) under the Wildlife and Countryside Act 1981, the New Forest constitutes the largest area of semi-natural vegetation in lowland England and comprises a mosaic of habits that were previously common, but now fragmented and rare in lowland western Europe (Cantarello et al. 2010). Through European designations, the New Forest is a Special Protection Area (SPA) and a Special Area of Conservation (SAC). Moreover, the Forest's global importance is recognised through its designation of a Ramsar site under the Convention of Wetlands of International Importance, Ramsar, Iran, 1971). Overall, the Forest is recognised as a hotspot for UK biodiversity, which can largely be attributed to the action of grazing livestock, maintained in the Forest by common rights (Tubbs, 2001, Carpenter et al., 2012).

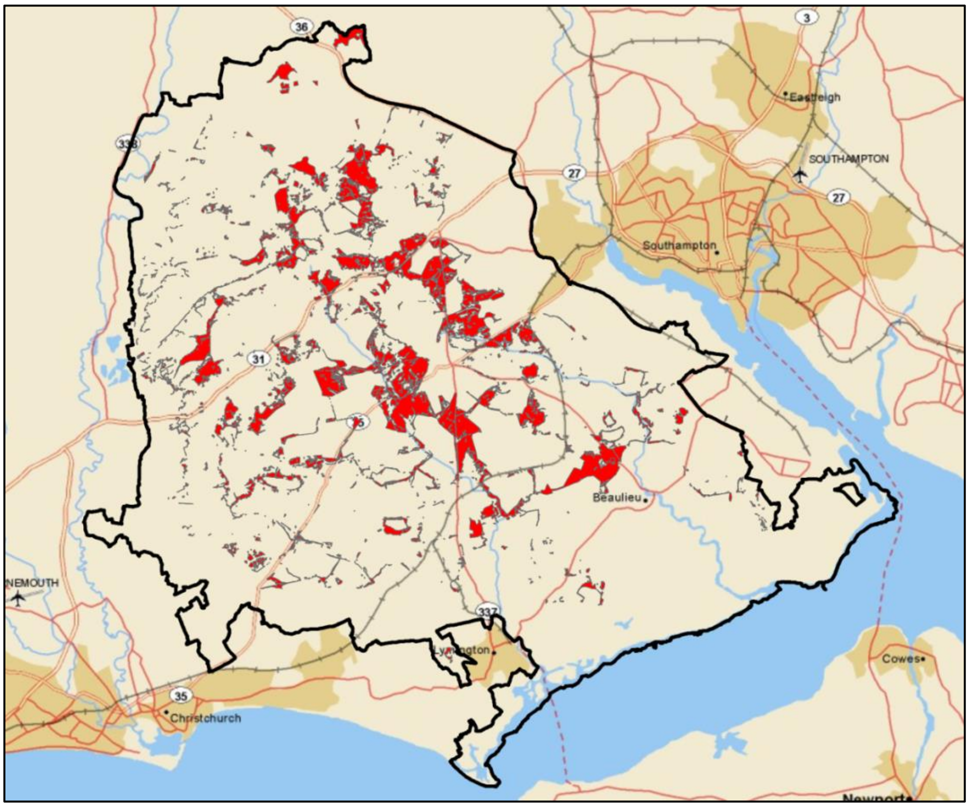

Figure 1.2 Map showing the extent of ancient woodland (i.e., >400 years old), in red, across the New Forest National Park. Black lines show the National Park designation boundary. From Carpenter et al. (2012).

1.2.2.5 Chapter 3 context and overview

Presently, there is much interest in setting aside overmature planted stands as a means of preserving species associated with old-growth forests (Humphrey, 2005, Lassauce et al., 2013). Old-growth forests are typified by long temporal continuity (typically multiples of the life-span of the dominant tree species), high proportions of large, old trees, multiple age-classes and high volumes of fallen and standing dead wood (Moning & Muller 2009). Set aside is a topical forest management strategy in Europe, where countries generally have a greater area of even-aged forests approaching biological maturity than old-growth forest (Barbati et al., 2012, Barbati et al., 2014). Indeed, for Europe, excluding the Russian Federation, even-aged forest >80 years of age now constitutes 18% of total forest area (Forest Europe et al. 2011). Forest ageing is a continuous process in which small-scale disturbances shape forest structural diversification (Barbati et al., 2012). Species associated with old-growth forest are expected to accumulate over time through the combined effects of this structural diversification, providing an ever-greater diversity of resources, and temporal continuity, favouring colonisation by dispersal-limited species (Norden and Appelqvist, 2001, Gibb et al., 2013).

EMF diversity is expected to increase with stand age (Humphrey et al., 2000, Ferris et al., 2000), as a result of increasing density of tree roots, leaf area (Simard and Durall, 2004), and associated carbon availability for ectomycorrhizal partners (Twieg et al., 2007). In addition, EMF are dispersal limited (Peay, 2010, Galante et al., 2011), requiring long periods of stand continuity for colonisation events to recover diversity to old-growth levels. In Chapter 2 we synthesised data from 17 studies measuring EMF richness in forest chronosequences (each a series of forest sites representing different stages of the forest cycle) in temperate and boreal regions, and showed that recovery of EMF richness to old-growth levels takes ~90 years on average. This estimate, however, is based exclusively on data from coniferous forest, primarily from North America, with the literature search finding no equivalent data from deciduous forests. EMF communities are sensitive to habitat fragmentation (Peay, 2010, Peay et al., 2012, Kranabetter et al., 2013), and it is therefore possible that richness recovery is faster in North America than in western Europe, where forests have been reduced to smaller remnants (Lassauce et al., 2011, Parviainen et al., 1999).

There is a need to assess recovery in broadleaved forests, which differ to coniferous forests in many ways that might influence the successional trajectories of EMF. For example, coniferous forests in general have larger volumes of coarse woody debris (CWD) than deciduous forests, due to better substrate quality and smaller diameter of angiosperm CWD on average (Gonzalez-Polo et al., 2013). The time needed for forests to reach different stages of stand development varies according to dominant species life history (longevity and growth rates) and site quality conditions (Barbati et al., 2012). For example, coniferous plantations typically attain canopy closure at younger ages than broadleaved forests. In oak (Quercus sp.) forests, old-growth characteristics are said to become significant after a stand age of about 200 years (Sanderson, 1996, Barbati et al., 2012).

Chapter 3 compares the species richness and composition of EMF between overmature planted 180 year-old and old-growth semi-natural oak forest, dating back at least 1000 years in the New Forest. The results show overmature planted forests support similar EMF communities and can therefore function as important reservoirs of old-growth communities in productive forest landscapes.

1.2.3 Chapter 4 – Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations

The objectives of chapter 4 are to assess the relative performance of traditional taxonomic metrics vs. functional metrics of biodiversity as indicators for use in monitoring in SFM schemes and investigate the drivers of carabid beetle functional trait composition and diversity in coniferous plantation forests. This is achieved through the analysis of the dataset of the UK Forestry Commission’s Biodiversity Assessment Project (BAP 1995-1999; Figure 1.1).

1.2.3.1 Chapter 4 context and overview

1.2.3.1.1 The use of indicator taxa in biodiversity monitoring

A central tenet to SFM is the integration of biodiversity conservation within production forests, a practice being increasingly implemented in Europe, North America and Australia (Rosenvald and Lohmus, 2008, Gustafsson et al., 2010, Lindenmayer and Franklin, 2002). Indicators of biodiversity are required for judging the success of management regimes intended to sustain biodiversity (Lindenmayer et al., 2000), and for prioritisation of protected areas (Larsen et al., 2009), as total biodiversity inventories and too costly and time-consuming. One approach being increasingly adopted is the use of indicator taxa, proxies that are typically metrics of richness or diversity of taxonomic units, assumed to be representative of broader biodiversity patterns (Westgate et al., 2014). In forests, ground layer plants are amongst the most commonly studied taxa when identifying potential surrogates for other taxa, typically invertebrates (Wolters et al., 2006). Indeed, the restoration of plant communities has become a major goal of restoration initiatives, with the assumption that the conditions that lead to more diverse plant communities will also lead to a restoration of insect communities (Babin-Fenske and Anand, 2010).

The use of indicator taxa rests on the assumption that cross-taxon congruency is high. A large literature has emerged quantifying the extent of cross-taxon congruence for a range of taxonomic groups, spatial locations and scales.Westgate et al. (2014) performed a global meta-analysis of these studies and revealed a high variance in cross-taxon congruence. Their analyses suggest that there are few circumstances in which pairs of taxa will be consistent surrogates for each other across a range of metrics, locations and spatial scales (Westgate et al., 2014). A key requirement of indicators is their ability to be applied with confidence in novel contexts (McGeoch, 1998), and so this lack of consistency puts into question the applicability of taxonomic surrogates to ecology and conservation planning (Westgate et al., 2014). The authors emphasise the need for novel approaches to the study of cross-taxon congruence and posit that functional metrics of biodiversity could be considered as potential means to improve surrogacy.

The use of functional metrics of biodiversity has a high potential to improve cross-taxon congruence. Cross-taxon congruence may occur for several reasons: (1) random coincidence; (2) interactions between taxa, (3) similar responses to common environmental variables, and (4) similar responses to different, but spatially covariant, environmental variables (Gaston, 1996, Wolters et al., 2006). Functional traits are the morphological, anatomical, biochemical, physiological or phenological traits associated with a species' ability to acquire resources, disperse, reproduce and persist in the environment (Violle et al., 2007). They represent physical interactions with the environment, and so it has been suggested that relationships between plant and invertebrate taxa and the environment are more likely to be revealed using trait data than species compositional data alone (Moretti and Legg, 2009).

In temperate forests, the majority of vascular plant species are restricted to the ground layer, where they form the trophic and structural template that supports a diversity of forest communities (Sabatini et al., 2014). Forest plant functional traits are particularly well characterised (Cornelissen et al., 2003), yet formal tests of the effectiveness of biodiversity indicators that incorporate functional traits are lacking. Just one study has investigated cross-taxon congruence between plants and animal diversity using functional traits. Gillison et al. (2013) explored the potential of functional and taxonomic descriptors of ground vegetation to function as indicators of bird, mammal and invertebrate taxonomic diversity in secondary tropical forests. They demonstrated correlations between vegetation functional traits (canopy height, woody basal area and litter depth) and taxonomic measures of vegetation diversity. Furthermore, structural measures of ground vegetation were found to be correlated with animal diversity.

More empirical tests of functional taxonomic indicators are needed before generalisations about their utility can be made. Chapter 4 assesses whether the use of functional biodiversity metrics improves cross-taxon surrogacy, over traditional taxonomic metrics (functional diversity vs. species richness and species diversity) in planted temperate coniferous forest stands in the UK. Congruence between ground layer plants and carabid beetles is assessed using a dataset from the Forestry Commission Biodiversity Assessment Project.

1.2.3.1.2 The Forestry Commission's Biodiversity Assessment Project

The Biodiversity Assessment Project (BAP) was established in 1995 in support of Forestry Commission policies relating to the conservation and enhancement of biodiversity in UK forests. It was a major component Forestry Commission's response to the UNCED Rio 1992 summit and sought to develop a biodiversity policy for the management of forests supported by a multidisciplinary biodiversity research programme. The particular objectives were to identify methods for improving biodiversity in managed forests, and to develop standards for managed forests (Humphrey et al., 2003). Assessments were conducted within planted conifer forests managed by clearfelling (when stands are approximately 40–80 years old) and restocking, a common silvicultural practice for commercial forests. Conifer plantation stands at 12 sites across the UK were selected for study in Chapter 4, although some broadleaved stands were also included in the BAP (Fig. 4.1; Table 4.1). These comprised four prominent commercial crop types grown in the UK: Sitka spruce (*Picea sitchensis* L. Bong. Carr.), Scots pine (*Pinus sylvestris* L.), Corsican pine (*Pinus nigra var. maritime* L.), and Norway spruce (*Picea abies* L. Karst.). A chronosequence approach was adopted in which comparisons were made between stands of different ages. The chronosequence stages used included (i) a pre-thicket restock stage (8–10 years); (ii) a mid-rotation stage (20–30 years); (iii) a mature stage (50–80 years); and (iv) an over-mature stage (60–250 years). Further details are given in Chapter 4. The biodiversity of multiple taxonomic groups (birds, fungi, beetles, plants, microbes) was characterised in a total of 44 coniferous plots across the 12 sites.

1.2.3.1.3 Investigation of the drivers of carabid trait composition and diversity

In addition to assessing the utility of trait-based diversity surrogates, Chapter 4 aims to investigate the relative importance of abiotic and biotic drivers of carabid functional trait diversity and composition across coniferous production forest stands sampled in the BAP. Quantifying the relative importance of mechanisms that drive community assembly is currently one of the most studied topics in ecology. Recent research on community assembly has shifted the emphasis away from taxonomic characterisations of species, to metrics that integrate species' functional traits. Such an approach facilitates an understanding of the mechanisms that underlie community responses to environmental change and determine ecosystem functioning (Diaz et al., 2007, Lavorel et al., 2008, Laliberte et al., 2010, Bachand et al., 2014). Much research has been devoted to identifying which traits make species more or less successful under given environmental conditions – broadly referred to as 'trait response' to the environment (Lavorel and Garnier, 2002, de Bello et al., 2009). The main interest in this approach is identification of which types of species will become more and less successful under future conditions imposed by land-use and climate change (de Bello et al., 2015).

To investigate drivers of carabid FD and trait distribution, Chapter 4 employs a frame-work that has been widely adopted across different taxonomic groups and ecosystems (Aubin et al., 2013, Bachand et al., 2014, Fountain-Jones et al., 2015). Figure 1.3 shows how it firstly involves the a priori generation of an appropriate list of functional traits. Selected traits were those thought to mediate direct responses of vegetation and beetle communities to the environmental changes imposed by forest management. I also selected traits that are likely to capture indirect effects of the forest cycle on beetle communities through bottom-up control by plants. These were traits related to morphology, reproduction, dispersal and resource use (Bachand et al., 2014). The traits were also commonly used in previous studies to allow for regional and global comparisons (Fountain-Jones et al., 2015). After trait selection, a species × site matrix (abundance data) is combined with the species × trait matrix to calculate a functional diversity index (Figure 1.3). Of the available indices, I chose Rao's quadratic entropy (Rao, 1982, Botta-Dukat, 2005) due to its widespread use and ability to identify habitat filtering mechanisms (de Bello et al., 2009, Aubin et al., 2013, Moretti and Legg, 2009). Models explaining variation in FD across sites can then be run to assess the relative importance of environmental variables (Figure 1.3). Chapter 4 also uses fourth corner analysis (Figure

1.2) to tests for trait–environment relationships using permutation models (Dray et al., 2014, Dray and Legendre, 2008).

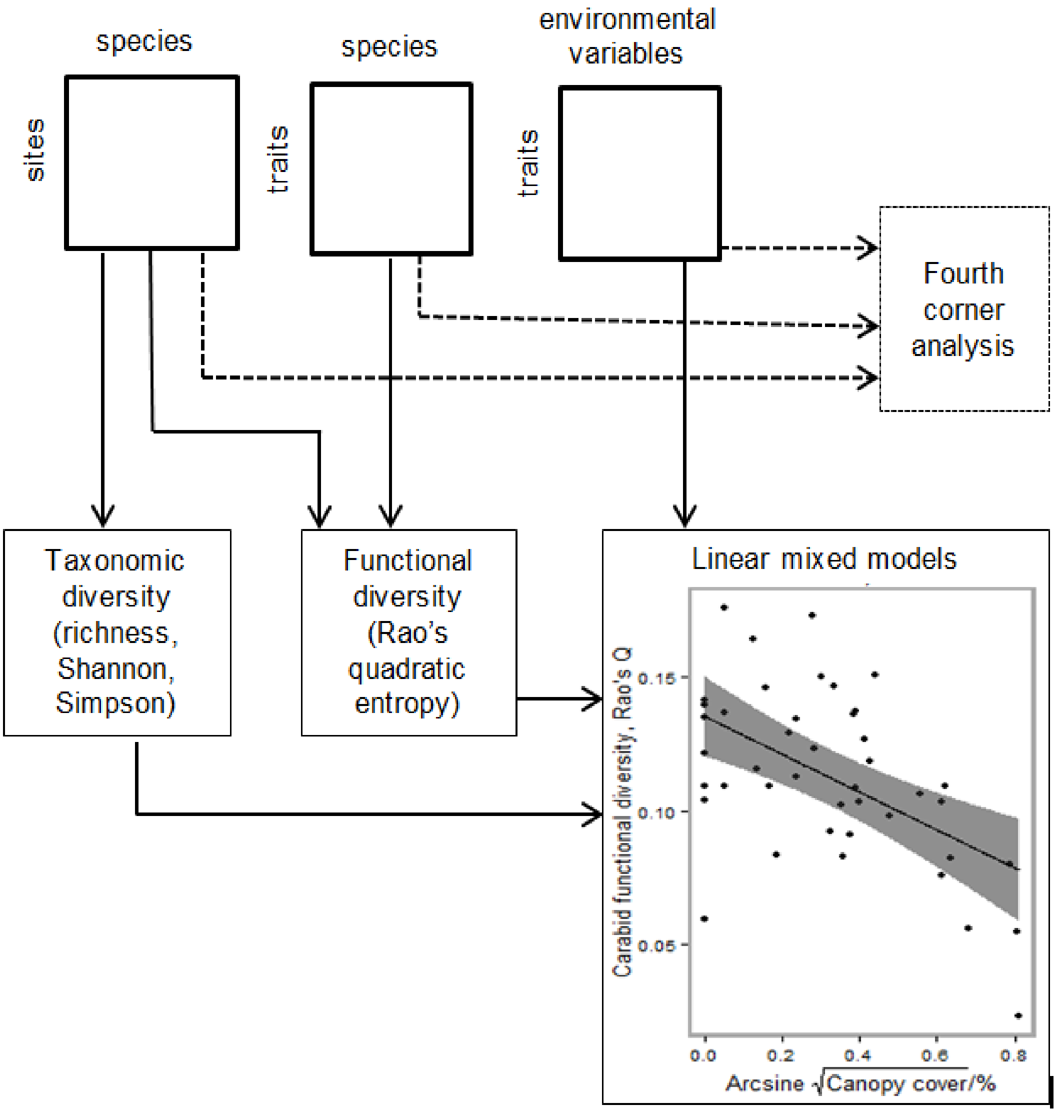

Figure 1.3 The methodological framework adopted in Chapter 4 to investigate the drivers of carabid functional trait diversity (solid lines) and distribution (broken lines) in UK coniferous production forests.

There is considerable uncertainty about if, and when, phylogenetic information is needed to answer various trait-based ecological questions (de Bello et al., 2015). Species are, necessarily, not phylogenetically independent of each other, and closely related species normally have similar functional traits and environmental preferences relative to distantly related species. As many statistical tests assume statistical independence amongst observations, some authors argue the importance of removing phylogenetic autocorrelation in trait data (Barton et al., 2011, Fountain-Jones et al., 2015). The majority of beetle trait studies, however, have not 'controlled' for phylogeny, partly due to the fact that correction requires a phylogeny for the target group, which for many beetle groups would be currently impossible at the species level (Fountain-Jones et al., 2015). Recently, de Bello et al. (2015) have argued that correction is not always required and that tests conducted with and without phylogeny focus on different questions. They argue that when assessing evolutionary mechanisms behind present trait-environment patterns, for example when asking whether (and which) traits have evolved as adaptations to environmental conditions, it might be useful to consider phylogeny, but phylogenetically ‘corrected’ results do not invalidate results obtained without phylogeny – they just highlight different aspects and evolutionary scales. Phylogemetic information is less important for questions concerning the short-term effects of environmental change on communities in terms of which species in a given regional species pool are going to be successful and which will be driven to (local) extinction. de Bello et al.’s (2015) reasoning for this is that the most important ongoing global change drivers operate on human time scales and therefore do not normally provide enough time for evolutionary processes to get ‘fixed’ in the phylogeny. Since the questions addressed in chapter 4 are interested in the effects of relatively short-term environmental changes, I decided not to correct for phylogeny; indeed evolutionary trait patterning was outside the scope of the study.

Chapter 4 found that neither functional nor taxonomic metrics of vegetation diversity correlated with carabid FD, arguing against the use of plant diversity as a surrogate UK coniferous production forests and suggesting that restoration of plant communities, a major goal of forest restoration efforts, will not necessarily enhance carabid FD in coniferous plantations. Chapter 4 observed a strongly negative relationship between canopy cover and carabid FD, suggesting that forest management could enhance carabid FD through initiatives that emulate natural disturbance regimes through gap creation.

1.2.4 Chapter 5 – Meta-analysis of forest management impacts on biodiversity in Japan

The objectives of Chapter 5 are to assess the effectiveness of various forest management strategies proposed in Japan’s National Biodiversity Strategy for enhancing biodiversity. This is achieved by the systematic review and meta-analysis of individual studies quantifying management impacts on species richness, abundance and composition (Figure 1.1).

1.2.4.1 Chapter 5 context and overview

Forests cover approximately 25 million hectares in Japan, constituting about two thirds of the total land area (Forestry Agency, 2009). The majority of Japan's forests are managed and include plantations and naturally regenerated coppiced and selectively cut forests (FRA 2010, table 1.2) . The most significant changes in Japanese forestry that has affected the relative extent and management of these forest types today occurred after the 1950s.

Table 1.2 The relative extent of different forest types in Japan. Adapted from FRA (2010).

National class	Definition	Area (1000 hectares)	% of forest area
Planted forest	Forest with standing trees established through planting or seeding	10,326	41.34
Naturally regenerated forest >80 years of age	Forest with standing trees other than planted forest, where there are clearly visible indications of management.	4,568	18.29
Naturally regenerated forest ≤80 years of age		8,744	35.01
Forest without standing trees	Forest without standing trees that has gone through final harvest	1,185	4.74
Bamboo forest	Forest dominated by bamboo	156	0.62

1.2.4.2 Planted forests

Planted forests account for over 40% of forest area in Japan (FRA, 2010, Table 1.2), much higher than the global average of 7% (FAO 2010). The majority of the plantations were established during 1950-1980, where large amounts of natural broad-leaved forests dominated by Fagaceae and Lauraceae were replaced by plantations of Japanese cedar (Cryptomeria japonica), Hinoki cypress (Chamaecyparis obtuse), and larch (Larix kaempferi) (Yamaura et al., 2012). Such large scale planting was promoted by a government program ('expansion of reforestation', 'Kakudai-zourin') launched in 1956 in response to increased wood demand.

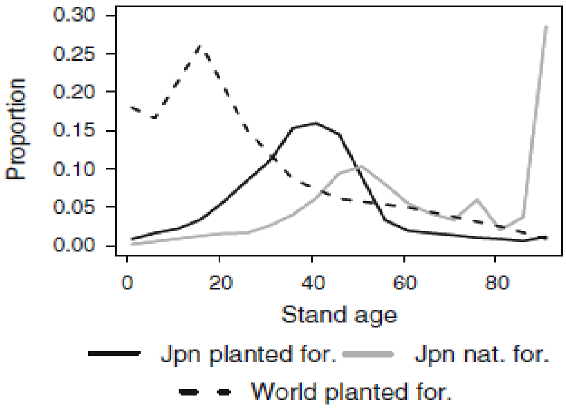

Figure 1.4 Present age-class distribution of Japanese planted and natural forests and world planted forests. Natural forests here are defined as forest with standing trees other than planted forest, where there are clearly visible indications of management. Note that resolutions of age-class distributions differ between Japanese and world forests. Sources: Japanese forests (Status of Forest Resources, Forestry Agency, Japan: http://www.rinya.maff.go.jp/toukei/genkyou/ index.htm); world planted forests (FAO 2006). The upper age class includes 91-year-old forests. From Yamaura et al. (2012).

A high proportion of planted forest area in Japan is now between 40 and 60 years of age, at economic felling age (Figure 1.4; Yamaura et al. 2012). The vast majority if these plantations forests, however, are currently unmanaged (Forest Agency 2009). Harvesting of plantations largely ceased during the 1970s for several socioeconomic reasons (Yamaura et al., 2009). These included: i) the high cost of harvesting owed to topographic complexity and the uncontrolled growth of shrubs and bamboos; ii) the importation of low-cost timber from North America and South East Asia; and iii) approximately 58% of Japanese forest area being privately owned by households, of which 57% own less than three hectares (Forest Agency 2009). The decline in profitability of forestry has made small-scale forest owners in particular reluctant to harvest their plantation forests (Forest Agency, 2009; Forest Agency, 2012). Indeed, despite the vast area of planted forest, Japan's self-sufficiency rate for wood supply has been around 20% in recent decades (Yamaura et al., 2012).

1.2.4.3 Secondary forests

Over half of forest area in Japan is classified as naturally regenerated (FRA, 2010; table 1), encompassing areas that have been selectively cut for saw timber and managed as coppices (Yamaura et al., 2009). A management regime known as 'satoyama' predominated during Japan's pre-development era, in which broad-leaved forests were clear-cut as coppices to provide a source of raw materials, such as charcoal, over cycles of 15 to 30 years

(Takeuchi, 2003). Management also included clearance of the undergrowth for fuel and compost, in addition to the collection of edible wild plants and mushrooms: ‘sansei’ (Chen and Qiu, 2012). Large-scale urban development and the ‘fuel revolution’ of the 1950s-60s, in which rapid economic development in Japan led to the replacement of fuelwood and green fertiliser in Japanese farms and markets with imported fossil fuels and chemical fertilisers (Yokohari and Bolthouse, 2011), resulting in the abandonment of many satoyama systems and their incorporation into suburban fringes (Iwata et al., 2011, Fukamachi et al., 2011). In many places, the abandonment of clearcut harvesting has produced mosaics of ageing secondary forests (Fukamachi et al., 2001); 35% of forest area in Japan that is currently classified as naturally regenerating is less than 80 years of age (FRA, 2010; table 1.2).

The collapse of the satoyama regime in Japan has triggered a reassessment of its value (Takeuchi, 2010). Since the 1980s, both national and international initiatives have been launched to restore satoyama through active management, not only in Japan, but throughout Asia, due to perceived benefits for biodiversity conservation and ecosystem service delivery. The definition of satoyama has recently expanded to encompass not only secondary broadleaved forests, but the mosaic landscape consisting of other habitat types that were also under traditional management during Japan’s pre-developmental era (Indrawan et al., 2014). These include plantation forests, rice paddy fields, grasslands, streams, reservoirs for irrigation and residential areas (Figure 1.5). Satoyama is epitomised as a ‘cultural landscape’ defined as the relationships between human activity and the environment have created ecological, socioeconomic, and cultural patterns and feedback mechanisms that govern the presence, distribution, and abundance of species assemblages (Farina, 2000). Indeed, the concept of satoyama figures prominently in popular and media discourse concerning the conservation of nature in Japan (Knight, 2010). The abandonment of satoyama systems in Japan is identified as a major driver of biodiversity loss in Japan’s National Biodiversity Strategy and Action Plan (Ministry of Environment, 2012). The Satoyama Initiative was recognised at the 10th meeting of the Conference of the Parties to the Convention on Biological Diversity (CBD) in 2010, together with the launch of the International Partnership for the Satoyama Initiative (IPSI).

Figure 1.5 Typical satoyama landscapes comprising mosaics of of forest, paddy fields, settlement and grasslands. Left: a village in the Kumano Mountains, Mie prefecture. Photo from Knight (2010). Right: a village from the Moriyama district. Shiga prefecture. Photo: Rebecca Spake

The Convention on Biological Diversity's Strategic Plan for Biodiversity and Aichi Biodiversity Targets (http://www.cbd.int/sp/) calls for substantial increases in the conservation, restoration and sustainable management of ecosystems by 2020. The restoration and integration of biodiversity conservation into the management of Japan's vast forest area will be central to Japan's effort to uphold its commitment to the Aichi Biodiversity Targets. Crucial policy issues have emerged concerning how forests should be managed to achieve these targets.

The future management of Japan's planted forest is currently being discussed by the forestry community in Japan. With the decreasing population size and demand for lumber and plywood over the last few decades in Japan, Yamaura et al. (2012) estimate the area of productive planted forest required to meet future domestic demand to be only 30% of the existing area. Several options are being discussed for plantation management, including rotation age extensions and rezoning of areas suitable for economic forest management. Ironically, restoration of planted forests into natural forests is being considered, and has been proposed as part of Japan's National Biodiversity Strategy (Ministry of Environment, 2012). Such restoration efforts have thus far taken a passive form, in which natural regeneration of broad-leaved forests has occurred on abandoned clear-cut stands. It has been suggested however that active measures subsidised by the government, involving planting native canopy tree species, might speed up the regeneration process at specific sites (Yamaura et al., 2012). Among the stand-level management options, thinning of planted forests has been proposed to enhance the natural regeneration of broadleaved tree species and biodiversity of various animal groups (Ministry of Environment, 2012; Yamaura et al. 2012).

For abandoned secondary forests, the management issue concerns whether to re-initiate their active management as promoted by initiatives such as ISPI, or whether to manage them passively by purchasing forests from private owners to set them aside for biodiversity conservation (Tsuchiya et al., 2014). In these deliberations, however, it must be recognised that satoyama is not necessarily a panacea for biodiversity conservation and the maintenance of ecosystem services. Indeed, the previous primary function of satoyama was for production rather the conservation of biodiversity per se (Takeuchi, 2003). The significance of the biodiversity benefits of satoyama management has remained an assumption (Indrawan et al., 2014). Policy documents from initiatives such as IPSI often fail to omit any systematic evidence of biodiversity benefits of active management. Furthermore, existing narrative reviews are not systematic, in that they synthesise data from an incomplete literature.

Sustainable restoration and management of forests requires a comprehensive understanding of the ecological impacts of interventions on biodiversity. A vast amount of empirical research has emerged in recent decades on biodiversity differences amongst forests under different management regimes in Japan. Systematic reviews offer an unbiased set of tools for accessing, appraising and collating robust scientific data into an evidence base to inform management and policy-making (Pullin and Knight, 2003). Several narrative syntheses exist summarising empirical findings of responses of biodiversity to forest management regimes in Japan (Inoue, 2005, Nagaike, 2012, Yamaura et al., 2011), yet a quantitative synthesis is lacking. Quantitative methods have been advocated for specifying the level of human interaction needed to use and manage biodiversity sustainably in satoyama landscapes (IPBES 2012). Furthermore, Yamaura et al. (2012) propose identifying thresholds of responses by components of biodiversity to stand-scale factors in plantation forests. The aim of Chapter 5 is to address these lacunae by synthesis and quantitative meta-analysis of forest management impacts on biodiversity in Japan.

Chapter 5 evaluates the effectiveness of plantation thinning and rotation age extension, and secondary forest satoyama management (clear-cutting and undergrowth clearance) on biodiversity. Taxonomic groups exhibit contrasting responses to different management interventions, except for thinning, which significantly increases the richness and abundance of several taxonomic groups.

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Chapter 2: A meta-analysis of functional group responses to forest recovery outside of the tropics

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2.1 Abstract

Both active and passive forest restoration schemes are used in degraded landscapes across the world to enhance biodiversity and ecosystem service provision. Restoration is increasingly also being implemented in biodiversity offset schemes as compensation for loss of natural habitat to anthropogenic development. This has raised concerns about the value of replacing old-growth forest with plantations, motivating research on biodiversity recovery as forest stands age. Functional diversity is now advocated as a key metric for restoration success, yet it has received little analytical attention to date. We conducted a meta-analysis of 90 studies that measured differences in species richness for functional groups of fungi, lichens, and beetles between old-growth control and planted or secondary treatment forests in temperate, boreal, and Mediterranean regions. We identified functional-group-specific relationships in the response of species richness to stand age after forest disturbance. Ectomycorrhizal fungi averaged 90 years for recovery to old-growth values (between 45 years and unrecoverable at 95% prediction limits), and epiphytic lichens took 180 years to reach 90% of old-growth values (between 140 years and never for recovery to old-growth values at 95% prediction limits). Non-saproxylic beetle richness, in contrast, decreased as stand age of broad-leaved forests increased. The slow recovery by some functional groups essential to ecosystem services makes old-growth forest an effectively irreplaceable biodiversity resource that should be exempt from biodiversity offsetting initiatives.

2.2 Introduction

The world's forests contain over 80% of global terrestrial biodiversity (Aerts and Honnay, 2011) and contribute crucial ecosystem services including carbon storage and protection of watersheds, fisheries, and soils (MA, 2005). Rates of deforestation are alarmingly high (FAO, 2010); 5.2 million ha of global forest area were lost each year from 2000 to 2010 (FAO, 2010). Currently, just 12% of global forest cover has biodiversity conservation designated as its primary function (FAO, 2010). While these protected reserves are essential to national and international strategies to counter biodiversity loss, they are insufficient to conserve forest biodiversity because they are too few, too isolated, and too inadequately protected from over-exploitation (Lindenmayer et al., 2006, Fischer et al., 2006). Therefore, conservation efforts are increasingly implementing forest restoration efforts worldwide, both within and outside reserves, to enhance biodiversity and ecosystem service provision in degraded landscapes (Chazdon, 2008, Benayas et al., 2009, Bullock et al., 2011). At the 11th Convention of the Parties, the Convention on Biological Diversity declared that ecological restoration and rehabilitation are crucial for the recovery of biological diversity and critical ecosystem services.

Forest restoration measures range from passive restoration, involving natural or unassisted forest recovery following the removal of environmental stressors such as grazing, to active restoration, involving human interventions such as planting to accelerate and influence the successional trajectory of recovery (Benayas et al., 2009, Holl and Aide, 2011, Morrison & Lindell, 2011). Forest restoration is also used as a biodiversity offsetting mechanism for mitigating the loss of natural area incurred by development. There are two major types of biodiversity offsets: restoration offsets and protection offsets. Restoration offsets aim to generate new habitat in an offset site to compensate for the loss of habitat due to development at the impact site. Protection offsets involve protecting existing biodiversity from further threats such as deforestation (Maron et al., 2012, Curran et al., 2014). The primary goal of biodiversity offsetting is to prevent change to species composition and habitat structure and to preserve ecosystem function or perceived cultural value associated with biodiversity (Bull et al. 2013).

A major criticism of restoration offset practice concerns the existence of time lags between the implementation of restoration action and the accrual of the intended benefits (Bull et al 2013). Several meta-analyses have quantified the recovery times required for biodiversity, including measures of species diversity and composition, to reach equivalence to some reference state. The reference state typically has attributes of an undegraded ecosystem (Bullock et al., 2011) characterized by relatively undisturbed old-growth forest. The majority of meta-analyses of stand age and biodiversity relationships have been produced for taxonomic groups including trees, epiphytes, birds, amphibians, mammals, ants, and other invertebrates in secondary tropical forests (Martin et al., 2013, Dunn, 2004, Chazdon et al., 2009). Fewer syntheses exist for forest recovery outside the tropics. A recent global synthesis by Curran et al. (2014) predicted century-long recovery times in species richness and composition within broad taxonomic groups including plants, trees, mammals, birds, herpetofauna, and invertebrates for naturally regenerating secondary forests in temperate, boreal, and tropical biomes. These syntheses indicate that different taxonomic groups exhibit contrasting patterns and rates of recovery over time (e.g., Dunn, 2004, Chazdon et al., 2009, Curran et al., 2014). This must be recognized in forest management strategies because different taxa make different contributions to ecosystem functioning (Hooper et al., 2002, Dirzo et al., 2014).

Syntheses to date have focused on charismatic taxa in tropical biomes. Evaluation of restoration objectives often pivots on the recovery of assemblages across broad taxonomic groups. The success of restoration programs, however, is being evaluated increasingly through assessments of functional diversity and critical ecosystem functions (Audino et al., 2014, Aerts & Honnay, 2011). In particular, one of the nine core success criteria suggested by the Society for Ecological Restoration is the representation of "all functional groups necessary for the continued development and/or stability of the restored ecosystem" (SER 2004). Distinguishing among the differential responses of different functional groups within broad groupings of taxa can facilitate an understanding of the mechanisms that underlie community responses to environmental change and determine ecosystem functioning (Diaz et al., 2007, Lavorel et al., 2008, Laliberte et al., 2010,).

We assessed the recovery of functional groups in restored forests outside the tropics, in temperate, boreal, and Mediterranean regions. We focused on lichens, fungi, and beetles because of their underrepresentation in existing quantitative syntheses of forest biodiversity recovery (Dunn, 2004, Chazdon et al., 2009, Curran et al., 2014). These taxa are well studied, relatively species rich, and sensitive to stand-level processes, and their communities perform vital functions in forest ecosystems. Lichens contribute to forest water and nutrient cycles through precipitation interception and nutrient sequestration (Ellis, 2012, Knops et al., 1996); fungi are the main agents of wood decomposition and thus carbon and nutrient cycling, and they form mycorrhizal associations with trees (Crockatt, 2012); beetle functional roles include herbivory, predation, decomposition, and microhabitat creation (Buse and Good, 1993, Barton et al., 2009). We differentiated functional groups by resource acquisition to reflect dependencies on resources or conditions that peak at different stages during forest recovery. For example, deadwood-dependent taxa were expected to benefit from forest succession because deadwood generally increases in volume and diversity as a stand ages (Humphrey et al., 2003). Furthermore, classification by resource acquisition, a process central to most biotic interactions, captures variation that is relevant to relationships between biodiversity and ecosystem (Flynn et al., 2009).

2.3 Methods

2.3.1 Systematic review scope

We followed standard systematic review methods (Pullin and Stewart, 2006) to collate empirical studies from temperate and boreal forests that compared biodiversity in planted or secondary forest with old-growth, primary, or mature controls. Temperate, boreal, and Mediterranean forest was defined as forest lying outside the -40° to +40° latitudinal band. Secondary forests (our treatment forests) had to have originated by planting or natural regeneration following major, stand-replacing disturbance including clearcutting and catastrophic wildfire. Controls had to have had little to no management over the past 50 years. Because passive restoration involves natural succession, studies that measured biodiversity at different stages of natural succession following disturbance were relevant to this analysis. Relevant studies published between 1970 and March 2015 were identified through literature searches in the ISI Web of Science. We used search terms relating to the focal taxa, forest type, and species richness data (see Appendix A.1 for the search query). Species richness was used as a proxy for biodiversity because species richness is the simplest and most widely used biodiversity measure (Magurran, 2004). For those studies that reported data in figures only, numerical information was extracted using DataThief (Tummers, 2006).

To ensure biologically meaningful comparisons, publications had to satisfy strict inclusion criteria. Treatment and control forest stands had to have similar composition and canopy dominants. Almost all of the collated studies featured treatment-control comparisons within observational chronosequences. Studies reporting only before-after comparisons were excluded because they lacked a true control (Duguid and Ashton, 2013). In agreement with Hurlbert's (1984) classification of acceptable and unacceptable study designs, we included studies that were definitively free of simple pseudoreplication so as to avoid spurious differences from confounding treatment variation with random site variation. We included studies that had replicate treatment forests spatially interspersed with replicates of control forests. Studies therefore had either completely randomized, randomized block, or systematic study designs (Hurlbert, 1984).

Beetles, lichens and fungi were assigned to functional groups according to resource acquisition. Beetles were categorized as saproxylic (species that depend on deadwood during some part of their life cycle [Speight, 1989] or non-saproxylic (groups not explicitly defined as saproxylic, e.g. ground beetles). Fungi were characterized as saprotrophic on deadwood, saprotrophic on litter, parasitic, or ectomycorrhizal (Humphrey et al., 2003, Ferris et al., 2000). Lichens were categorized as epiphytic (species that grow on the bark of trees) or terricolous (species growing on soil).

2.3.2 Statistical analyses

For each biodiversity comparison, the log response ratio (ln*R*) of species richness was calculated between secondary forest (treatment group) and old-growth forest (control group):

$$\ln R = \ln(\bar{x}_2) - \ln(\bar{x}_1), \qquad (1)$$

where $\bar{x}_2$ is the mean species richness of treatment forest stands and $\bar{x}_1$ is the mean species richness of old-growth stands. The ln*R* describes the proportional difference in species richness between control and treatment groups. The natural log transformation of the response ratio both linearizes the metric, treating deviations in the denominator and the numerator as equal, and normalises its otherwise skewed distribution (Hedges et al., 1999).

All statistical analyses and calculations were performed in R (version3.1.1) (R Core Team, 2014). Publication bias may be suspected if small positive effect sizes are present without small negative effect sizes (Newton et al., 2009). We tested this in the METAFOR package (Viechtbauer, 2010) by assessing a funnel plot of effect size versus standard error of the effect size (Sterne and Egger, 2001, output in Appendix A.4). Weighted regression with multiplicative dispersion and standard error as the predictor did not detect funnel plot asymmetry, (t_{88}= -0.53, p = 0.54), indicating no evidence of publication bias.

To quantify how the species richness of different functional groups varies with stand age, we constructed linear mixed models containing an interaction between stand age and functional group. Latitude and transition category, which are consistently reported in the literature, were added to the model. Transitions included clearcut to planted, clearcut to regenerated, fire to planted, and fire to regenerated. Treatment forest stands were either managed or unmanaged, where managed forests were secondary forests from which many trees had been removed (e.g., thinning since initial planting or regeneration). We included quadratic or $\log_{10}$ relationships and stand age to test for possible nonlinear biodiversity recovery with stand age. To account for possible pseudoreplication from multiple biodiversity comparisons (studies) per observational chronosequence, each model included chronosequence as a random factor.

Meta-analyses may weight study-wise effect sizes to improve precision of the estimate of overall mean effect and the power of tests (Gurevitch & Hedges, 1999). Effect sizes are commonly weighted by the inverse of within-group variance to raise the relative contributions of studies with lower unmeasured variation, on the principle that these will have higher precision (Koricheva & Gurevitch, 2014). In the absence of a suitable measure of within-group variation being provided by primary studies, some meta-analyses weight by sample size, on the principle that variance is expected to decrease with sample size, all else being equal. We did not weight effect sizes because of two issues relating to variance estimation and sample size that occur frequently in ecological study design (see Appendix A.5 for reasoning). Differences between weighted and unweighted statistics are generally small for meta-analysis (Cardinale et al., 2006, Marvier et al., 2007, Benayas et al., 2009). Furthermore, unweighted meta-regression is often more robust because it does not use potentially misleading estimation of error variances (Fletcher & Dixon 2012).

All possible additive models were constructed using maximum likelihood methods in package MuMIn (Barton, 2013). Power was insufficient to test for interactions other than stand age*functional group. We used Akaike's information criterion (AIC) with small-sample correction (AICc) to identify support for each model (Burnham & Anderson, 2002). The AICc gives a parsimonious quantification of model fit by incorporating both deviance explained and number of parameters used. Fit of selected models was assessed by calculating marginal R^2 following Nakagawa and Schielzeth (2013). Latitudes were centred to improve the interpretability of regression coefficients (Schielzeth, 2010). Graphics were produced using ggplot2 (Wickham, 2009), with ln*R* values transformed to show change more intuitively as percentage difference from old-growth forest stands. Planned orthogonal contrasts were applied to the best model (with the lowest AICc value) in order to interpret differences among functional groups and their interaction with stand age (Doncaster and Davey, 2007).

2.4 Results

The literature search yielded 3810 publications. Of these, 47 satisfied inclusion criteria concerning study taxa and latitude and appropriateness of control and treatment stands. Fifteen of these had unclear or pseudoreplicated study designs (covered in Methods). We included the remaining 33 publications in the analysis (Appendix A2). These provided 90 separate biodiversity comparisons, hereafter referred to as studies (Table 2.1). Of these studies, 40 (44%) were from Europe, 45 (50%) from North America, and 5 (5%) from Asia and Australia (Table 2.1 & Appendix A3). Biases existed in terms of the forest type and the functional groups investigated. Of the 90 studies, 19 (21%) were from broadleaved forest, and 13 of these 19 were on non-saproxylic beetles. The non-saproxylic beetle group was therefore divided into broadleaved and coniferous subgroups. Authors indicated some degree of harvesting (e.g., thinning operations) in the treatment stands of 5 out of 90 studies. The influence of management was therefore not assessed. The single study on terricolous lichens that satisfied inclusion criteria was grouped with epiphytic lichens. No suitable data were found on parasitic fungi.

Table 2.1 Geographic origin and focal functional groups of studies used in the meta-analysis of functional group richness recovery with stand age

Group	Number of studies by continent				Total
	N. America	Europe	Asia	Australia	
Epiphytic lichens	12	7	0	0	19
Ectomycorrhizal fungi	14	3	0	0	17
Deadwood fungi	5	7	0	0	12
Litter fungi	3	4	0	0	7
Saproxylic beetles	3	5	2	0	10
Non-saproxylic beetles	8	14	1	2	25
Total	45	40	3	2	90

The minimum adequate model selected to explain recovery of species richness in secondary forests included functional group ($F_{6,45} = 8.92$, $p < 0.001$) and $\log_{10}$ stand age ($F_{1,45} = 5.91$, $p = 0.019$), their interaction ($F_{6,45} = 4.41$, $p < 0.002$; Table 2.2), and latitude ($F_{1,30} = 1.75$, $p = 0.196$; Table 2.2). This model had the lowest AICc score (the next best model had ΔAICc 4.9) and explained 56% of the variation among studies (Table 2.2). Transition category did not feature in the best model. Planned orthogonal contrasts revealed significant differences in recovery between broadleaved non-saproxylic beetles and pooled coniferous saproxylic and non-saproxylic beetles and between saproxylic and coniferous non-saproxylic beetle groups (Table 2.3).

Table 2.2 Variables included in linear mixed models developed to explain variation in the log response ratio of species richness in planted and secondary forest stands relative to old-growth forest.

	Variables in model[*]					df	AICc	ΔAICc	Marginal R^2
Null model[a]	group	$\log_{10}$(age)	group*$\log_{10}$(age)	lat	trans				
Null						3	94.81	20.01	0.17
1	+	+	+	+		17	74.80	0.00	0.56
2	+	+	+			16	79.70	4.90	0.54
3	+	+	+	+	+	20	80.83	6.03	0.58

*Abbreviations: ‘group’, functional groups comprising lichens, ectomycorrhizal fungi, litter fungi, deadwood fungi, saproxylic beetles, and non-saproxylic beetles in coniferous and broadleaved forest; ‘log10(age)’, log10 of stand age in years; ‘lat’, centred latitude; ‘trans’, transition category representing the origin of the treatment stands, including clearcut planted, clearcut secondary, fire planted, and fire secondary. In addition to the null model, only models with ΔAICc < 7 are shown (i.e., those with considerable support [Burnham and Anderson, 2002].

Different functional groups showed different directions and rates of recovery following disturbance. For ectomycorrhizal fungi, a best estimate of recovery to undisturbed old-growth values of species richness was 90 years (between 45 years and unrecoverable at 95% prediction limits) (Fig. 2.1). The best estimate for lichens was 180 years to reach 90% of undisturbed forest values (between 140 years and never for full recovery) (Fig. 2.1). Saproxylic beetles had a best estimate of about 60 years to reach 90% of old-growth values (between 10 years and never for full recovery). In coniferous forest, non-saproxylic beetle species richness did not differ detectably between control and treatment forest. In broadleaved forest by contrast, non-saproxylic beetle species richness appeared to benefit from early successional stages; treatment forest exhibited about twice (from 1.4 to 2.5 times) the species richness of old-growth forest immediately following major disturbance. Deadwood and litter fungi species richness did not differ detectably between old-growth and treatment stands (Fig. 2.1).

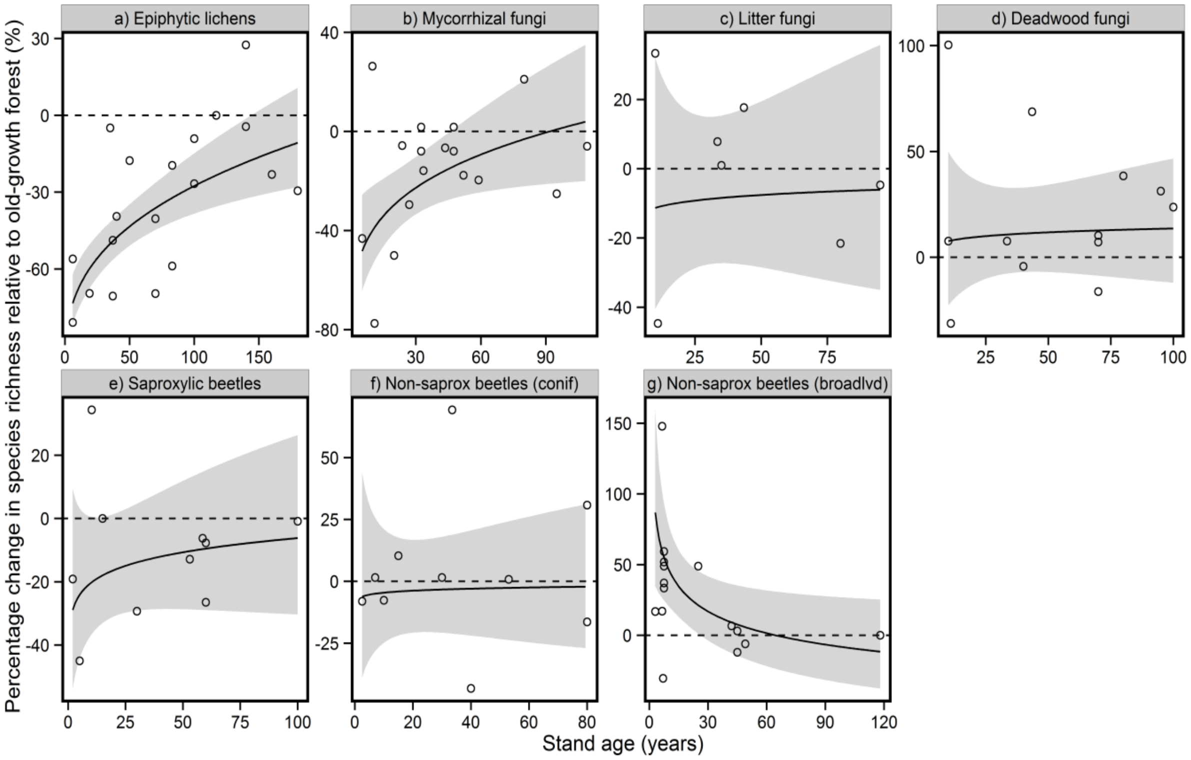

Figure 2.1 Influence of stand age on percent change in species richness for 7 functional groups in planted and secondary forest relative to old-growth forest stands (horizontal dashed line, no difference between undisturbed old-growth forest and treatment [planted and secondary] forest stands; grey, 95% prediction intervals based on uncertainty in fixed effects only; 'saprox', saproxylic; 'conif', coniferous; 'broadlvd', broad-leaved). Regressions had coefficients of the best model based on AICc. Latitude was fixed at its mean value for all predictions.

Table 2.3 Planned orthogonal contrasts among 7 functional groups in the best model of species-richness recovery in planted and secondary forests*

Comparison	Main effect of group		Interaction with $\log_{10}$(age)	
	t	*p*	*t*	*p*
Coniferous and broadleaved non-saproxylic beetles and saproxylic beetles vs. all other groups	-0.59	0.555	-0.06	0.952
Broadleaved non-saproxylic beetles vs. pooled coniferous non-saproxylic beetles and saproxylic beetles	5.65	<0.001	-3.93	<0.001
Saproxylic beetles vs. coniferous non-saproxylic beetles	-3.59	<0.001	2.45	0.018
Lichens vs. pooled coniferous litter, deadwood and ectomycorrhizal fungi	0.87	0.390	-0.74	0.464
Litter fungi vs. pooled deadwood and ectomycorrhizal fungi	1.26	0.215	-0.77	0.445
Deadwood fungi vs. ectomycorrhizal fungi	-1.40	0.168	1.20	0.237

*All comparisons had 45 error df. Negative *t* values indicate lower coefficients for the first group than the second group, and positive values indicate higher coefficients for the first group than the second group.

2.5 Discussion

2.5.1 Recovery of species richness of functional groups

We found functional group-specific relationships between species richness and stand age following forest disturbance. Lichen, ectomycorrhizal fungi, and saproxylic beetle richness was much lower in early successional or young planted forest than undisturbed old-growth forest (Fig. 2.1). Recovery to old-growth values of species richness required 90 years for ectomycorrhizal fungi, 60 years for saproxylic beetles, and >100 years for lichens. Non-saproxylic broadleaved beetle communities benefited from major disturbance; early successional forest contained around twice the species richness of undisturbed forest (1.4-2.5 times; Fig. 2.1). Our result of taxon-specific responses to stand age extended this pattern from tropical multi-taxon syntheses. Dunn (2004) synthesized data across a wide range of animal taxa, including bats, birds, and invertebrates, and found that faunal species richness in tropical secondary forest can rapidly resemble that of old-growth forest within just 20-40 years following major disturbance. Martin et al. (2013) found that tropical epiphytic plants took considerably longer; over 100 years were needed for species richness to recover in forest regenerating from agricultural clearance.

The increase in lichen richness with stand age is likely attributable to the combined effects of time, which favored colonisation by dispersal-limited species, and changes in substrate conditions associated with tree ageing (increased surface availability, changes in bark pH and texture, and increased stable substrate due to reduced growth rates) (Nascimbene et al., 2013). Johansson (2008) investigated lichen-stand age relationships in boreal chronosequences by meta-regressing stand age with the species richness of forest age class as a proportion of the total species pool richness (all age classes combined). Using this approach, no relationship was found between proportional richness and stand age, which is likely due to compositional differences between younger and older stands (Johansson, 2008). Ectomycorrhizal fungi form mutualistic symbioses with tree hosts by forming a sheath around the root tip of the tree that exchanges soil-derived nutrients for carbohydrates from host trees (Smith and Read, 2008). Ectomycorrhizal diversity is expected to increase with stand age (Humphrey et al., 2000, Ferris et al., 2000), as found in this study (Fig. 2.1), in response to increasing density of tree roots, leaf area (Simard & Durall, 2004), and associated carbon availability for ectomycorrhizal partners (Twieg et al., 2007). Deadwood-dependent richness, including deadwood fungi and saproxylic beetles, is expected to rise with stand age, owing to the increase in deadwood volume and decay stage over time, and therefore as a function of the species-area relationship and provision of diverse microhabitats (Heilmann-Clausen and Christensen, 2004, Lonsdale et al., 2008). While saproxylic beetle richness increased steadily as stand age increased, species richness of deadwood fungi differed little between old-growth controls and planted and secondary forest (Fig. 1). Little deadwood is produced in young forest stands, and its presence in these studies may have been a product of the major disturbance event that initiated the stand or due to deadwood created through self-thinning of young stands. Higher deadwood volumes in young treatment stands may therefore be responsible for the comparable richness of deadwood fungi in treatment and old-growth stands.

Studies investigating the succession of non-saproxylic beetle groups attribute higher biodiversity values in early successional forest to high numbers of open-habitat and generalist species, favoured by conditions afforded by open canopies (da Silva et al., 2008, Taboada et al., 2008). Although we did not examine compositional differences between treatment and old-growth forest, this may be the case here for broadleaved non-saproxylic beetles (Fig. 2.1), which decreased in richness as stand age increased (see also Lange et al., 2014). Coniferous non-saproxylic beetle richness differed little between old-growth and treatment stands. More data are needed to understand compositional differences that might explain this pattern.

The inclusion of latitude improved the goodness of fit and explanatory power of the best model (Table 2.2). Latitude is a coarse proxy for changes among many local environmental descriptors. For example, high-latitude soils generally contain fewer nutrients than low-latitude soils (Zvereva et al., 2008), and latitude can alter the slope of species-area relationships on islands (Solymos & Lele, 2012). Furthermore, spatial continuity of forest at the landscape scale is less likely to be a limiting factor for dispersal in widely forested regions such as boreal Fennoscandia, as opposed to other areas in temperate western Europe where forests have been reduced to smaller remnants (Parviainen et al., 1999). Further identification of latitudinal components that cause species richness differences between old-growth and treatment forest is problematic because of the high co-linearity among the components that underpin the broad latitudinal gradient.

We found that functional groups within broad taxonomic groups exhibited varying responses to forest recovery (Fig. 2.1). This might suggest that previous meta-analyses investigating biodiversity variation relative to environmental variables in which organisms were classified into uniform taxonomic groups may have undervalued some patterns of biodiversity-by-environment relationships. We found that functional groups were not equivalent to broad taxonomic groups for fungi and beetles (Fig. 2.1). For example, pooling saproxylic and non-saproxylic beetles, which showed contrasting responses to stand age, may wrongly suggest that forest stand age has negligible effects on beetle biodiversity, which was clearly not the case.

2.5.2 Knowledge gaps

Our systematic review yielded just 33 publications (90 individual studies) in which old-growth was compared with planted or secondary forests in a statistically robust way. For some functional groups, this led to small sample sizes and low precision in ln*R* values (Fig. 2.1). The small number of publications suggests a continuing lacuna of empirical data for evaluating biodiversity indicators. Sustainable forest management requires effective biodiversity indicators for monitoring (Lindenmayer et al., 2000), and there is therefore an urgent need for more carefully designed studies to identify and evaluate such indicators. Of the 90 suitable studies suitable, 79% were conducted in coniferous forest. More data are needed from broad-leaved successional chronosequences, which are underrepresented in the literature.

2.5.3 Conservation implications

The primary goal of biodiversity offsetting is to achieve no net loss of biodiversity. Our results show that through restoration offsetting, this goal is unachievable within a reasonable time frame. Functional groups in secondary forest require over a century for lichens and almost a century for ectomycorrhizal fungi to recover species richness values equivalent to old-growth forest (Fig. 2.1). The slow recovery of species richness for some functional groups essential to ecosystem services makes old-growth forest an effectively irreplaceable biodiversity resource that should be exempted from restoration offset initiatives. Interim losses of old-growth forest from landscapes over century-long time scales disable their function as biodiversity donors to developing forests, lead to the loss of functional groups, and jeopardize ecosystem function (Wardle & Zackrisson, 2005).

Our results support the findings of Curran et al. (2014), who also demonstrated long recovery times in their global analysis across broad taxonomic groupings in secondary forests. They found that species richness converges to old-growth reference values within a century, species similarity takes about twice as long, whilst assemblage composition takes up to an order of magnitude longer (hundreds to thousands of years). Our finer-scale analysis showed significant differences in the responses of different functional groups within broad taxonomic groupings and century-long recovery times for some functional groups.

These results support the value of protecting old-growth forest through reserve creation, set-aside of overmature stands for biodiversity conservation, and implementation of schemes that extend rotation-length of secondary forests within production forest landscapes. Examples of the latter include woodland key habitats (WKHs) and green tree retention (GTR) practices in Fennoscandia and the creation of temporary “ageing islands” in French high forests (Lassauce et al., 2013).

Our observation of varying responses of different functional groups to forest recovery has important implications not only for restoration initiatives but also for sustainable forest management of productive forests. Sustainable forest management represents a paradigm of forest management strategies that balance timber provision with the production of other goods and services that human society needs through the integration biodiversity conservation within productive forest landscapes (Lindenmayer et al., 2012). Forest successional stages that support different functional groups must be represented in production landscapes because different groups make different contributions to ecosystem functioning (Hooper et al., 2002).

Our results apply to the scale of forest stands and therefore to alpha diversity. With different functional groups exhibiting contrasting species richness levels in different successional stages, it is possible that diversity at the landscape scale may be higher in a mosaic of lower richness patches than in a homogeneous landscape with higher alpha diversity (Duguid & Ashton, 2013). For example, the decline of broadleaved non-saproxylic beetles as stand age increased (Fig. 2.1) supports suggestions that young secondary forest must be included in managed forest mosaics for invertebrate conservation (de Warnaffe & Lebrun, 2004).

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2.7 Co-author contribution

Contributor	Contribution
RS	Formulated original research question and study deign, performed systematic review and data extraction, statistical analysis and write up
THGE	Advised on statistical analaysis and presentation in R
PAM	Advised on statistical analaysis and presentation in R
ACN	Advised on question formulation and write-up
CPD	Advised on question formulation and study design and contributed to statistical analysis and write-up.

2.8 Chapter 2 Addendum

This addendum addresses an omission and two possible caveats to chapter 2.

2.8.1 Omission of the clarification that 'within-sample species richness' was measured across studies

For the purposes of comparing species richness among sites, sample- or individual-based rarefaction may be used to standardise datasets to a common number of individuals (Gotelli & Colwell 2001). However, the majority of empirical research comparing the number of species among sites standardise measures of richness on the basis of area or sampling effort, by employing an equal sampling intensity across sites. Such comparisons are actually comparisons of species density: the number of species per unit area (Simpson 1964; Gotelli & Colwell 2001), or 'within-sample species richness' (Newbold et al. 2015). Such studies therefore assume that samples are drawn from populations of individuals with similar densities (Gotelli & Colwell 2001). Chapter 2 employed within-sample species richness as a measure of species richness, and this was not clarified in the published version (Spake et al. 2015). It is important to note that it is possible that differences in species richness between old-growth forest control and secondary forest stands could be partly driven by effects on overall abundance of individuals (A. Purvis, pers. comm).

2.8.2 Possible caveat relating to exclusion of studies with simple pseudoreplication

I decided to exclude studies with simple pseudoreplication from the meta-analysis, using Hurlbert's (1984) classification of acceptable and unacceptable study designs. We therefore only included studies that had replicate treatment forests spatially interspersed with replicates of control forests in the form of completely randomized, randomized block, or systematic study designs (Hurlbert, 1984). The original reasoning for this exclusion was to avoid the inclusion of spurious differences that might arise from confounding treatment variation with random site variation, which can occur in studies with simply pseudoreplicated designs. This decision was perhaps unnecessary for two reasons. Firstly, meta-analysis could be perceived as a solution to a pseudo-replicated literature, as it is a means by which individual studies can be combined and analysed to detect consistent patterns (Hargrove and Pickering, 1992; Cottenie and De Meester 2003; Davies & Gray, 2015). Indeed, univariate directional effects, such as decreases in the species richness across a particular management intervention, are formative collectively (Ramage et al. 2014) and meta-analysis can be seen as statistical tool which effectively replicates the studied systems (Cottenie and De Meester, 2003). Secondly, the meta-analysis was unweighted. Effect sizes are commonly weighted by the inverse of within-group variance to raise the relative contributions of studies with lower unmeasured variation, on the principle that these will have higher precision (Koricheva & Gurevitch, 2014). Because low variation among simply pseudo-replicated samples can arise as an artefact of the study design, whereby replicates are actually interdependent samples of the same species pool (Halme et al., 2010), they may be awarded a relatively high weighting in a meta-analytical model, potentially inflating mean parameter estimates. Given the decision to perform an unweighted meta-analysis, excluding studies that contained pseudoreplication was therefore perhaps unnecessary.

2.8.3 Possible caveat relating to criterion used to assess whether species richness had recovered to old-growth levels

We considered species richness of secondary forest stands to have recovered to old-growth levels when the species richness difference between them became zero, i.e. when recovery curves crossed the dashed line Figure 2.1. We reported mean recovery times with respect to their 95% prediction limits (Figure 2.1). Subgroups with larger sample sizes (epiphytic lichens had the largest *n*) will have had smaller confidence bands surrounding the mean recovery curves. Larger sample sizes will have led to longer recovery estimates at lower prediction limits and shorter recovery times at upper prediction limits. To avoid recovery estimates that are artefactual of sample size, vote counting of studies that have ‘recovered’, i.e. with a 0-10% difference in richness between old-growth and secondary stands, within successive forest age classes could have been done and compared across subgroups.

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Chapter 3: Similar biodiversity of ectomycorrhizal fungi in set-aside plantations and ancient old-growth broadleaved forests

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except for the addendum on page 89.

3.1 Abstract

Setting aside overmature planted forests is currently seen as an option for preserving species associated with old-growth forests, such as those with dispersal-limitation. Few data exist, however, on the utility of set-aside plantations for this purpose, or the value of this habitat type for biodiversity relative to old-growth semi-natural ecosystems. Here we evaluate the contribution of forest type relative to habitat characteristics in determining species richness and composition in seven forest blocks, each containing an ancient old-growth stand (>1000 yrs) paired with a set-aside even-aged planted stand (ca. 180 yrs). We investigated the functionally important yet relatively neglected ectomycorrhizal fungi (EMF), a group for which the importance of forest age has not been assessed in broadleaved forests. We found that forest type was not an important determinant of EMF species richness or composition, demonstrating that set-aside can be an effective option for conserving ancient EMF communities. Species richness of above-ground EMF fruiting bodies was principally related to the basal area of the stand (a correlate of canopy cover) and tree species diversity, whilst richness of below-ground ectomycorrhizae was driven only by tree diversity. Our results suggest that overmature planted forest stands, particularly those that are mixed-woods with high basal area, are an effective means to connect and expand ecological networks of ancient old-growth forests in historically deforested and fragmented landscapes, for ectomycorrhizal fungi.

3.2 Introduction

High structural diversity and long continuity of old-growth forests make them irreplaceable biodiversity resources (Gibson et al., 2011, Spake et al., 2015). Planted or regenerated forests of relatively young and even age now constitute 73% of total forest cover in Europe (San-Miguel-Ayanz et al., 2011). Throughout Europe, timber-orientated forest management has shortened forest stand development to just 10–40% of the potential lifespan of dominant tree species (Bauhus et al., 2009, Barbati et al., 2012). These forests consequently lack the continuity and many of the structural attributes typical of old-growth forests, including high variation in tree size, the presence of large dying trees and irregular gap size and distribution (Bauhus et al., 2009).

Concern about the global decline of old-growth forest and the associated loss of biodiversity has motivated initiatives to increase the area of protected old-growth (CBD, 2011). Although strict protection of natural forests will likely remain a conservation priority throughout the world, management options increasingly recognise the additional potential for other types of forests to support biodiversity (Gibson et al., 2011, Putz et al., 2012). Presently, there is much interest in the setting aside of overmature planted stands as a means of preserving species associated with old-growth forests (Humphrey, 2005, Lassauce et al., 2013). Set-aside is a topical forest management strategy in Europe, where countries generally have a greater area of even-aged planted forests approaching biological maturity than old-growth forest (Barbati et al., 2014). The ageing of even-aged forest stands is a continuous process in which small-scale disturbances shape forest structural diversification (Barbati et al., 2012), with consequences for biodiversity conservation, carbon storage and the ways energy, gas and nutrients are cycled through the forest (Parker et al. 2004).

Species associated with old-growth forest are predicted to accumulate over time in set-aside in response to the increasing structural diversification as a forest ages. The temporal continuity and ever-enriching diversity of resources particularly favours colonisation by the dispersal-limited species characteristic of old-growth forest (Norden and Appelqvist, 2001). Indeed, several studies of dispersal-limited groups have demonstrated that ecological communities from older forests are generally, but not invariably, richer than those of more recent forests. For example, Peterken (1974) and Rose (1974) showed that the occurrences of certain vascular plants and epiphytic lichens could distinguish ancient semi-natural forests (old-growth forest that has been continuously wooded since 1600 A.D.)

from more recent, secondary forest stands. Whilst differences in species composition between ancient and more recent forests can be attributed to differences in stand structure and microhabitat composition, many studies emphasise the importance of time *per se*; evidenced by certain species being absent from young forest despite the presence of suitable habitats (Norden and Appelqvist, 2002). For example, many cyanobacterial macrolichens are rare in recent stands even if seemingly suitable substrate is available (Kuusinen 1996). It is therefore thought to be the longer residence time that is important in allowing dispersal limited species to reach and establish in a habitat (Goward 1994).

Despite the perceived importance of overmature planted forest in supporting old-growth forest communities, empirical data are lacking on their relative biodiversity values for many taxonomic groups (Sverdrup-Thygeson et al., 2015). A recent meta-analysis synthesising species richness relationships with stand age in temperate and boreal forests demonstrated functional group-specific responses to stand age, owing to specific dependencies on resources or environmental conditions that become available at different times during succession (Spake et al., 2015). This synthesis showed that species richness in planted and regenerating forests can eventually achieve equivalence to old-growth forests for some functional groups, including epiphytic lichens and fungi. Compositional differences have yet to be investigated, however, and the potential for planted forests to support old-growth forest communities remains poorly understood. Here we investigate empirically the value of planted, economically overmature forests to ectomycorrhizal fungal communities, relative to ancient old-growth forest in the New Forest National Park, UK.

Ectomycorrhizal fungi (EMF) comprise a functional group that forms mutualistic associations with most economically and ecologically important temperate tree species (Smith and Read, 2008). Approximately 90% of species rely on mycelial networks intimately connected with their roots, ectomycorrhizae, for the uptake of water and N, P, and other minerals from soil (Heilmann-Clausen et al. 2014). EMF form a highly diverse biota in boreal and temperate forests, which is sensitive to natural and anthropogenic disturbances, such as nitrogen deposition (Barker et al., 2013). High EMF diversity is important both to the vigour of individual hosts and to the functioning of the forest ecosystem. At the individual level, the diverse capacities amongst EMF species for mobilising nutrients from soil mineral and organic matter (Nygren et al., 2007) insure a host tree against environmental stresses (Courty et al., 2010). At the ecosystem level, EMF are not only important for nutrient cycling, but high EMF diversity can facilitate resistance to disease and drought (Kernaghan, 2005), and contribute to net primary productivity, mineral weathering and soil carbon storage (Smith and Read, 2008).

Whilst the relative biodiversity value of ancient old-growth and more recent secondary forest has been established for groups including vascular plants and epiphytic lichens (Rose, 1974; Peterken, 1974), we still lack sufficient empirical assessments of the relative biodiversity value of planted and old-growth forest for EMF. To date, studies have reported only from coniferous forest in North America (e.g. Kranabetter et al., 2005, Twieg et al., 2007), where they show that EMF exhibit much lower species richness in young secondary forest. Meta-analysis of these studies shows an average time of 90 years to recover EMF richness to old-growth values (between 45 years to unrecoverable at 95% prediction limits: Spake et al., 2015). No previous study has examined EMF-stand age relationships in broadleaved forests with a statistically robust study design. Dispersal limitation is important in structuring EMF communities, despite the fact that fungal fruit bodies produce large numbers of spores with high potential for long distance travel (Peay et al. 2010). Indeed, red-lists and field observations suggest that numerous species are likely to be confined to old-growth forests due to infrequent dispersal (Dickson and Leonard, 1996; Senn-Irlet et al. 2007).

In historically deforested regions such as the UK, where the proportion of forest has declined to just 12% of total land area, ~80% of this forested area is planted and just 5% is classified as ancient (UK National Ecosystem Assessment, 2011), the setting-aside of planted forests presents a particularly pertinent opportunity for increasing the area of forest that can support the biodiversity and functions that characterise old-growth forests (Bauhus et al., 2009). The aims of this study were to (1) compare EMF biodiversity and species associations among overmature planted and ancient old-growth forest stands; and (2) determine what stand characteristics explain the differences in species richness and composition in order to identify opportunities for enhancing EMF diversity in overmature planted stands.

3.3 Methods

3.3.1 Study area

The study area was located in the New Forest National Park in southern England, UK (Figure B1.1). The New Forest lies within the Warm Dry climatic zone with mild winters and warm summers. Temperatures range from 2.3°C (mean February minima) to 20.8°C (mean July maxima). Annual precipitation is 760 mm. Soils are mainly brown earths above Barton clays and Chama sands overlying Tertiary gravels. The old-growth forests in this study are ancient *sensu* Peterken (1977), in that they have originated before a threshold date of 1600 A.D.; a time before which secondary forests were rarely established through planting. In fact, the New Forest's ancient forests include remnants of post-glacial forest that have never been completely cleared (Tubbs, 2001), and the ancient stands under study all had stand continuity of >1000 years. They are also deemed semi-natural, in that they have been selectively felled for timber in the past, but allowed to regenerate naturally, without any major tree removal since the mid-20th century. The canopies of the ancient and planted stands under study are dominated by English oak (*Quercus robur* L.), sessile oak (*Q. petraea*) and beech (*Fagus sylvatica*) with the understory consisting largely of holly (*Ilex aquifolium*) (Tubbs, 2001).

The plantations under study were on average 180 years old. Plantation ages were considered equal to the number of years since planting (Appendix B1). Plantations were established following clear-cutting of partially forested (deer parks) to completely forested grounds. All sites likely underwent the same preparation procedure following clear-cutting, involving the upturning of soil and trench formation for water drainage (see Appendix B1 for a detailed description). The management histories of the ancient old-growth stands under study were elucidated using historic maps, Forestry Commission management plans, pollen records and consultation with local experts. The stand ages refer to the oldest record available indicating that the site was forested (Table B1.1), and since then have not experienced major tree removal.

3.3.2 Study design

In order to compare EMF communities in overmature planted set-asides and ancient old-growth forest communities, locations were selected that paired forest types in a randomised block design (Hurlbert, 1984). Seven forest locations containing both a planted stand and an ancient stand were identified. In order to minimise extraneous variation, paired stands were matched for canopy species (oak dominated), elevation and underlying geology, and separated by < 1 km. Within each stand at each location, five 10×10-m permanent assessment plots were selected inside a 2-ha area using stratified random coordinates. Stratification met selection criteria of oak dominance, homogeneous tree and vegetation cover, relatively flat topography and absence of atypical or exotic tree species.

3.3.3 Sampling of EMF communities

We used two methods to obtain representative samples of EMF communities in plots: surveys of above-ground sporocarps (‘mushrooms’), and soil cores for analysis of below-ground EMF on root tips (Taylor, 2002; henceforth ‘ectomycorrhizae’).

3.3.3.1 Above-ground sampling of sporocarps

The incidence of all visible above-ground EMF macrofungal sporocarps was recorded across all assessment plots. We define macrofungi as species with fruiting bodies large enough to be collected in the field without the aid of a hand lens, including the majority of basidiomycetes, boletes and many and ascomycetes (Balmford et al. 2000). Plots were surveyed during autumn 2012, 2013 and 2014 (September-November) to coincide with the main time of sporocarp production. Three visits were made to each plot at approximately monthly intervals over this period. Species identifications were made using a compound microscope and standard texts (Phillips 2006; Moser 1983), and more specialised texts for *Lactarius* (Heilmann-Clausen et al., 1998), *Inocybe* (Outen and Cullington, 2009), *Cortinarius* (Knudsen and Vesterholdt, 2012), *Russula* (Kibby, 2012c), *Boletus* (Kibby, 2012a), and *Amanita* (Kibby, 2012b). To obtain a measure of species richness, sporocarp incidence data were pooled to the plot level across all plot visits.

3.3.3.2 Below-ground sampling of ectomycorrhizae

Below-ground sampling took place between February and July 2014, in locations 1-4 only (Table B1.1). These were a random selection of the available seven locations. Each plot was divided into a 10×10 grid, and every intersection given a coordinate. Sixteen soil cores (2-cm diameter, 30-cm length) were taken at randomly generated coordinates. Samples were stored at 4°C until root tip analysis could be undertaken, always within 5 days. Cores were soaked in tap water for 15 minutes and washed through a 500 µm sieve. After manual removal of coarse woody debris and senescent roots, live roots were extracted from the core for five minutes under a dissecting microscope. To minimize observer bias, three of the largest roots were selected at random, and one living root tip was randomly selected from each of these following Cox et al. 2010 and Suz et al. (2014). This sampling intensity was justified from the results of preliminary sampling in January 2014, which recorded >60% of the Chao2 estimate of EMF species (Figure B3.1).

3.3.3.3 Molecular identification of ectomycorrhizae on root tips

Identification of ectomycorrhizae followed the methodology of Suz et al. (2014). Fungal DNA was extracted from the selected EMF tips with the Extract-N-Amp™ Plant PCR kit (Sigma-Aldrich, St. Louis, USA) with some modifications of the protocol: EMF tips were incubated in 8-µL of extraction solution and diluted in 8-µL of dilution solution. The internal transcribed spacer (ITS) region of the rDNA was amplified by polymerase chain reaction (PCR) on 0.5 µL of the freshly extracted DNA, mixed with 3.5-µL of the Extract-N-Amp PCR ReadyMix™ (Sigma-Aldrich, St. Louis, USA), 0.1 µL of each primer at 10 µM and 3.8 µL of distilled water. All PCR reactions were performed using the primer pair ITS1-F (Gardes and Bruns, 1993) and ITS4 (White et al., 1990).

Fungal ITS sequences were analysed and edited with Geneious version R7, Biomatters, available from http://www.geneious.com/. Edited sequences were identified using the BLAST algorithm in GenBank and the UNITE database (http://unite.ut.ee/). The best BLAST identification was reported for each fungal taxon. The UNITE species name was validated only when (i) the similarity between the submitted sequence and the sequence in the database exceeded 97%, and (ii) the UNITE identification was plausible taking into account ecological considerations and known geographical distributions of related species (Richard et al., 2011). Sequences with < 97% of similarity with the nearest blast, or for which the UNITE species name was considered too uncertain, were ascribed to an undetermined operational taxonomic unit (OTU).

3.3.4 Quantification of environmental variables

Soil was sampled from all plots during a consistently dry period with minimal spatio-temporal variation in rainfall during May 2014. Five random soil cores (2-cm diameter, 30-cm length) were taken from each 10×10-m fungal assessment plot and were pooled to the stand level. Samples were sent to the Forest Research Soil Analysis Service (Surrey, UK), for analysis. The following soil variables were measured: (i) pH; (ii) moisture content (loss in fresh mass after 2 day at 105°C); (iii) organic matter (loss on ignition after 1 day at 450°C); (iv) water-soluble anions, NO3-N, NH4-N, PO4-; (v) exchangeable cations, K+, Mg+, Ca+; (vi) total N; and (vii) total C. See Humphrey et al. (2003) for further details of soil analytical procedures. All vascular plants rooted in the plots below 1-m in height were sampled to obtain a measure of understory richness (Gilliam, 2007). For stand structural assessments, the 10×10-m plots were nested within 30×30-m plots. Each 30×30-m plot was assessed for stand basal area, tree species diversity (Shannon-Weiner, using basal area as a measure of species' relative abundances) and canopy closure. Assessments of diameter at breast height were inclusive of all trees >5-cm diameter and followed standard protocols (Newton, 2008). Canopy closure, the proportion of the sky hemisphere obscured by vegetation when viewed from a single point (Jennings et al. 1999), was estimated by taking the average of five measurements using a spherical densiometer at each plot corner and centre. Details of stand environmental variables are given in Table B2.1.

3.3.5 Statistical analysis

3.3.5.1 Variation of species richness with forest type and other environmental variables

All analyses were computed in R 3.00 software (R Core Team, 2013). Prior to analysis, environmental variables were centred and scaled to improve the interpretability of regression coefficients, following Schielzeth (2010). Basal area was square rooted. Principal component analysis (PCA) was used to produce orthogonal axes (soil1, soil2, soil3), representing >70% of variation in the soil chemistry data for both sporocarp and ectomycorrhizae datasets. Because not all EMF root tips were sequenced successfully, below-ground sampling intensity was unequal across plots. We therefore estimated individual-based sporocarp species richness at plot-level with Chao1 (Chao, 1984), using the vegan package (Oksanen et al., 2013).

The simultaneous effects of environmental variables on EMF richness were quantified using mixed effects models. Two response variables were investigated: sporocarp and ectomycorrhizae richness, the former using a generalized mixed model with Poisson error distribution and logarithmic link function, and the latter using a linear mixed model on log-transformed Chao1 estimated richness. Explanatory variables included: forest type (planted or ancient old-growth), tree species diversity, understory species richness, tree basal area soil1, soil2 and soil3. Canopy closure was not included due to co-linearity with the more precisely measured basal area (Pearson's $r = 0.80$, $P < 0.001$).

Location was included as a random factor crossed with forest type, reflecting the designed pairing of the two types in each location. All possible additive models were constructed by maximum likelihood methods using packages lme4 (Bates et al., 2014), and MuMIn (Barton, 2013). Akaike's Information Criterion (AIC) with small sample correction bias (AICc) was used to identify the best model and all plausible models, with ΔAICc < 7

(Burnham and Anderson, 2004; Aho et al., 2014). Random intercepts were featured in the mixed models only, as allowing for slopes caused a large positive ΔAICc. Goodness of model fits of the minimum adequate model and other plausible models was estimated by calculating the marginal R^2, following Nakagawa and Schielzeth (2013). The relative importance values of the explanatory variables were calculated by summing up the Akaike weights of all plausible models (with ΔAICc < 7), that included the variable in question (Burnham and Anderson, 2004).

3.3.5.2 Community composition in planted and ancient old-growth stands

All analyses of community composition used the ‘vegan’ R package (Oksanen et al. 2013). Tests of compositional differences between planted and ancient forest types used a non-parametric multi-response permutation procedure (MRPP) (Zimmerman et al., 1985), based on the Sørensen (Bray–Curtis) distance measure (McCune and Grace, 200, Promis et al., 2012). Its statistic *A* describes within-group homogeneity relative to random expectation. $A = 1$ signifies that all items are identical within groups; $A = 0$ signifies that heterogeneity within groups equals chance expectation; $A < 0$ signifies less agreement within groups than chance expectation (Promis et al., 2012).

Differences in EMF composition across forest types were visualised with nonmetric multidimensional scaling (NMDS). NMDS reflects similarities (or dissimilarities) between assemblages (Oxbrough et al., 2005). The Sørensen distance measure was used for species presence-absence data. Two-dimensional solutions were produced with 999 iterations, as the reduction in stress was small beyond the second axis.

Species fidelities to each forest type were identified by indicator species analysis (ISA; Dufrene and Legendre, 1997) extended by De Caceres et al. (2010), using package IndicSpecies (De Caceres and Legendre, 2009). Indicator values determine how strongly each species associates to a forest type, based on two probabilities: (i) the probability that a surveyed plot belongs to the target forest type (specificity), and (ii) the probability of finding the species in plots belonging to the forest type (sensitivity). Indicator values range from 0 (no indication) to 1 (maximum indication). Statistical significances of indicator values were tested using a randomisation procedure based on 999 permutations.

We estimated the Chao similarity index to quantify the compositional similarity between EMF communities as sampled as sporocarps and ectomycorrhizae following Chao et al. (2005). We used the proportion of sampled plots that species occurred in as a measure of relative abundance. This method calculates a Jaccard- or Sørensen-type dissimilarity index that accounts for the effect of unseen shared species, based on replicated incidence or abundance sample data, respectively. Values range between 0 (no similarity) and 1 (complete similarity).

3.4 Results

A total of 225 EMF taxa were identified across all plots, with 122 species identified in the sporocarp survey and 136 OTUs characterised using the molecular analysis (Appendix B4). The same four species were most frequently observed in the sporocarp and ectomycorrhizae surveys, in terms of the percentage of plots containing them: *Lactarius tabidus* (79% sporocarp, 37% ectomycorrhizae), *Lactarius quietus* (74%, 48%), *Laccaria amethystina* (73%, 29%) and *Russula ochroleuca* (53%, 31%). Visual examination of species' ranked abundance distributions suggests that the EMF communities from both forest types followed a Zipf-Mandelbrot distribution, indicating that communities have a few species that are very abundant, and a long tail of rarer species (Figure B4.1). The ancient old-growth stand at location 2 and the planted stand at location 7 were disregarded from the analysis, after the PCA analysis of soil chemistry revealed unrepresentative soil conditions in extreme outliers (Figure B5.1).

3.4.1 Environmental drivers of EMF richness

Forest type was not found to be an important determinant of either sporocarp or ectomycorrhizae richness, as shown by its low relative importance values, summed over plausible models with ΔAICc < 7 (Tables 3.1 & 3.2, Figures 1a & 1b). The most important variables explaining EMF richness were basal area and tree diversity (Tables 3.1 & 3.2). For sporocarps, basal area was the most important predictor of species richness (Table 3.1a), with a strong positive effect (Figure 1c) and a relative importance value of 1.00 (Table 3.2). For ectomycorrhizae, tree diversity was a major positive driver of EMF richness (Table 3.1b, Figure 1d), which had a relative importance value of 0.60 (Table 3.2) and was the only variable included in the minimum adequate model (Table 3.1b) explaining below-ground richness. Marginal R^2 values were higher for models explaining sporocarp richness (0.30 for the best model; Table 3.1a) than below-ground richness (0.15 for the minimum adequate model; Table 3.1b).

Sporocarp richness was also positively driven by tree diversity and understory richness (importance values of 0.54 and 0.40; Table 3.2), and the richness of ectomycorrhizae was also influenced by soil2 and soil3, though moderately so (relative importance values 0.47 and 0.39; Table 3.2). soil2, the second PCA axis of the soil chemistry data, indicated a gradient of increasing ratio of carbon to nitrogen, and decreasing ammonium, sulphate and soil pH. See Appendix B6 for a more detailed description of the soil PCA axes.

Table 3.1. Fixed variables included in mixed models explaining variation in sporocarp and ectomycorrhizae species richness of overmature planted and ancient old-growth forest stands. Only models with ΔAICc < 2 are shown. See methods for model details.

Variables included in model								df	ΔAICc	Marginal R^2
	forest type	basal area	tree div	Understory richness	soil1	soil2	soil3			
(a) Sporocarp										
1		+	+					4	0.00	0.30
2		+	+	+				6	0.26	0.32
3		+						4	0.83	0.24
4		+			+			5	1.19	0.29
5		+		+				5	1.41	0.26
6		+	+		+			6	1.67	0.32
7	+	+						5	1.72	0.30
8		+	+			+		6	1.73	0.29
9	+	+	+					6	1.79	0.29
(b) Ectomycorrhizae										
1			+					5	0.00	0.15
2			+			+		6	0.19	0.27
3						+	+	6	0.85	0.27
4			+			+	+	7	1.11	0.34
5								4	1.13	0.00
6			+				+	6	1.54	0.26
7	+		+					6	1.60	0.21

Table 3.2 Relative importance values for explanatory variables contained within plausible models (ΔAIC < 7) explaining sporocarp and ectomycorrhizae species richness.

Explanatory variable	Sporocarp richness	Ectomycorrhizae richness
Forest type	0.27	0.19
Basal area	1.00	0.22
Tree diversity	0.54	0.60
soil1	0.31	0.15
soil2	0.23	0.47
soil3	0.22	0.39
Understory richness	0.40	0.13

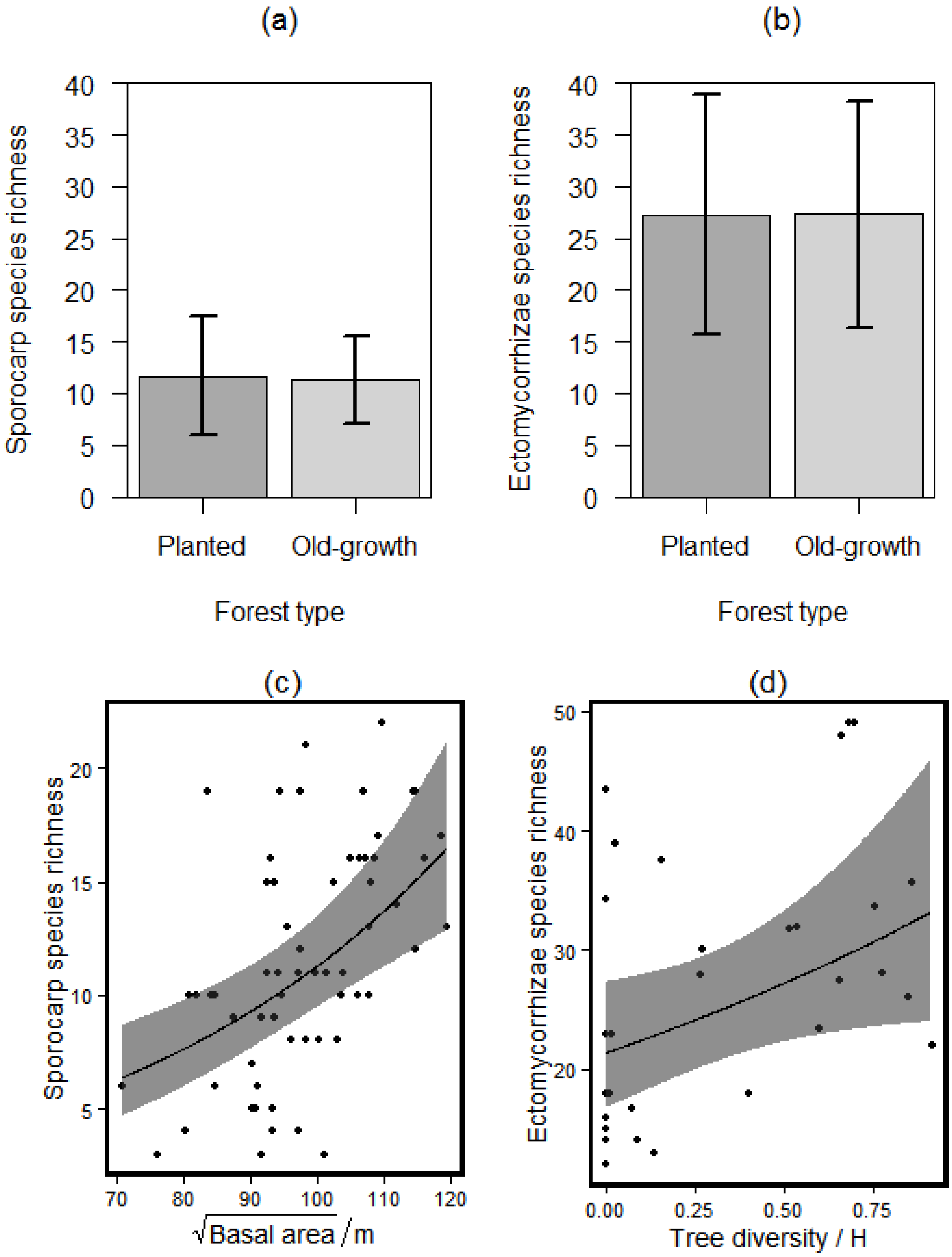

Figure 3.1 The influence of forest type, (a) and (b), and the most important environmental variables on EMF richness (c) and (d). Neither sporocarp (a) nor ectomycorrhizae (b) richness varied detectably by forest type (bars show mean +SD). (c) Influence of square-rooted basal area on sporocarp richness; (d) influence of tree diversity (Shannon-Wiener H) on richness of ectomycorrhizae. Regression coefficients are for minimum adequate models based on AICc, with 95% prediction interval (grey shading) based on uncertainty in the fixed effects.

3.4.2 EMF community composition

MRPP analysis revealed no differences in EMF species composition between overmature planted and ancient old-growth forest plots, for communities of either sporocarp or ectomycorrhizae ($A < 0.01$, $P = 0.41$ and $A = 0.00$, $P = 0.73$, respectively). The NMDS ordination confirmed these results, finding no separation in species composition according to forest type (Figure 3.2; $R^2 = 0.02$; $P = 0.28$ and $R^2 = 0.00$; $P = 0.91$ for sporocarp and ectomycorrhizae, respectively). A two-dimensional solution described 63% and 66% of the variance in the species composition for sporocarp and ectomycorrhizae datasets, respectively (Figure 3.2).

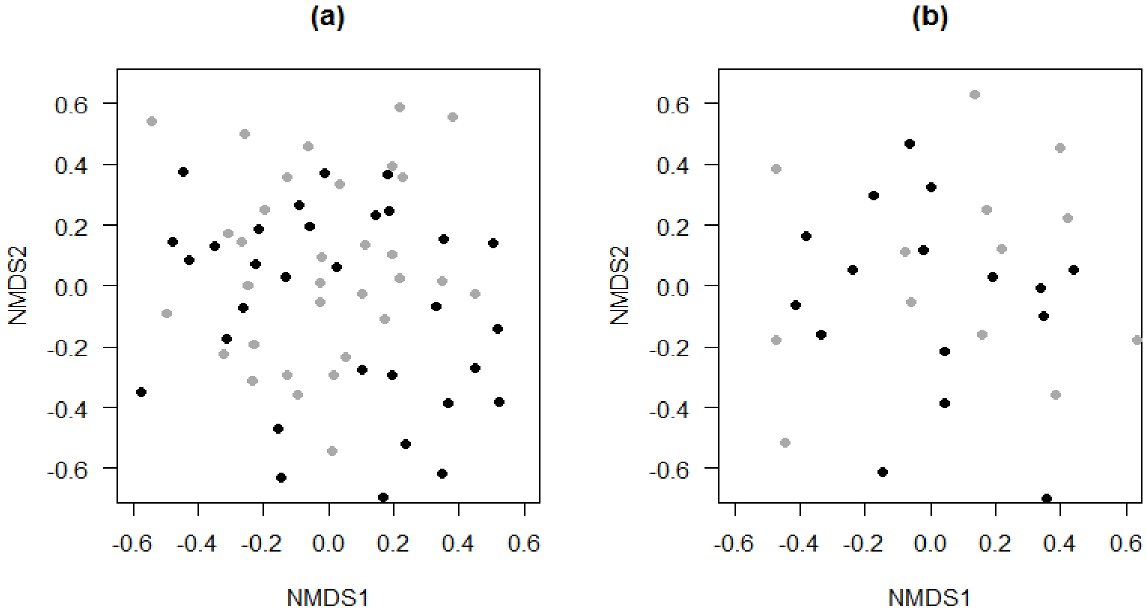

Figure 3.2 NMDS ordination on (a) sporocarp and (b) ectomycorrhizae communities, using Sørensen distance of ancient (black) and overmature planted (grey) forest plots based on plot-level EMF presence-absence data.

Indicator species analysis detected associations of a single species with each forest type from the sporocarp surveys, and of a single species with ancient old-growth forest from the ectomycorrhizae samples (Table 3.3). Indicator values were only moderate, however (Table 3.3; De Caceres & Legendre, 2009). Two of the species recorded are on the Red List for British fungi (Evans et al. 2006). Both species, *Cortinarius orellanus* (Vulnerable) and *Cortinarius violaceus* (Near Threatened), were found as sporocarps in ancient old-growth stands at locations 1 and 2, respectively. Due to their incidences within single plots, they had low sensitivities to forest type, and so did not have significant indicator values.

Table 3.3 Indicator values representing associations by forest type, for species with P < 0.05.

Forest type	Species	Indicator value	*P*
(a) Sporocarp			
Overmature planted	*Cortinarius flexipes*	0.51	0.008
Old growth	*Hydnum rufescens*	0.41	0.048
(b) Ectomycorrhizae			
Old growth	*Laccaria proxima*	0.55	0.034

Compositional similarity between communities sampled as sporocarps and ectomycorrhizae was only moderate with Chao similarity indices of 0.41 for ancient and 0.37 for planted forest (Chao et al. 2005).

3.5 Discussion

3.5.1 The effectiveness of set-aside overmature planted forest at conserving ancient forest ectomycorrhizal communities

This investigation found similar richness and composition of EMF in set-aside plantation and neighbouring ancient stands. It has been suggested that increasing the proportion of overmature planted forests could offer alternative habitats for species typical of old-growth forests, but this possibility lacks empirical evaluation (Martikainen et al. 2000; Sverdrup-Thygeson et al. 2015). Many EMF species require long periods of stand continuity for colonisation events to recover richness to old-growth levels, consistent with strong dispersal limitation (Peay, 2010). Despite the fact that fungal fruit bodies produce large numbers of spores with high potential for long-distance travel, relatively recent evidence suggest that dispersal limitation is significant in EMF assemblages (Peay et al. 2010). A meta-analysis of EMF recovery in planted and secondary forests showed that recovery of species richness is possible after ~90 years in temperate and boreal regions (Spake et al., 2015). This estimate, however, is based exclusively on data from coniferous forest, and from secondary forests less than a century old. Our empirical study has shown that set-aside overmature broadleaved plantations ~180 years old can attain the species richness of old-growth semi-natural forests > 1000 years old.

The EMF communities in the overmature plantations were indistinguishable from those of ancient old-growth forests (Figure 3.2). Our findings concord with studies of regeneration following harvest of mixed coniferous forests in the USA (Twieg et al. 2007) and tropical forest in China (Gao et al. 2015). Both of these studies found significant changes in the compositions of EMF communities between young and intermediate-aged or old forest stands, but no significant differences between intermediate-aged and old forests.

EMF communities observed within samples of sporocarps and ectomycorrhizae had only moderate overlap in species composition, in contrast to the complete overlap between forest types. Other studies using both methods often report a poor correspondence between them in terms of species richness and community composition (Dahlberg et al., 1997; Horton and Bruns, 2001). Such differences have been attributed to differences in modes of reproduction, but also differences in methodological caveats (discussed below) and sampling effort between the techniques; sampling of ectomycorrhizae typically spans a much a shorter time period than sporocarp surveys (five months vs. three years in our study). Indeed, temporal partitioning amongst EMF species has been observed (Koide et al. 2007), which may cause many species to be missed by the short and infrequent sampling of ectomycorrhizae on root tips (Toth and Barta, 2010).

Different variables were important in predicting sporocarp and ectomycorrhizae species richness patterns, with sporocarp richness driven by basal area as a proxy for canopy closure and tree diversity, and the richness of ectomycorrhizae driven by tree diversity only (Figure 3.1). It is possible that these differences may reflect differences in the communities sampled by above- ground sporocarp and below-ground ectomycorrhizae sampling methods. Up to 80% of EMF biomass in forest soils is in the form of external mycelia (Wallander et al. 2001). Patterns of resource allocation by a fungus to the production of sporocarps versus ectomycorrhizal root tip formation vary amongst species (Gardes and Bruns, 1996). It is therefore likely that the sampled above-ground richness is more responsive than below-ground richness to changes in carbon allocation, which increases with canopy closure: at canopy closure, tree growth rates are rapid and leaf area maximal, with correspondingly high potential for carbon allocation to roots and ectomycorrhizal partners (Twieg et al. 2007). It is not surprising that EMF richness increased with tree diversity; different tree hosts provide unique habitats for host-specific taxa (Tedersoo et al., 2012).

3.5.2 Methodological caveats

We sampled both sporocarps and ectomycorrhizae in our attempt to acquire an accurate unbiased representation of the EMF communities within our plots. Each technique has limitations. Sporocarp production is sensitive to a host of environmental factors, and consequently sporadic annual fruiting patterns necessitate long term monitoring (Dahlberg et al., 1997). In mesic temperate climates, 3-8 years is considered the minimum sampling period necessary to obtain a reasonable representation of fungal community structure (Vogt et al. 1992; Gardes and Bruns, 1996). We sampled only macrofungal sporocarps, those that are large enough to be collected in the field without the aid of a hand lens (Balmford et al. 2000); but the sporocarps of many species are inconspicuous (e.g. corticoid species) or hypogeous (e.g. truffles; Peter et al., 2001, Richard et al., 2004), leading to underestimates of diversity if sporocarp surveys are used alone. The sampling of ectomycorrhizae in our study complemented the sporocarp surveys and enabled the discovery of species that are inconspicuous above-ground e.g. *Cenococcum geophilum*. However, the molecular sequencing of ectomycorrhizae is expensive and time-consuming resulting in relatively small volumes of soil being screened (Peter et al., 2001).

Sporocarp surveys are essential for detecting those rare species that form conspicuous sporocarps (Smith et al., 2002). It is thought that there is high variation in fruiting activity amongst species, ranging from annual fruiting, where species rely heavily on spores for propagation, e.g. Lactarius and Russula genera; or sporadic fruiting, in which species do not produce sporocarps every year (O'Hanlon, 2012). Smith et al. (2002) have suggested that older forest stands comprise rare species that fruit infrequently, due to decreasing net primary production (NPP) and corresponding below-ground carbon allocation with stand age. They compared sporocarp richness and composition in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in Canada, and found old-growth stands contained many species of fungi that infrequently produce sporocarps. With sporocarp surveys disadvantaged by the inherent sporadicity of EMF fruiting and ectomycorrhizae surveys limited by the small volume of soil sampled, either sampling method may have omitted the inclusion of rarer EMF species that fruit infrequently. Indeed, two species of conservation concern were recorded only once, both in ancient old-growth stands. It is possible that further sampling may reveal more rare species, particularly within ancient stands: Smith et al. (2002) sampled over 4 years, whilst we present 3 years of sampling.

A study of EMF communities in forests across the UK in the 1990s (Humphrey et al. 2000) surveyed 100×100-m plots each within eight stands of ‘mature’ to ‘overmature’ oak forest (~200 years) for sporocarps over 3 years, and found a mean of ~14 species per stand. Comparing this value with the mean of ~30 species per stand from sporocarp surveys in this study (after pooling the five, smaller 10×10-m plots to the stand level), we are confident that our sampling was adequate in obtaining a representative sample of EMF richness. Species accumulation curves using both methods support this assertion (Figure A3.2). Furthermore, the combination of two sampling techniques, used simultaneously across replicate sites of interest, increases the validity of the comparisons we have drawn between communities from ancient and set-aside planted stands .

It is possible that the ancient old-growth forests of the New Forest National Park comprise a depauperate subset of the EMF community that was once supported in the past. Indeed, potential threats to EMF including nitrogen deposition, selective tree felling and soil compaction by high herbivore densities (Newton, 2010), might have diminished EMF diversity in the park. If this were the case, the generalization of our results to other areas where EMF diversity has not been diminished may be inappropriate. Nevertheless, the New Forest has been designated as an Important Fungus Area by national assessment, due to its high diversity (~2,600 species of fungi across all functional groups and habitat types have been recorded across the New Forest; Dickson & Leonard 1996), the persistence of populations of conservation concern and the presence of habitats of known mycological importance (Evans, 2001; Newton, 2010).

3.5.3 Conservation and management implications

The setting aside of overmature planted forest is an effective means of conserving EMF communities associated with ancient old-growth forests, given temporal continuity in the order of a century. This holds out particular promise for historically deforested regions such as the UK, where little ancient forest remains and much planted forest exceeds a century in age. In our study, the paired ancient and set-aside planted stands were separated by less than 1 km. Given that many EMF are dispersal limited, it is possible that the ability of overmature plantations to function as reservoirs for old-growth EMF communities may depend on the degree of connectivity with old-growth propagule sources. Indeed, Humphrey et al. (2004) observed a negative relationship between EMF species richness of conifer plantations with distance from the nearest ancient woodland across the UK. This finding has relevance to the development of ecological networks, a major policy driver in many countries that aims to mitigate against biodiversity loss in highly fragmented landscapes (Jongman, 2004; Opdam, 2006; Lawton, 2010). Ecological networks represent a suite of core areas of habitat connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules (Lawton et al. 2010; Humphrey et al. 2015). Our study suggests that set-aside, overmature planted stands can function as effective stepping stones in connecting ancient forest stands. The protection of overmature planted forest stands located near or adjacent to ancient semi-natural forest should therefore represent a conservation priority.

Our study has identified influences of habitat variables that suggest opportunities for enhancing EMF diversity in planted forest. EMF distribution and composition have been shown to be influenced by the relative proportions of host tree species, indicating a degree of host preference or specificity for some EMF species or genera (Newton and Haigh, 1998). In this study, tree diversity was important in driving sporocarp and ectomycorrhizae richness (Figure 3.1). Correlations between host richness and EMF richness are a common finding in empirical research comparing monocultures with mixed woods (Cavard et al., 2011), probably due to a higher host richness providing more unique habitats for host-specific taxa (Tedersoo et al., 2012), or more facilitation of EMF taxa that associate with multiple hosts (Cavard et al., 2011). Our findings support sustainable forest management strategies that promote mixed-wood management, which will likely enhance EMF richness. Understory richness was also important in driving up sporocarp richness, suggesting that that restoration of plant communities, a major goal of forest restoration efforts, may simultaneously enhance EMF sporocarp richness.

Basal area correlated positively with sporocarp richness (Figure 3.1). Although we cannot distinguish between the effects of basal area and canopy closure (with which it strongly correlates), the positive response is likely due to the combined effects of increasing density of roots (and therefore a function of the species-area relationship), and the associated increased carbon availability for EMF partners with increasing canopy closure (Twieg et al., 2007). Furthermore, EMF richness patterns revealed by sporocarp surveys also shed light on the influence of environmental variation on sporocarp production, on which canopy closure has been shown to be a key driver, as it affects precipitation interception (Santos-Silva et al. 2011). Increases in tree stress and mortality and associated declines in basal area have been observed in both managed and unmanaged forest stands across the world (Allen et al. 2006; McIntyre et al 2015). These are driven by direct impacts of climate change on drought frequency and severity (Gonzalez et al. 2010), and on the dynamics of forest insects and pathogens (Allen et al. 2006), and by inhibited regeneration due to recreation and over-grazing (Mountford and Peterken 2003). Our results suggest that EMF richness will likely benefit from conservation measures designed to sustain basal area within set-asides and ancient stands.

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3.7 Co-author contribution

Contributor	Contribution
RS	Devised the study design, carried out fieldwork, laboratory work, sequence analysis, statistical analysis and the write up.
SVDL	Advised on below-ground sampling strategy, laboratory work and sequence analysis
LMS	Advised on study design and laboratory work.
MIB	Advised on study design.
ACN	Advised on study design and write up and contributed to fruit body identifications
CPD	Advised on study design and statistical analysis, and contributed to fieldwork and write up.

3.8 Chapter 3 Addendum

This addendum outlines a caveat related to the interpretation of results for Chapter 3.

A principle outcome of chapter 3 was the finding that set-aside even-aged planted stands (ca. 180 yrs) adjacent to ancient old-growth forest stands (>1000 yrs) were similar in the species richness and composition of ectomycorrhizal fungi. We concluded that the setting aside of overmature planted forest represents an effective means of conserving ectomycorrhizal communities associated with ancient old-growth forests, given temporal continuity in the order of a century. We suggested that this finding has relevance to the expansion of ecological networks, whereby overmature planted stands can function as effective stepping stones in connecting ancient forest stands. Further to this, we made the argument that the protection of overmature planted forest stands located near or adjacent to ancient semi-natural forest should represent a conservation priority. This last statement assumes that younger stands would have lower ectomycorrhizal diversity, which was not demonstrated. It may not be appropriate to prioritise 180-yr overmature stands over younger planted forest stands, for example.

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Chapter 4: Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations

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4.1 Abstract

Functional diversity (FD) is increasingly used as a metric to evaluate the impact of forest management strategies on ecosystem functioning. Management interventions that aim to maximise FD require knowledge of multiple environmental drivers of FD, which have not been studied to date in temperate coniferous production forests. We quantified the relative importance of abiotic (forest management) and biotic (ground vegetation community) drivers of carabid FD and trait distribution in 44 coniferous plantation forest stands across the UK. Carabid FD declined with canopy cover and carabid body length correlated negatively with the percentage of open semi-natural area surrounding a plot. We conclude that forest management could enhance carabid FD through initiatives that emulate natural disturbance regimes through gap creation. We found that neither functional nor taxonomic metrics of vegetation diversity correlated with carabid FD, suggesting that restoration of plant communities, a major goal of forest restoration efforts, will not necessarily enhance carabid FD in coniferous plantations.

Keywords: carabids; functional diversity, functional traits; plants, plantation forest; trait-based approach.

4.2 Introduction

Research on the impacts of environmental change on invertebrate biodiversity has traditionally adopted a taxonomic approach by focusing on the composition and diversity of particular groups of species in a community (Fountain-Jones et al. 2015). This approach has limited scope for generalisations, especially when comparing different regions with different species pools (McGill et al. 2006). A recent shift towards consideration of functional traits has focused attention on the morphological, anatomical, biochemical, physiological or phenological traits of a species that influence its ability to acquire resources, disperse, reproduce and persist in the environment (Violle et al., 2007; Pavoine and Bonsall, 2011). Functional-trait analysis offers several advantages over taxonomic composition analysis for both conceptual and management purposes (McGill et al., 2006; Kleyer et al., 2012). It facilitates an understanding of the mechanisms that underlie both community responses to environmental change and ecosystem functioning (Diaz et al., 2007, Lavorel et al., 2008, Laliberte et al., 2010, Bachand et al., 2014).

Quantitative measures have been developed that use multivariate methods to integrate multiple traits into a single continuous trait diversity index. These measures capture the value, range or distribution of functional traits in a community (hereafter ‘functional diversity’; FD; Hooper et al., 2005, Diaz et al., 2007). Unlike traditional taxonomic measures of species richness or diversity, FD presupposes a mechanistic link between diversity and the ecological phenomena in question (Cadotte et al., 2011), and it has become apparent that FD is more directly relevant to ecosystem functioning than taxonomic diversity (TD; Hooper et al. 2002; Díaz et al. 2004; Vandewalle et al. 2010). It is thought that predator assemblages exhibiting high diversity in functional traits are likely to have high levels of complementarity in traits associated with natural enemy capture and consumption (Petchey and Gaston, 2002). Conversely, assemblages with low FD may be more likely to exhibit niche overlap, increasing interference competition and limited potential for biological control (Woodcock et al., 2010). A quantitative review by Gagic et al. (2015) revealed that functional trait-based indices of animal diversity consistently provided greater explanatory power than species richness or abundance in predicting various ecosystem functions including pollination and pest control. It follows that estimates of invertebrate FD may provide surrogate measures of such services (Woodcock et al., 2014).

Considering that species differ in their response to environmental factors and effects on ecosystem functioning, it is important to understand the impacts of environmental changes on biotic communities. In this study, we investigate the diversity and distribution of functional traits for carabid beetles and ground layer plants, in relation to environmental variation imposed by forest management in coniferous production forests in the UK. Carabid beetles are a diverse and abundant group of insects ubiquitous to most terrestrial ecosystems (Thiele, 1977), where they contribute to ecosystem functioning through predation of other invertebrates and granivory of plant seeds (Lang et al., 1999; Kotze et al., 2011). In forest ecosystems, carabid beetles are important natural enemies of insect pests (Alalouni et al., 2013) and contribute to nutrient cycling (Loreau, 1995; Prather et al., 2013). Carabids have experienced general declines in diversity and abundance across the UK, but have remained relatively stable in forest and hedgerow habitats (Brooks et al., 2012), presenting opportunities for forest management to increase their value as carabid biodiversity refuges at the landscape level (Brooks et al., 2012).

Management of plantation forests requires an understanding of the environmental drivers affecting FD across taxonomic groups in order to sustain the multifunctional roles of these forests. It has been suggested this appreciation will require unravelling complex biotic interactions (Gilman et al., 2010; Brooks et al., 2012). Trait-based extensions to multi-taxa assessments are consequently being advocated as a means to further our understanding of community assembly following disturbance (Moretti and Legg, 2009; Aubin et al., 2013; Bachand et al., 2014). In temperate forests, most vascular plant species occupy the ground layer, where they form the trophic and structural template for a diversity of invertebrate communities (Sabatini et al., 2014). Plant functional traits mediate interactions with the physical environment, which suggests that data on plant and invertebrate traits may reveal more than species compositional data about the relationships between these taxa and their interactions with the environment (Moretti and Legg, 2009). Trait-based multi-taxa approaches therefore permit analyses of the relative influences of abiotic drivers (e.g. forest management) and biotic drivers (e.g. the plant community) on responses by animal communities to disturbance events (Pakeman and Stockan, 2014).

In this study, we investigate the diversity and distribution of carabid and ground layer plant functional traits, in relation to environmental variation imposed by forest management. We use data from the Biodiversity Assessment Project, which has previously been analysed only from a taxonomic perspective (Jukes et al. 2001; Humphrey et al. 2003). The BAP found that carabid species diversity declined with increasing canopy cover and soil organic matter content, and that the abundance of forest specialist carabid species increased with stand age whilst non-woodland species declined (Jukes et al. 2001). The influence of forest management on carabid FD has received less attention. Aubin et al. (2013) studied the FD of several taxa, including carabids, in boreal plantation forests, in relation to the single environmental variable of stand age. Pakeman and Stockan (2014) considered multiple abiotic and biotic drivers of carabid in arable fields, pasture and moorland. Our study is the first to analyse responses of carabid functional trait composition and diversity in relation to environmental drivers in planted coniferous production forests. This type of forest comprises around a half (52%) of total UK forest area (Forestry Commission, 2012). Our objective is to determine the processes driving carabid community dynamics in coniferous forest plantations. We use chronosequence data from 44 conifer plantations distributed widely across the UK (Humphrey et al. 2003). Specifically, we set out to: (i) compare the relative importance of a number of abiotic and biotic drivers of carabid FD in plantation forests; (ii) test whether meaningful correlations exist between carabid FD and taxonomic and functional metrics of ground vegetation diversity (species richness, Shannon-Wiener, Simpson diversity and Rao's quadratic entropy); and (iii) identify a combination of functional traits in ground layer plant and carabid species that are most sensitive to forest management and which could potentially be used to characterise priority groups for conservation action.

4.3 Materials and methods

4.3.1 The Biodiversity Assessment Project

All analyses used the dataset of the UK Forestry Commission's Biodiversity Assessment Project (BAP) which ran from 1995 to 1999. Here we summarise relevant features of sampling design (Humphrey et al., 2003).

4.3.2 Study location and design

Conifer plantation stands at 12 sites across the UK were selected for study (Fig. 4.1; Table 4.1). These comprised four prominent commercial crop types grown in the UK: Sitka spruce (*Picea sitchensis* L. Bong. Carr.), Scots pine (*Pinus sylvestris* L.), Corsican pine (*Pinus nigra* var. maritime L.), and Norway spruce (*Picea abies* L. Karst.).

Table 4.1 Metrics of sample sites used in assessment of carabid community composition, 1995–1997.

	Site	UK grid referencea	Forest category	Tree species	Sampling years
1	Glen Affric, Highland	NH 317363	Foothills	Scots pine	1996–1997
2	Strathspey, Highland	NH 853084	Foothills	Scots pine	1996–1997
3	Thetford, Norfolk	TL 833901	Lowland	Scots pine	1995–1996
4	New Forest, Hants.	SU 254064	Lowland	Scots pine	1995–1997*
5	Knapdale, Argyll	NR 814907	Upland	Sitka spruce	1995–1996
6	Clunes, Highland	NN 257938	Upland	Sitka spruce	1995–1996
7	Forest of Dean, Gloucs.	SO 608130	Lowland	Norway spruce	1995–1996
8	Fineshade, Northants.	SP 982978	Lowland	Norway spruce	1995–1996
9	Kielder, Northumberland	NY 715860	Foothills	Sitka spruce	1996–1997
10	Glentress, Borders	NN 257938	Foothills	Sitka spruce	1996–1997
11	Thetford, Norfolk	TL 815760	Lowland	Corsican pine	1996–1997
12	Sherwood, Notts.	SK 606621	Lowland	Corsican pine	1996–1997

* Plots within site #4 were sampled in 1995-1996, except for the over-mature plot which was sampled in 1996-1997.

At the 12 sites, 1-ha permanent sample plots were established in four forest stands, reflecting four growth stages of a typical commercial timber crop rotation. Humphrey et al. (1999) provide a full description of these structure classes. Each site comprised of plots dominated by a single crop type. The chronosequence stages used included (i) a pre-thicket restock stage, crop height 2–4 m, age 8–10 years, incomplete canopy closure; (ii) a mid-rotation stage – crop height 10–20 m, age 20–30 years, canopy closure, no understorey; (iii) a mature stage – crop height 20–25 m, age 50–80 years, canopy closure, some development of understorey layers; and (iv) an over-mature stage (beyond economic maturity and acquiring some of the ecological characteristics of natural old-growth forests *sensu* Oliver, 1981) – crop height >25 m, age 60–250 years, canopy break-up, well-developed understorey layers, accumulation of deadwood. A randomised-block design was used to assign the four growth stages to each site. In practice, the overmature age class was not present at four of the sites, resulting in a working total of 44 plots. Furthermore, sites were not equally distributed across climatic zones in the BAP project, meaning that not all combinations of tree species and bioclimatic zones were represented, leading to these factors being confounded.

Figure 4.1 Location of the 12 coniferous sites assessed by the Biodiversity Assessment Project; 44 plots representing four stand age classes across chronosequences (see text) were sampled over a 4-year period.

Table 4.2 Environmental variables and vegetation functional diversity used to explain variation in carabid functional diversity.

Variable code	Description	Range or levels
stage	Chronosequence stage	Pre-thicket (Pre) / Mid-rotation (Mid) / Mature (Mat) / Overmature (Omat)
treesp	Crop type	Scots pine / Norway spruce / Corsican pine / Sitka spruce
clim	Bioclimatic zone	Uplands / foothills / lowlands
%open	Percentage cover of open semi-natural area including farmland, grassland and heathland within 1-km radius of plot	0 – 50; continuous
S1	Field, 10 cm –1.9 m high	0-75; continuous
S2	Shrub, 2–5 m high	0-40; continuous
S3	Lower canopy, 5.1–15 m high	0-55; continuous
S4	Upper canopy, 15.1–20 m high	0-30; continuous
soil	Soil type	Podzolic / Peaty gleys / Surface water gleys / Acid brown earths / Calcareous brown earths and clays
vegFDQ	Ground vegetation diversity calculated as Rao’s quadratic entropy.	0.000 – 0.144; continuous

4.3.2.1 Ground vegetation sampling

Two 10×10-m quadrats were arranged diagonally across the centre of each 50×50-m quarter of the 1-ha plot, giving eight quadrats in total per plot. The composition of ground vegetation (vascular plants) was assessed visually using the DOMIN cover-abundance scale *sensu* Dahl and Hadač (1941), within eight 2×2-m quadrats nested within the 10×10-m quadrats. To aggregate quadrat values to the plot level, each quadrat DOMIN score was converted to an average percentage, the percentages were summed and divided by eight. This value was then assigned the appropriate score on the DOMIN scale.

4.3.2.2 Ground beetle sampling

Ground beetles were sampled by pitfall trapping. Five traps were positioned 10 m apart on a north-south transect through the centre of each 1-ha plot and trapping was carried out over a 20-week period from May to September for two consecutive years (Table 4.1) and emptied at fortnightly intervals. Pitfall trap catches were pooled to the plot level for analysis. Carabid identification was based on Forsythe (1987) and Lindroth (1974). Due to difficulties with taxonomy, *Pterostichus rhaeticus* Heer (Luff, 1990) was recorded as

Pterostichus nigrita (Paykull). Similarly, *Asaphidion curtum* Heyden and *Asaphidiom stierlini* Heyden (Speight et al., 1986) were not separated from *Asaphidion flavipes* (L.).

4.3.2.3 Environmental data

Environmental variables that have previously been observed to affect carabid diversity and composition in plantation forests (Jukes et al., 2001), were selected to interpret differences in carabid FD and trait composition between stands (Table 4.2). Bioclimatic zones were uplands, foothills and lowlands, delineated by annual rainfall totals of: >1500 mm (uplands); 800–1500 mm (foothills); and <800 mm (lowlands), following the Forestry Commission's Ecological Site Classification (ESC –Pyatt et al., 2001). Four vegetation strata S1 to S4 were defined, covering field, shrub, lower canopy and upper canopy layers. Percentage cover of vegetation within each vertical stratum was described to the nearest 5%. A general measure of canopy cover for carabids was given by the percentage cover of vegetation in S3: lower canopy, due to its correlation with leaf area index and consequent influence over light levels at the forest floor (Ferris et al. 2000; Jukes et al. 2001).

4.3.3 Trait selection and calculation of functional diversity

4.3.3.1 Trait selection criteria and trait databases

Functional traits were selected *a priori* using published literature (Table 4.3), within the constraints of data availability. We selected traits thought to mediate direct responses of vegetation and beetle communities to the environmental changes imposed by forest management. These were traits related to morphology, reproduction, dispersal and resource use (Bachand et al., 2014). We also selected traits thought likely to capture indirect effects of the forest cycle on beetle communities through bottom-up control by plants. The 'structural heterogeneity hypothesis' posits that bottom-up control of invertebrate communities is exerted through the physical structure of the vegetation, by affecting microhabitat specialisation, hunting efficiency and vulnerability of invertebrates to their predators (Brose, 2003). We selected traits thought to underpin these mechanisms (Table 4.3).

4.3.3.2 Calculation of functional diversity

Rao's quadratic entropy (FD_Q; Rao, 1982; Botta- Dukát, 2005) is a multi-trait FD metric that describes the variation of species trait composition within the community. It sums pairwise distances between species in a community weighted by their relative abundances.

We calculated FD_Q for each plot as: $FD_Q = \sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij}p_ip_j$ where N is the number of species in a plot, d_{ij} is the difference in trait values between the *i*th and *j*th species; p_i and p_j are the proportions of the *i*th and *j*th species, calculated as number of individuals per species relative to the total number of individuals in the community. Functional distances between species were calculated using Gower's distance metric, which allows for a mixture of continuous, ordinal, and categorical variables, and accommodates missing trait values (Laliberte and Legendre, 2010; Sonnier et al., 2014). Continuous trait data were scaled by range to assign equal weighting amongst traits (Botta-Dukát, 2005). FD_Q possesses all of the necessary properties of a FD index including its representation of the range of character values present and its ability to be relatively unaffected when a minor species with an extreme character value decreases in abundance (Botta-Dukát, 2005). It has widespread use and has been shown to successfully identify habitat filtering patterns (de Bello et al., 2009; Moretti and Legg, 2009; Aubin et al., 2013).

Table 4.3 Plant and beetle traits used to calculate functional diversity metrics.

Trait (code)	Type / unit	Trait range or category	Trait data source(s)
Plants			
Height (height)	Continuous / mm	10 – 600	(3), (8)
Leaf area (lf.area)	Continuous / mm		(3), (8)
Raunkier life form (life)	Ordinal	Geophyte / therophyte / hemicryptophyte / chamaephtye / phanerophyte	(3)
Ellenberg shade tolerance (light)	Ordinal	1-9 (1= plant in deep shade; 9 = plant in full light)	(3)
Stem woodiness (woody)	Categorical	Woody/non-woody	(3)
Wind dispersal (wind)	Categorical	Yes / no	(4)
Ground beetles			
Body length (length)	Continuous / mm	2.95 – 30	(2)
Adult feeding guild (diet)	Categorical	Collembola specialist / generalist predator / phytophagous / omnivorous	(2), (5), (10)
Hind-wing morphology (wing)	Categorical	Macropterous / dimorphic / apterous or brachypterous	(2), (5), (7)
Activity pattern (active)	Categorical	Diurnal / nocturnal	(9), (10)
Adult habitat affinity	Categorical	Forest / open / generalist	(1), (6), (12)
Breeding season	Categorical	Spring / summer / autumn or winter	(1), (10), (12)
Overwinter type	Categorical	Adult only / larvae or adult	(10), (11)

(1) Desender et al. (1994); (2) Edgar & Purvis (2014); (3) Fitter & Peat (1994); (4) Hintze et al. (2013); (5) Homburg et al. (2014); (6) Jukes et al. (2001); (7) Luff (2007); (8) Kleyer et al. (2008); (9) Pakeman & Stockan (2014); (10) Ribera et al. (2001); (11) Stork (1990); (12) Thiele (1977).

4.3.4 Statistical analyses

4.3.4.1 Abiotic and biotic drivers of carabid functional diversity

All analyses were computed in R 3.00 software (R Core Team, 2013). Linear mixed models were used to quantify the effects of environmental variables on carabid FD_Q. Explanatory variables included forest stage, tree species, bioclimatic zone, % open ground and cover by vegetation strata, soil type, and vegetative FD_Q (Table 4.2). Missing combinations of tree species across climatic zones precluded cross-factoring of these variables; we therefore ran these partially crossed factors as a single combined factor 'treesp_clim' with as many levels as existing combinations of these factors. We fitted our mixed model following the protocol of Zuur et al. (2013). In our global model, site was incorporated as a random factor since plots within a given location were expected to be similar and should not be considered independent. We fitted appropriate dependency structures *a priori* that allowed for different slopes of the relationships between carabid FD and covariates across sites where appropriate. All possible additive models were constructed using maximum likelihood methods in package MuMIn (Barton, 2013), to allow model comparisons based on Akaike's Information Criterion with small-sample correction (AICc; Burnham and Anderson, 2004). We applied full model averaging (Lukacs et al. 2009) across all plausible models – those with Akaike weights summing to at least 0.95 – because the minimum adequate model as selected by AICc was not strongly weighted (Symonds and Moussalli 2011). The goodness of fit of each plausible model was estimated by calculating the marginal R^2 following Nakagawa and Schielzeth (2013). Relationships between carabid and FD and covariates were graphed using coefficients from the minimum adequate model refitted using restricted maximum likelihood.

Key requirements of indicators include their ease of application and ability to be applied with confidence in novel contexts (McGeoch, 1998). This means that they should correlate with biodiversity independently of other factors. Therefore, we explored simple bivariate relationships to investigate whether taxonomic or functional metrics of vegetation diversity ($vegFD_Q$) were better predictors of carabid FD. We tested for a meaningful correlation of Carabid FD_Q with measures of vegetation diversity based on Pearson's *r*, or Spearman's rho when variables violated parametric assumptions. For taxonomic measures of vegetation diversity, we used species richness, and the Shannon-Wiener and Simpsons diversity indices which account for species' relative abundances.

4.3.4.2 Functional trait associations with environmental variables

Prior to analysis, abundance values were log-transformed to reduce the effect of dominant species (Ribera et al., 2001). We applied fourth-corner analysis (Dray and Legendre, 2008; Dray et al., 2014) to measure and test directly the correlation between the variations in carabid and vegetation species traits and the environmental variables using the ‘ade4’ package (Dray and Dufour, 2007). Two permutation tests were applied to determine correlation as recommended by Dray and Legendre (2008). Firstly, we tested the null hypothesis that species assemblages are randomly attributed to plots, irrespective of plot environmental conditions, using 4999 permutations of plot vectors (Model 2 of Dray and Legendre, 2008). Secondly, we tested the null hypothesis that species traits have no influence on species composition of samples with fixed environmental conditions, by permuting species vectors (Model 4 of Dray and Legendre, 2008). From these models, we chose the larger of the two P values as the most conservative approach (ter Braak et al., 2012). To account for multiple testing of environmental variables and multiple traits, we adjusted P values to account for false discovery rates**.** We report results both with and without this correction, because correction can increase the likelihood of a type II error rate (Rothman, 1990).

4.4 Results

4.4.1 Environmental drivers of carabid functional diversity

Model selection and multimodel inference suggested that the most important variable controlling carabid FD_Q was cover within the S3 stratum (hereafter ‘canopy cover’; tables 4.4 & 4.5), which negatively affected carabid FD (Figure 4.2). Canopy cover featured in all plausible models. $VegFD_Q$, %open, and treesp_clim did not appear consistently across these models (table 4.4), contributing to their relatively low importance values of 0.40 to 0.45 (table 4.5). The model containing canopy cover as the only fixed effect had a marginal R^2 value of 0.35 (table 4.4). The variables S1, S2 and stage had barely any importance in explaining variation in carabid FD across plots (table 4.5) and did not appear in models with $\Delta AICc < 2$, i.e. models with substantial support (Burnham and Anderson, 2004). Full model averaging revealed canopy cover to be the only variable to significantly explain carabid FD (table 4.5).

Our analysis of simple bivariate relationships between carabid FD and vegetation diversity metrics found no detectable correlation with carabid FD_Q for either functional or taxonomic metrics of vegetation diversity (*r* values of 0.24 to 0.26; Figure 4.2 and Appendix C).

Table 4.4 Most parsimonious linear mixed models of carabid functional diversity as measured using Rao's quadratic entropy (FDQ). Only models with substantial support are shown, with ∆AICc < 2, ranked by AICc weight (Burnham and Anderson, 2004).

Model	Fixed explanatory variables included in model*	df	∆AICc	AICc weight	Marginal R^2
1	S3 + vegFD$_Q$	6	0.00	0.11	0.37
2	S3	5	0.20	0.10	0.35
3	S3 + clim	10	0.44	0.09	0.30
4	S3 + %open + treesp + vegFD$_Q$	12	1.00	0.07	0.61
5	S3 + %open + treesp	11	1.25	0.06	0.58
6	S3 + %open	6	1.27	0.06	0.32
7	S3 + %open + vegFD$_Q$	7	1.42	0.05	0.36
8	S3 + treesp + vegFD$_Q$	11	1.61	0.05	0.58
Null		4	15.25	0.00	0.00
Global	vegFD$_Q$ + S3 + %open + stage + soil + treesp	17	15.44	0.00	0.69

*See table 4.2 for variable codes.

Table 4.5 Full model-averaged parameter estimates and importance values for models of carabid functional diversity whose cumulative Akaike weight summed to 0.95, calculated by multiplying the estimates for individual models which contain parameters by their weight

Explanatory variable	Parameter estimate	Standard error	*P*	Importance value
Intercept	0.126	0.013	<0.001	
S3	-0.074	0.017	<0.001	1.00
vegFD$_Q$	0.111	0.154	0.711	0.45
Sitka spruce_foothill	0.000	0.008	0.976	0.41
Sitka spruce_uplands	0.006	0.010	0.563	
Corsican pine_lowland	0.018	0.021	0.403	
Norway spruce_lowland	0.009	0.013	0.486	
Scots pine_lowland	0.018	0.022	0.404	
perc	0.011	0.017	0.528	0.41
S1	0.002	0.008	0.850	0.18
S2	-0.001	0.009	0.891	0.15
Stage_Pre	-0.001	0.005	0.798	0.08
Stage_Mid	-0.001	0.004	0.852	
Stage_Overmature	-0.001	0.004	0.838	

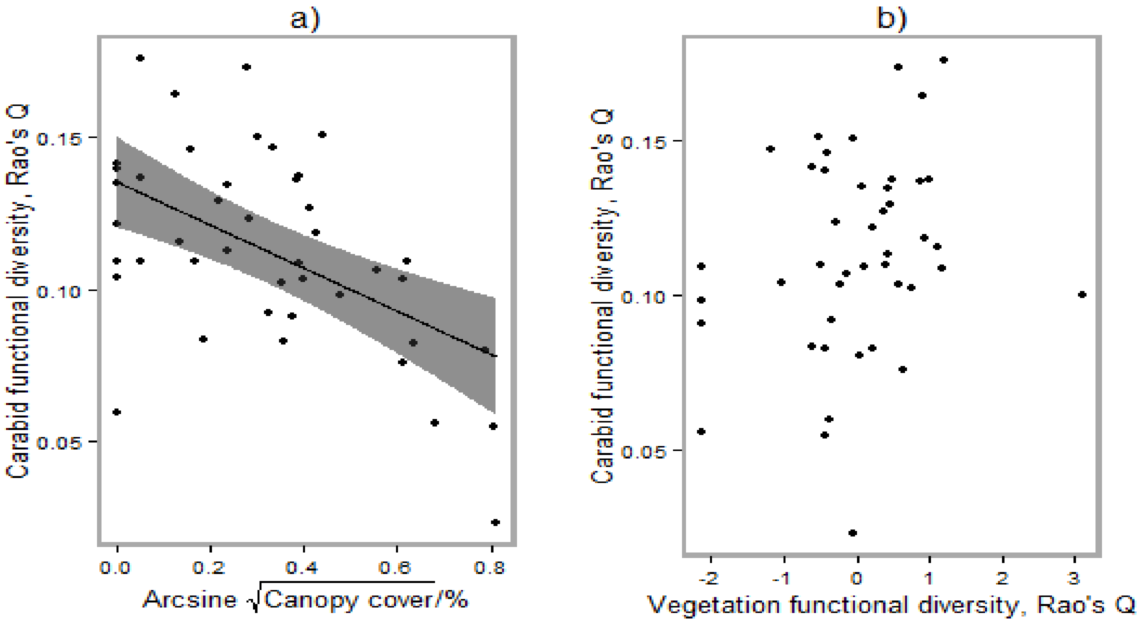

Figure 4.2 Carabid functional diversity variation with (a) canopy cover, and (b) vegetation functional diversity. Vegetation diversity has been centred and scaled. Regressions used coefficients of the minimum adequate model based on AICc and REML estimation. Grey shading shows 95% prediction intervals based on uncertainty in fixed effects only.

4.4.2 Environmental drivers of species trait distributions

Fourth corner analysis detected correlations of environmental variables with vegetation and carabid functional traits. The correlation matrix of classes of vegetation traits by classes of environmental variables detected four significant correlations. Plots with high percentage canopy cover associated with vegetation communities that had low tolerance to light ($P < 0.01$), and that dispersed by means other than wind dispersal ($P < 0.01$); Scot's pine plots were dominated by woody species ($P < 0.01$), and Norway spruce stands by phanaerophytic plant species ($P = 0.01$). The correlation matrix of classes of carabid traits by classes of environmental variables detected four significant correlations. Carabid communities that overwinter as adults dominated in plots with high percentage canopy cover ($P = 0.02$); carabid body length correlated negatively with the percentage of open semi-natural area surrounding a plot ($P = 0.04$); omnivorous carabid communities dominated in Norway spruce plots ($P = 0.04$); carabid communities that favoured open habitats correlated negatively with Sitka spruce plots ($P = 0.04$). None of these eight associations remained detectable after correcting for multiple comparisons using the false discovery rate, except the association of Scot's pine plots with woody species ($P < 0.01$).

4.5 Discussion

4.5.1 Environmental drivers of functional diversity and trait distribution

Our study reveals that canopy cover is the most important driver of carabid FD in UK coniferous production forests, tending to drive down carabid FD (Fig. 4.2). Other studies, including a taxonomic analysis of this dataset, have found that carabid TD declines with canopy cover or stand age (Jukes et al., 2001; Vanbergen et al., 2005; Gibb and Cunningham, 2010; Spake et al., in press). Open-habitat specialists are expected to decrease with increasing canopy cover, and to re-establish as plantations approach, or pass, maturity when the canopy becomes less continuous through tree mortality and/removal through management. This response may be mediated by gap size and proximity to open habitat (Jukes et al., 2001; Toigo et al., 2013). Open-habitat specialists have functional traits that differ from those of forest specialists, for example tending to be winged and smaller in size, reflecting higher dispersal abilities (Jelaska and Durbesic, 2009). Our observation of declining overall carabid FD with canopy cover can be attributed to an absence of open-habitat species in plots with high canopy cover. This was observed in the fourth corner analysis, with the negative association between open-habitat species and

Sitka spruce plots prior to correction for multiple comparisons; it was also observed in the taxonomic community analysis of the same dataset by Jukes et al. (2001). Sitka spruce plots exhibited a larger mean and range in canopy cover than the other tree species, which each had similar mean values of canopy cover. Previous studies have found a positive correlation of carabid body size with canopy cover (Gibb and Cunningham, 2010) and percentage forest cover in the surrounding landscape (Vandewalle et al., 2010). Our results support the latter finding, with fourth corner analysis revealing a negative correlation between body size and the percentage of open habitat surrounding landscape. We found high cover to be associated with species that overwinter as adults. Such species will complete their larval stages during the summer, and may therefore select habitat with high cover to reduce the risk of larval desiccation.

Ground vegetation was not an important driver of carabid FD, with a relatively low importance value of 0.45 (Fig. 2; table 4.5). Previous taxonomic analysis of the dataset found that vegetation diversity (Shannon-Wiener) was not important in determining carabid species richness or diversity (Jukes et al. 2001). This finding is contrary to Moretti and Legg's (2009) assertion that relationships between taxa are more likely to be revealed when using a functional, rather than a taxonomic approach, as functional traits represent interactions between organisms and their environment. Indeed, Pakeman and Stockan (2014) demonstrated positive correlations between measures of vegetation and carabid FD in agricultural setting in the UK. In their study and ours, traits used to calculate vegetation and carabid FD were related to morphology, reproduction, dispersal and resource use. For plants, these were mostly broad morphological traits, suggesting that ground vegetation FD is likely to reflect the degree of structural heterogeneity. Brose (2003) outlines three hypotheses that may underpin a direct relationship between assemblages of invertebrate and structural aspects of the vegetation. These are: (i) microhabitat specialisation, in which vertical or horizontal zonation is higher in architecturally complex plant communities that offer microsites for oviposition, hibernation and shelter; (ii) hunting efficiency, in which vegetation structure changes the efficiency of different hunting strategies causing large predators to be more efficient in sparse vegetation; and (iii) enemy-free space, in which vegetation structure affects the vulnerability of prey species that have more chance of escaping from natural enemies in dense vegetation. It is also possible that higher vegetation FD supports increasing numbers of specialised invertebrate consumers (Murdoch et al., 1972), which through cascade effects can encourage predator assemblages with greater divergence in traits related to consumption (Hunter and Price, 1992).

4.5.2 Management implications

4.5.2.1 Maintaining high carabid FD in production forests

The capacity for forests to sustain diverse and stable carabid communities suggests that forest management could aim to maximise their value as carabid refuges in agricultural landscapes (Brooks et al. 2012). The decline of carabid FD with cover observed in our study supports the implementation of silvicultural treatments that emulate natural disturbance regimes through canopy gap creation, such as close-to-nature forestry. Gap-based management has been included in proposals for managing forests across the world (Muscolo et al., 2014). Canopy gap creation will also benefit ground layer plant communities in UK coniferous plantations. Plant species with high levels of tolerance to light could be lost in productive landscapes with high canopy cover, as shown by the negative correlation between light tolerance and cover in this study. That being said, the value of gaps in terms of the communities they contain depends on a host of factors including gap size (Latty et al. 2006), spatio-temporal distribution (Marthews et al. 2008) and shape (Garbarino et al. 2012), which were not considered in this study and must be addressed by gap-based management regimes.

The restoration of plant communities has become a major goal of forest conservation efforts such as restoration initiatives, with the assumption that the conditions that lead to more diverse vegetation will also lead to a restoration of insect communities (Babin-Fenske and Anand, 2010). Our observation of no relationship between vegetation diversity (either taxonomic or functional; figures 4.2 and C1) and carabid FD suggests that management strategies that aim to promote a functionally diverse understorey shrub layer will not necessarily enhance carabid FD in coniferous plantations.

4.5.2.2 4.2.2 Utility of vegetation FD as an indicator of carabid functional diversity

Indicators of biodiversity are required for judging the success of management regimes intended to sustain biodiversity (Lindenmayer et al., 2000), and for prioritisation of protected areas (Larsen et al., 2009), as a surrogate for costly and time-consuming inventories of total biodiversity. In forests, ground layer plants are amongst the most commonly studied taxa when identifying potential surrogates for other taxa, typically invertebrates (Wolters et al., 2006). A large literature has emerged quantifying the extent of cross-taxon congruence for a range of taxonomic groups, spatial locations and scales. Westgate et al. (2014) performed a global meta-analysis of these studies and revealed a high variance in cross-taxon congruence. Their analyses suggest that there are few circumstances in which pairs of taxa will be consistent surrogates for each other across a range of metrics, locations and spatial scales (Westgate et al., 2014). Given that a key requirement of indicators is their ability to be applied with confidence in novel contexts (McGeoch, 1998), this lack of consistency casts doubt on the generalizability of taxonomic surrogates in ecology and conservation planning (Westgate et al., 2014). The authors emphasise the need for novel approaches to the study of cross-taxon congruence and posit that functional metrics of biodiversity could be considered as potential means to improve surrogacy.

Cross-taxon congruence is thought to have any of several causes: (i) random coincidence; (ii) interactions between taxa, (iii) similar responses to common environmental variables, and (iv) similar responses to different, but spatially covariant, environmental variables (Gaston, 1996; Wolters et al., 2006). Functional metrics are likely to perform better as surrogates than taxonomic metrics, as they incorporate species' morphological, anatomical, biochemical, physiological or phenological traits associated with a species' ability to acquire resources, disperse, reproduce and persist in the environment (Violle et al., 2007), and therefore reflect interactions with the environment and between species (Moretti and Legg, 2009; Gillison et al. 2013). Our results show that the incorporation of functional traits commonly used to assess community responses to the environment does not necessarily improve cross-taxon congruence, particularly in circumstances where other environmental variables (in our case, canopy cover) have a high importance in determining biodiversity.

4.6 Conclusion

Invertebrate functional diversity (FD) is directly relevant to ecosystem functions including pollination and pest control and is therefore being increasingly used as a metric to evaluate the impact of forest management strategies. Despite this, the majority of research on the impacts forestry on invertebrate biodiversity has focussed on drivers of taxonomic diversity. Our investigation of the drivers of carabid FD amongst temperate coniferous production forest stands across the UK which vary in environmental conditions as imposed by forest management including crop species, stand developmental stage and variation in canopy cover has shown that canopy cover is an important driver of carabid FD, with increasing cover tending to drive down FD. Contrary to previous studies, we found that ground vegetation diversity is not an important determinant of carabid FD, and its performance as a surrogate is not improved when functional metrics of ground vegetation are used over taxonomic metrics. This suggests that conservation or management efforts that restore diverse plant communities will not necessary benefit carabid communities, but those that emulate natural disturbance through canopy gap creation will.

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4.8 Co-author contribution

Contributor	Contribution
RS	Collated trait data, formulated question, performed statistical analyses and write-up
NB	Provided datset and advised on question formulation and write-up
ACN	Provided information on datset and advised on write up
CPD	Advised on question formulation, statistical analysis and contributed to write up

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Chapter 5: Meta-analysis of forest management impacts on biodiversity in Japan

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5.1 Abstract

Sustainable forest management strategies that aim to balance resource extraction with biodiversity conservation must be informed by a scientifically credible evidence base. The forestry community of Japan is currently discussing the future management of its vast area of unmanaged planted and secondary forests, which cover more than two thirds of the nation's land area. Japan's National Biodiversity Strategy states that the underuse of the nation's forests resources is responsible for widespread declines in biodiversity and proposes the revival of traditional management practices in planted and secondary forests to promote the recovery of species dependent on early successional habitats. Management interventions for coniferous plantations include thinning and extended rotation cycles, whilst for secondary broadleaved forests, a traditional management regime known as 'satoyama' is currently being revived across the nation, involving clear-cutting and clearance of undergrowth. In this paper we use systematic review methodology to collate an evidence base of robust scientific data to inform forest biodiversity conservation and policy-making in Japan. We used meta-analysis to quantify the impacts of the proposed management regimes on species richness, abundance and composition, both at stand- and landscape-scales. We found that plantation thinning significantly increases the richness and abundance of several taxonomic groups, although effect sizes for abundance of plant taxa decline with the time since thinning. Taxonomic groups exhibited variable relationships with stand age in both planted and secondary forests, suggesting that both young and old forest stands must be included in managed forest mosaics. The removal of undergrowth, a common practise in satoyama secondary forests, negatively affected the richness of soil invertebrates but increased their abundance. We highlight the understudied impact of this common management intervention on other taxonomic groups.

5.2 Introduction

Forests cover approximately 25 million hectares in Japan, constituting more than two thirds of the total land area (Forestry Agency, 2009). The majority of Japan's forests have been managed in the past and are dominated by coniferous plantations and secondary broadleaved forests. Planted forests constitute over 40% of forest area (FRA, 2010), much higher than the global average of 7% (FAO 2010). The majority were established in the period 1950-1980, by replacing natural broad-leaved forests with high-productivity conifers, namely Japanese cedar (*Cryptomeria japonica*), Hinoki cypress (*Chamaecyparis obtuse*), and larch (*Larix* sp.) to meet increased housing and timber demands following World War II (Yamaura et al., 2012). Secondary forests comprise more than 50% of Japan's forest area and are a product of a management regime known as 'satoyama' that predominated during Japan's pre-development era, when broad-leaved forests were clear-cut as coppices over cycles of 15 to 30 years to provide a source of raw materials including charcoal, and the undergrowth was cleared for fuel and compost (Takeuchi, 2003, Yokohari and Bolthouse, 2011).

A high proportion of planted forests are now between 40 and 60 years of age, at economic felling age (Yamaura et al., 2012), yet the vast majority of planted and secondary forests in Japan have remained unmanaged since the 1970s for socioeconomic reasons. These include the high cost of harvesting due to topographic complexity and uncontrolled bamboo growth, the importation of low-cost timber from North America and South East Asia, and difficulties with co-ordinating the management of small-scale privately owned forests (Yamaura et al., 2012). The cessation of satoyama management across Japan coincided with large-scale urban development and the 'fuel revolution', in which rapid economic development led to the replacement of fuelwood and green fertiliser with imported fossil fuels and chemical fertilisers (Iwata et al., 2011). Thus plantations and secondary forests have largely been abandoned, and Japanese forests are becoming more mature, even though their area remains constant (Kauppi et al., 2006, Yamaura et al., 2009).

The future management of Japan's forests is currently being discussed by the forestry community in Japan (e.g. Forest Agency, 2009; Yamaura et al. 2012). Due to their vast extent, their conservation and management will be integral to the nation's commitment to the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 which calls for substantial increases in the conservation, restoration and sustainable management of ecosystems by 2020. Japan's National Biodiversity Strategy states that the underuse of the nation's forests resources is responsible for widespread declines in biodiversity. It proposes the revival of traditional management practices in planted and secondary forests to promote the recovery of species dependent on early successional habitats. For abandoned plantation forests, proposed management interventions include thinning and extended rotation cycles. For secondary forests, both national and international initiatives have been launched to restore satoyama through their active management, not only in Japan, but throughout Asia (Takeuchi, 2010). This includes the return of clear-cutting and coppicing (traditional management) and undergrowth clearance and selective logging (contemporary management). In addition to these stand-scale management propositions for planted and secondary forests, landscape-scale considerations are also being made. For example the National Biodiversity Strategy recognises that restoring well-connected ecological networks is essential for implementing biodiversity conservation in urbanized lowlands of Japan, where fragmented forest remnants in the precincts of shrines and temples are scattered among residential areas, rice paddies and farmland.

It is essential that forest management strategies are informed by a scientifically credible evidence base. A vast amount of empirical research has emerged in recent decades investigating biodiversity responses to forest management regimes in Japan. Several narrative syntheses of such studies exist (Inoue, 2005, Nagaike, 2012, Yamaura et al., 2011), yet a robust systematic and quantitative synthesis is lacking. The Intergovernmental Panel on Biodiversity and Ecosystem Services have advocated the need for quantitative methods to specify the level of human interaction needed to and manage biodiversity sustainably in satoyama landscapes (IPBES 2012). Furthermore, Yamaura et al. (2012) emphasise the importance of the identification of thresholds of biodiversity responses to stand-scale factors in plantation forests. Here we attempt to describe and quantify the effects of various management interventions on biodiversity in a systematic review and meta-analysis at the national scale. In particular, we examine the impact of stand-scale forest management interventions proposed in Japan's National Biodiversity Strategy, on species richness, abundance and composition of various taxonomic groups. The management types are: i) plantation thinning; ii) extended rotation cycles (plantation age); iii) traditional satoyama forest management (secondary forest age); iv) contemporary satoyama forest management (understory clearance) and also investigate the effect of forest patch size on species richness.

5.3 Methods

5.3.1.1 Literature search and data extraction

We followed standard systematic review methodologies (Pullin and Stewart, 2006) to collate published empirical studies that evaluated the impacts of the proposed management interventions of interest on biodiversity. We conducted literature searches in English and Japanese using the ISI Web of Science, Google Scholar and J-Stage. We searched for studies conducted in Japan, and also in South Korea which is similar to Japan in terms of forest management regimes. For example, South Korea has similar planted forest composition and has a secondary satoyama forest equivalent known as 'maeulsoop', which is managed in similar ways (Kwon et al. 2006; Takeuchi, 2010). We used search terms relating to Japan and South Korea, the forest management interventions and biodiversity data (see Appendix S1 for the search queries). We used the R package 'metagear' (Lajeunesse, 2015), to screen abstracts of potentially relevant papers returned by the searches.

Studies compared biodiversity in planted or secondary forest with appropriate controls, given in Table 5.1. Species richness was used as a proxy for biodiversity, being the simplest and most widely used biodiversity measure (Magurran, 2004). Abundance measures included mean values of vegetation cover (percentage cover, summed frequency, density), number of individuals or measures of activity. We extracted species compositional data from each study based on species lists, which were aggregated either across forest types (i.e. across replicate sites of control and treatment groups), or more preferably at the sampling site level. Most articles contributed more than one observation to our analysis, for example when several taxonomic groups and thinning intensities were included in the same study. Observations from different taxonomic groups were considered independent of each other (Fedrowitz et al. 2014).

Table 5.1 Descriptors of treatment and control groups used in our systematic review of the impact of four forest management interventions on biodiversity in Japan.

Management intervention	Treatment group	Control group	Moderator variables in quantitative synthesis
Plantation forest			
Thinning	Thinned plantation	Unthinned plantation	Taxon, stand age, taxon, thinning intensity, canopy dominant, thinning intensity.
Extended rotation cycles (stand age)	Young plantation	Overmature plantation beyond economic felling age (typically >65 years)	Taxon, treatment stand age, canopy dominant.
Secondary forests			
Traditional satoyama management (stand age)	Unmanaged secondary forest that has not been clearcut for >100 years	Secondary forest regenerating from clearcutting	Taxon, treatment stand age, canopy dominant
Contemporary satoyama management	Unmanaged secondary forest	Secondary forest that has undergone selective logging and/or understory removal	-
Lowland forest fragments			
Patch size	N/a. Investigating correlations between patch area and richness.		Functional group (forest specialist/non-specialist), surrounding landscape type (urban or satoyama)

5.3.1.2 Review methods of studies on plantation thinning

To ensure meaningful comparisons across studies, we searched for studies that compared unthinned control and thinned treatment stands with the same canopy dominant and of a similar age. For each richness and abundance comparison, the log response ratio (lnR) was calculated:

$$lnR \;=\; ln(\bar{x}_T) - ln(\bar{x}_C)$$

where $\bar{x}_\mathrm{T}$ is the mean species richness or abundance of treatment forest stands and $\bar{x}_C$ is the mean value for control stands. The lnR describes the proportional difference in species richness or abundance between control and treatment groups. The natural log transformation of the response ratio both linearizes the metric, treating deviations in the denominator and the numerator as equal, and normalises its otherwise skewed distribution (Hedges et al., 1999). Since a response ratio cannot be calculated when a treatment or control mean is equal to zero, we added 1% of the value that was >0 to each treatment and control mean before calculating the response ratio.

We extracted data on the following moderator variables: taxon (understory plants/saplings and seedlings/invertebrates), thinning stand age, years since thinning and thinning intensity (percentage volume of trees removed). All statistical analyses and calculations were performed in R v.3.2 (R Core Team, 2014). We used the metafor package (Viechtbauer 2009) to estimate the mean effect sizes for species richness and abundance of each taxonomic group by using random-effects models, which include both the within-study variance (sampling error) and between-study variance, the latter estimated by the restricted maximum likelihood estimator (REML). Study-specific effect sizes were weighted by the inverse of study variance. The weighted mean effect was calculated as the sum of the products (study-specific effect sizes multiplied by weights) divided by the sum of weights. The SE of the mean effect was calculated as a square root of the variance (calculated as the reciprocal of the sum of the weights) adjusted by the sample size. Mean effect sizes were transformed from log response ratios to the more intuitive percentage differences between thinned and unthinned plantations, and were considered significantly different from 0 if their confidence intervals did not include 0. The magnitude and significance of heterogeneity across studies was quantified by the Q statistic (Hedges et al., 1999) as implemented by the metafor package (Viechtbauer 2009). We used mixed effects models to investigate the influence of moderators on effect sizes. Random effects were used to identify observations from the same study, which used a common control, to avoid problems of non-independence. The minimum adequate model was identified by sequential backward elimination of non-significant parameters (Crawley, 2009).

5.3.1.3 Meta-analysis of extended rotation cycles for plantations and traditional management of secondary forest as satoyama

Studies investigating the impact of traditional stand-scale satoyama management in Japan have typically measured biodiversity in broadleaved secondary stands of varying age following clearance, whilst plantations of varying age have been compared in studies investigating the impact of extended rotation cycles. For satoyama stands, we included studies that used a reference stand of >100 years old (median age: 128 years). For planted stands, we used overmature plantations with extended rotation cycles (median age: 75 years) as the control group to compare against younger plantations of the same canopy dominant.

Whilst all studies included a common reference stand (>100 years old), studies varied widely in their approach, with stand age being treated as both a continuous and categorical variable across studies. We therefore adopted the meta-analytical approach of previous stand-age biodiversity syntheses by Curran et al. (2014) and Martin et al. (2014), which synthesised pair-wise comparisons between single treatment stands and replicated reference stands. We calculated *lnR* as the effect size for abundance and richness comparisons. We grouped taxa into the following groups: butterflies and moths, bees and wasps, epigeous invertebrates (beetles, bugs and ants), soil invertebrates (collembola and springtails) and ground layer plants (including groups termed vascular, shrub or herb species).

To measure pairwise compositional similarity between control and treatment groups, we calculated the abundance-based Morisita-horn index using R package 'vegan' (ref; see Appendix S2 for index formulae). Similarity indices have been used as effect sizes in previous quantitative reviews (Soininen et al., 2007; Dent et al. 2009; Curran et al., 2014). Similarity values for comparisons among forest stands represent pairwise averages where multiple comparisons were possible (i.e. when compositional data were available at the sampling site level). Raw similarity indices are unstandardized because background patterns of compositional change vary across taxa, spatial scales, forest type, among other factors (Dent and Wright, 2009). For studies that reported site-level compositional data, it was possible to adjust for this background compositional change by calculating a similarity response ratio, *RRsim*, following Curran et al. (2014). This expresses control and treatment forest community similarity ($\mathrm{Sim}_{\mathrm{C\text{-}T}}$) as a proportion of average background similarity in control comparisons ($\mathrm{Sim}_{\mathrm{C\text{-}C}}$):

$$\mathrm{RR}_{\mathrm{sim}} = \log_{10}\left(\frac{Sim_{C-T}}{Sim_{C-C}}\right).$$

We used linear mixed models in R package 'lme4' (Bates et al., 2014) to investigate variation in effect size with stand age and other moderator variables. For each intervention, three response variables were modelled: two log response ratios (*lnR*) representing proportional differences in species richness and abundance and the similarity response ratio RR_{sim}. Moderator variables included taxon, stand age, their interaction, and canopy dominant (Table 5.2). We included quadratic or $\log_{10}$ relationships with stand age to test for possible nonlinear biodiversity recovery with stand age. The studies varied too widely in their design to investigate the influence of all possible study characteristics on the impact of management interventions on biodiversity. We therefore used a random-effects framework, where each study-specific true effect is subject to random variation (Viechtbauer 2009). Effect sizes were weighted by the log of sample size, to reduce the overweighting of studies with much higher sample size. Random effects were used to identify observations from the same study, which used a common control, to avoid problems of non-independence. We identified the minimum adequate model from stepwise model simplification of global linear mixed models using the likelihood ratio test (Crawley, 2009). Relationships between effect sizes and covariates were explored by graphing coefficients from the minimum adequate mode with R package ‘ggplot2’ (Wickham, 2009).

5.3.1.4 Meta-analysis of contemporary satoyama management

The most common management interventions practised today in satoyama secondary broadleaved is undergrowth clearance (Tsuchiya et al. 2014). We retrieved studies that investigated the influence of undergrowth clearance by comparing abandoned and managed stands (selectively logged or undergrowth cleared) that were of a similar stand age and canopy dominant. We summarised them quantitatively using random-effects meta-analysis of log response ratios for species richness and abundance.

5.3.1.5 Meta-analysis of patch-size relationships with biodiversity

We sought studies that investigated the relationship between forest patch area and richness in Japan and South Korea. English- and Japanese-language papers were identified from ISI Web of Science, Google Scholar and J-Stage using relevant search terms (listed in Appendix S1). In the literature, the most common method for assessing the area-richness relationship has been to sample the abundance of a species in different habitat patches within a landscape, and then to test for a correlation between patch area and population density or richness (Bender et al. 1998). We chose the Pearson correlation coefficient r to represent the strength of the relationship between patch size and richness. Coefficient values were converted from conventional test statistics such as regression slopes and R^2 values following Lajeunesse (2013). Test statistics were not used from multivariate regressions where coefficients are affected by additional covariates, as this would lead to poor comparability across studies (Stein et al. 2014).

We used Fisher's z to quantify the effect size of landscape diversity–richness relationships. We derived z from r using Fisher's r-to-z transformation (following Borenstein et al. 2009):

$$z = \frac{1}{2} \times \ln \frac{1 + r}{1 - r}$$

This transformation is normalising and variance stabilising so that the variance v_z depends only on sample size n and not on the strength of the correlation itself (Shadish & Haddock 2009): $v_z = 1/(n - 3)$. Sample sizes were too low to group by taxonomic group. Observations were therefore grouped into three broad functional categories: forest specialists, non-forest specialists, and all species (where studies presented linear relationships between patch size and species richness for all species and did not differentiate species by a habitat association). We estimated mean effect sizes for each functional group using weighted random-effects meta-analysis. Random effects were used to identify observations from the same study to avoid problems of non-independence.

5.4 Results

5.4.1 Effects of plantation thinning on richness and abundance

We retrieved 18 publications that compared biodiversity in thinned and unthinned plantations, which spanned a range of taxonomic groups and thinning intensities (Appendix S3). All stands were planted as monocultures. These amounted to 45 richness and 61 abundance comparisons across all taxonomic groups. Plantation thinning significantly increased the abundance of tree saplings/seedlings, understory plants and invertebrates, by 218%, 217% and 51%, respectively ($P < 0.05$; Figure 5.1). Thinning also significantly increased richness of the studied groups, by 151%, 79% and 45% respectively ($P < 0.05$; Figure 5.1). Studies varied widely in thinning attributes such as stand age and thinning intensity, causing significant heterogeneity amongst studies across all taxonomic groups ($P < 0.001$; Figure 5.1). Collinearity between taxonomic group and stand age and thinning intensity restricted our mixed effects modelling of abundance effect sizes to saplings and seedlings and ground layer plants only. Moderator collinearity precluded mixed-effects analysis of species richness effect sizes. Thinning intensity, stand age and taxonomic group were not important predictors of abundance effect sizes: only the $\log_{10}$ of years since thinning featured in the minimum adequate model explaining effect size variation for understory plants, saplings and seedlings, where effect sizes declined with time since thinning ($F_{1,13} = 14.06$, $P = 0.023$; Figure 5.2).

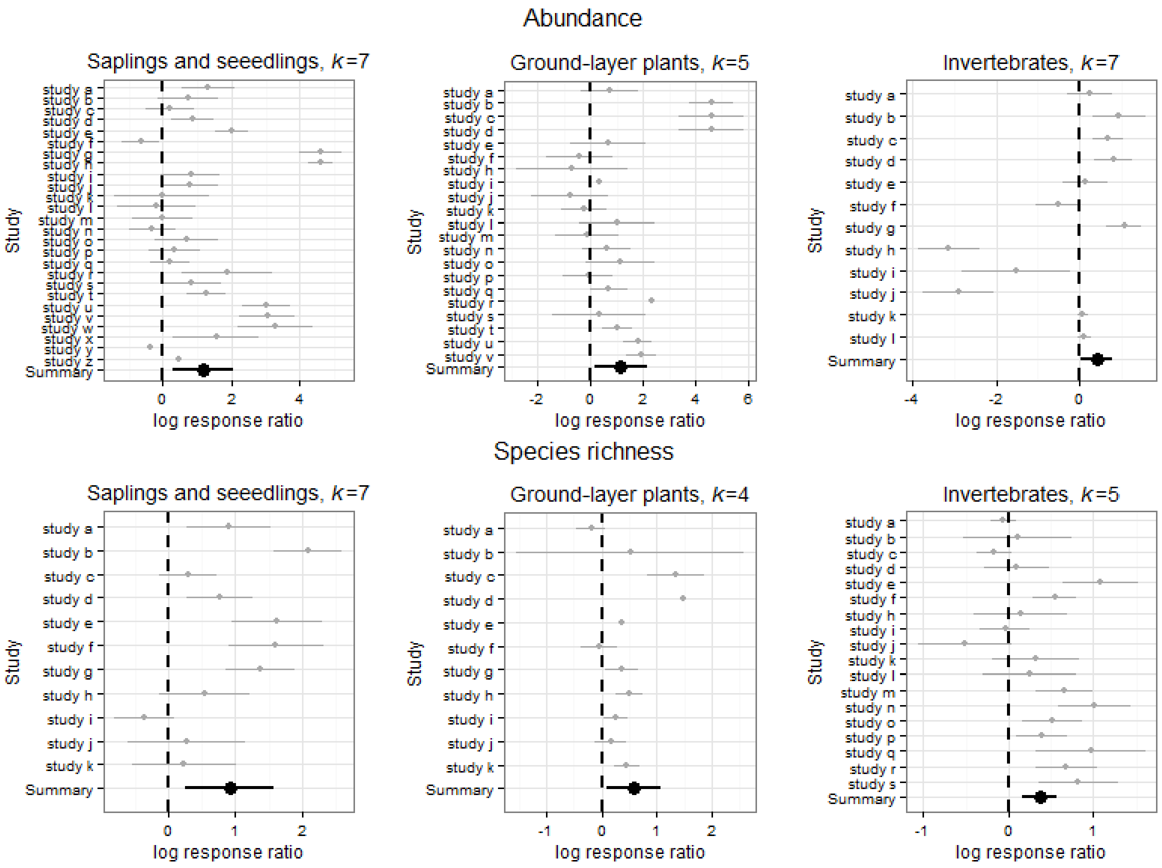

Figure 5.1 Effect of thinning on abundance and species richness, from *k* studies. Summary mean effects in bold differ significantly from zero when their 95% CIs do not cross the dashed line of zero difference between thinned and unthinned stands.

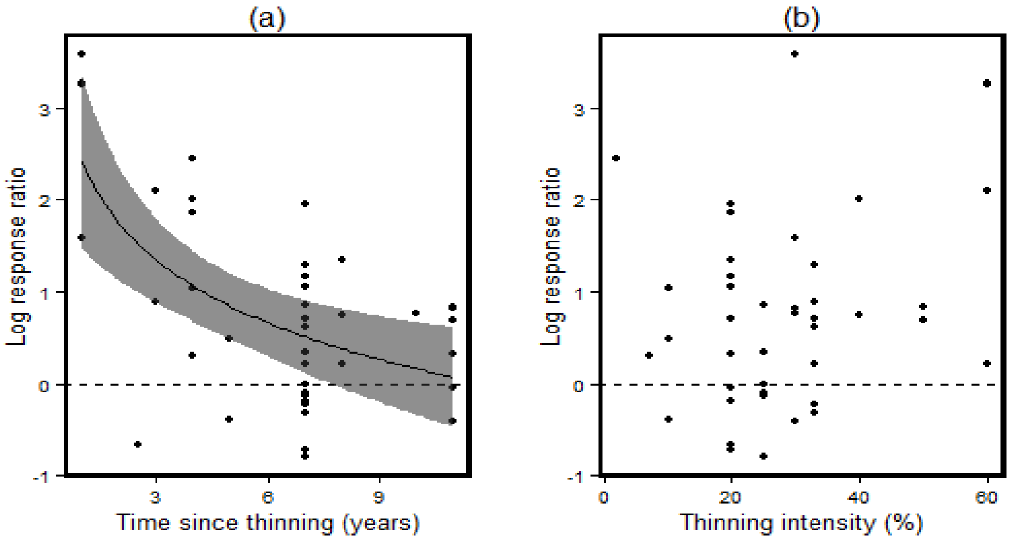

Figure 5.2 Influence of (a) years since thinning and (b) thinning intensity on abundance differences between thinned and unthinned forest stands for ground layer plants and saplings and seedlings (horizontal dashed line means no difference). Regression used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on uncertainty in fixed effects only.

5.4.2 Effects of stand age on richness, abundance and composition in plantations

We retrieved data on 72 planted forest sites from 14 publications each describing species richness, abundance or composition in comparison to a reference overmature planted forest stand. With most studies reporting on multiple taxonomic groups, these yielded 114 richness, 57 abundance and 37 species composition comparisons. One study that measured tree composition in stands from 20-250 years old was excluded from the quantitative synthesis because its stand age values were outliers (Suzuki et al. 2005). The minimum adequate models selected to explain species richness and abundance differences between extended rotation and younger planted forest stands contained taxonomic group (species richness: $F_{1,103} = 8.87$; $P < 0.001$; abundance: $F_{1,41} = 13.15$; $P < 0.001$), $\log_{10}$ stand age (species richness: $F_{1,98} = 1.50$; $P = 0.223$; abundance: $F_{1,52} = 2.40$; $P = 0.128$), and their interaction (specie richness: $F_{1,98} = 6.81$; $P < 0.001$; abundance: $F_{1,37} = 8.98$; $P < 0.001$). These models had marginal R^2 values of 0.30 and 0.61 for species richness and abundance effect sizes, respectively. Climbing plants, and terricolous invertebrates exhibited consistently higher species richness and abundance levels in younger planted stands than overmature planted stands, while fungi were consistently richer and abundant in overmature stands (Figure 5.3). The interaction reflects opposing relationships of species richness and abundance with stand age (explaining the non-significance of the stand-age main effect). Birds and shrubs and trees demonstrated positive relationships, whilst flying and terricolous invertebrate and ground layer plant richness and abundance declined with stand age (Figure 5.3). Fungi richness and abundance did not vary with stand age.

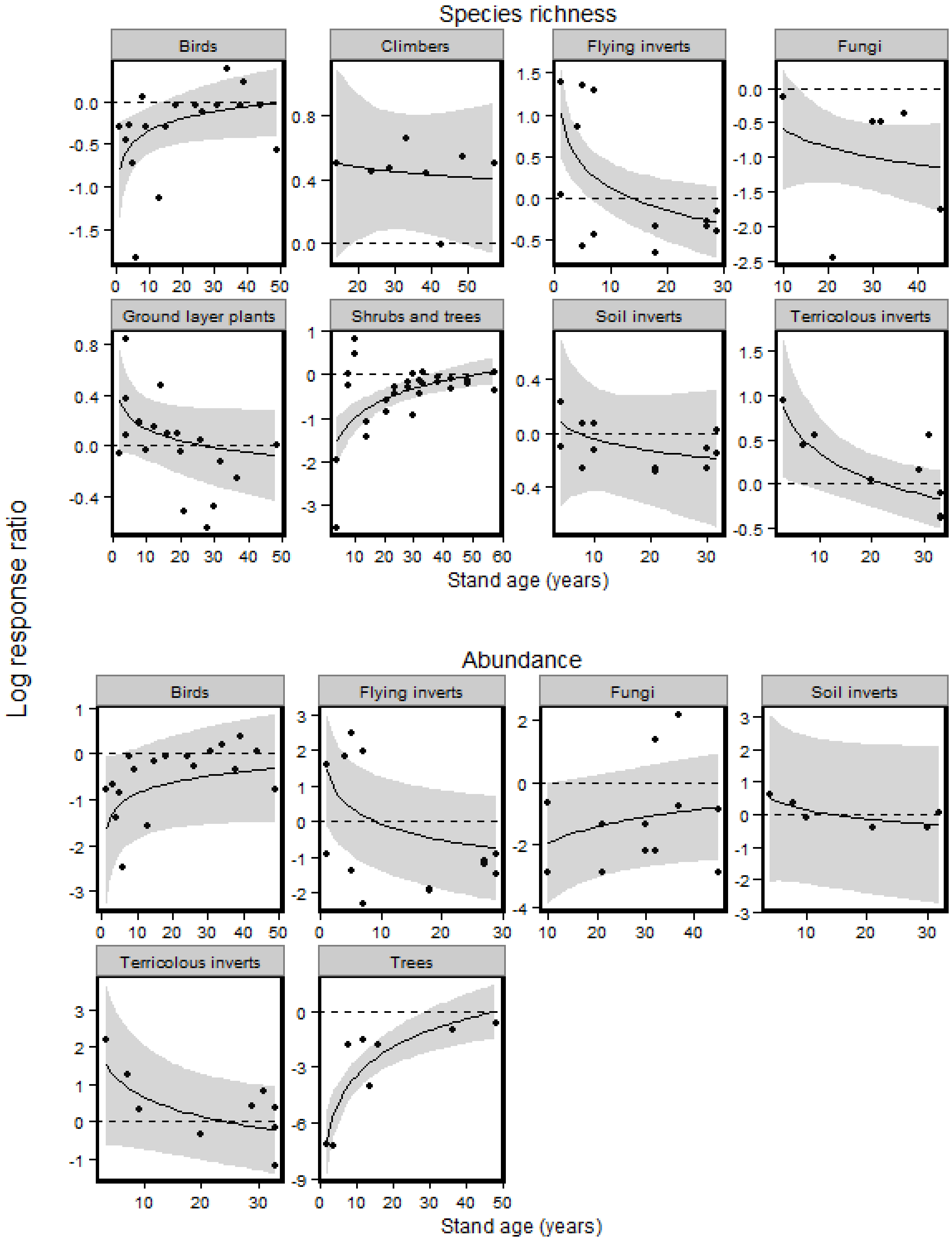

Figure 5.3 Influence of stand age on species richness and abundance effect sizes in planted stands relative to extended rotation planted stands. The horizontal dashed lines show no difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on uncertainty in fixed effects only.

Investigation of compositional similarity across extended rotation and younger planted stands was possible for birds and insects only. The minimum adequate model selected to explain compositional similarity between extended rotation and younger planted forest stands included $\log_{10}$ stand age only (t_{33}= 5.23; P <0.001) and had a marginal R^2 of 0.42. Compositional similarity between younger and overmature planted forests increased with stand age, and younger planted stands achieved equivalence with extended rotation stands after approximately 50 years (95% prediction intervals encompassing 28 years and never; Figure 5.4).

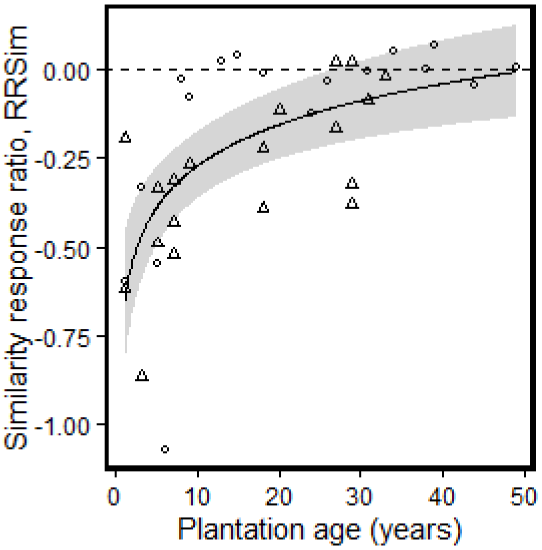

Figure 5.4 Influence of stand age on pair-wise compositional similarity between planted and extended rotation planted forest stands for birds (o) and insects (Δ). The horizontal dashed line shows no compositional difference between extended rotation and younger treatment forest stands. Grey shading shows 95% prediction intervals based on uncertainty in fixed effects only.

5.4.3 Effects of traditional satoyama management of secondary forests on richness and abundance

We retrieved data on 66 secondary forest sites from 17 studies that each described species richness, abundance or composition in comparison to a reference secondary forest stand > 100 years old. With most studies reporting on multiple taxonomic groups, these yielded 94 richness, 69 abundance and 23 species composition comparisons. The minimum adequate model selected to explain species richness differences between abandoned older and younger secondary forest stands contained taxonomic group ($F_{5,21}$ = 2.21; P = 0.091), stand age ($F_{1,70}$ = 0.91; P = 0.341), and their interaction ($F_{5,68}$ = 5.57; P = 0.006). This model had a marginal R^2 of 0.25. The interaction reflects a balanced opposition of stand-age effects amongst taxonomic groups (explaining the non-significance of their main effects). Flying invertebrates and ground-layer plant richness benefited from early successional conditions and declined with stand age, whilst soil invertebrates, birds and terricolous invertebrates exhibited lower richness and abundance levels in younger planted forest stands relative to overmature stands and tended to increase with stand age. The minimum adequate model explaining abundance effects size variation contained taxonomic group only ($F_{4,64} = 4.42$; $P = 0.003$), which had a marginal R^2 of 0.34.

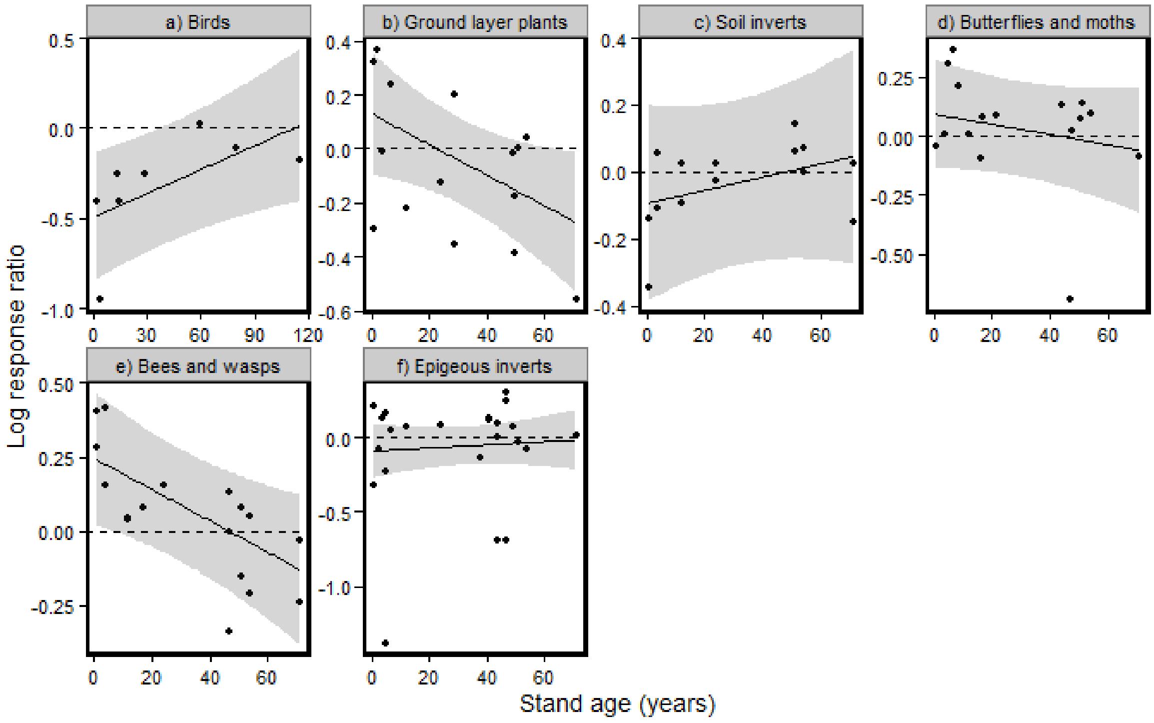

Figure 5.5 Influence of stand age on species richness effect sizes in younger secondary forest stands relative to older (>100-yr) abandoned forest stands. The horizontal dashed lines show no difference between extended rotation and younger treatment forest stands. Regressions used coefficients of the minimum adequate model. Grey shading shows 95% prediction intervals based on uncertainty in fixed effects only.

5.4.4 Effects of contemporary satoyama management of secondary forests on richness and abundance

We retrieved only four studies that investigated the impact of undergrowth removal on species richness and abundance, all of which were on invertebrates. Three studies were from the same study site in Okinawa, and one from Hiroshima (Yamamoto, 2001). One study contributed biodiversity data for two taxonomic groups, amounting to five richness and abundance comparisons. Four out of five comparisons were on soil dwelling invertebrates. Data were insufficient for compositional analysis. Random-effects meta-analysis showed a negative effect of undergrowth clearance on species richness, resulting in a 12% reduction in richness (*P* < 0.01; Figure 5.6). This relationship was consistent across studies (between-study effect *P* = 0.583). In contrast, abundance varied between studies (*P* = 0.049), with an with no evidence of change due to management (*P* = 0.339).

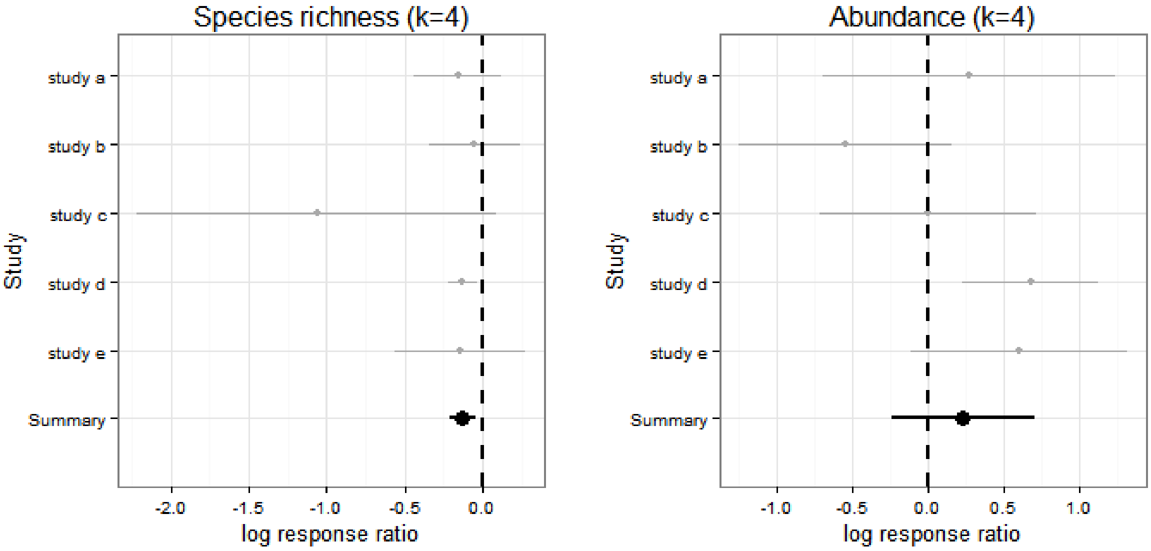

Figure 5.6 Effects of undergrowth clearance on species richness and abundance of invertebrates in secondary broadleaved forests, from *k* studies. Summary mean effects in bold differ significantly from zero when their 95% CIs do not cross the dashed line of zero difference between treatment and control stands.

5.4.5 Effects of patch area on species richness

We retrieved data from 12 publications that investigated the relationship between patch area and species richness (Appendix S3). These amounted to 9 forest specialist, 11 non-forest specialist and 11 patch size-richness relationships for all taxonomic groups. All but two studies (forest specialist study 3 and all taxa study 4 in Figure 5.7) adopted an area-independent sampling strategy by maintaining an equal sampling area across different sized patches. The species richness of biotic communities exhibited variable relationships with patch size according to habitat specialisations, from strongly positive for forest specialists (*r* = 0.77; *P* <0.001), to negligible for non-forest specialists (*r* = -0.17; *P* = 436) and intermediate for groups with species of all habitat associations (*r* = 0.61; *P* < 0.001; Figure 5.7). High heterogeneity existed across effect sizes of non-forest specialists (P<0.001; Figure 5.7).

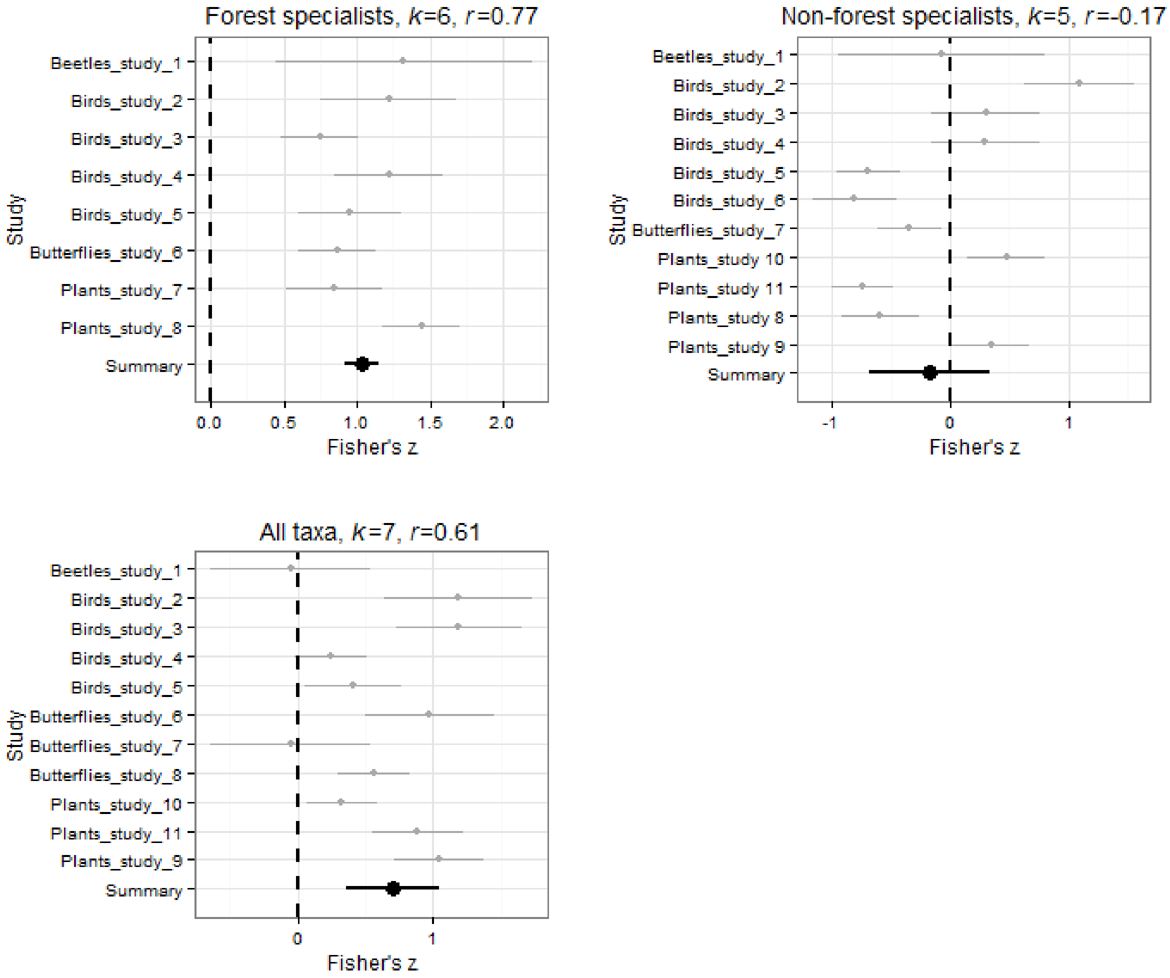

Figure 5.7 Relationships between forest patch area and species richness (random-effects) for forest specialists, non-forest specialists and all species. Mean effect size estimates are back-transformed from *z* to *r*.

5.5 Discussion

The challenges that Japan faces in managing its forest resources sustainably are broadly similar to those of other nations; indeed, coppice abandonment is a concern across Europe (Müllerová et al. 2015). Japan has unique cultural influences of land use, however, that have resulted in its exclusion from pan-global quantitative syntheses of forest management impacts on biodiversity (Higuchi and Primack, 2009; Curran et al. 2014; Spake et al. 2014). These reviews used relatively undisturbed old-growth forest as a reference state, a forest type which is extremely rare and therefore inappropriate for Japan. In this study, we have collated and synthesised studies that have investigated biodiversity responses to management interventions relevant to Japan's National Biodiversity Strategy.

5.5.1 Effects of plantation thinning on richness and abundance

Plantation thinning positively impacted species richness and abundance of invertebrates, ground layer plants and saplings and seedlings (Figure 5.1). One objective of plantation thinning in Japan is, ironically, to encourage the regeneration of natural broadleaved forest species that were replaced when the coniferous plantations were established (Yamaura et al. 2012). Plantation thinning substantially increased sapling and seedling abundance and richness (Figure 5.1), although with declining effect in the years following thinning, with no effect remaining after around 10 years (Figure 5.2). This finding might suggest that whilst thinning encourages the regeneration of broadleaved species, repeated thinning may be required to ensure the survival and establishment of broadleaved species. Surprisingly, neither thinning intensity nor stand age influenced abundance (Figure 5.2), suggesting an absence of generally applicable thresholds for maximising positive effects on species richness or abundance. Individual studies that have measured biodiversity in stands encompassing a range of thinning intensities have reported a strong effect of thinning on biodiversity; Seiwa et al. (2012) showed that species diversity and abundance of hardwood saplings and seedlings was higher in intensively thinned Japanese cedar plantations than weakly thinned stands. This relationship did not hold out when all studies were combined, perhaps due to interactions between thinning intensity and crop species, although power was insufficient to test this.

Overall, plantation thinning was the only management intervention studied in this review that tended to benefit all of the studied taxonomic groups simultaneously. However, it is important to consider the impacts of thinning on ecosystem services other than biodiversity conservation in multi-functional-orientated forest management. For example, Dung et al. (2010) found that thinning Japanese cypress plantations on hillslopes in central Japan compromised the soil's water retention capacity and increased overland flow in plantations due to soil compaction from the thinning operation and reduced canopy interception. Further research is needed to better understand the impact of plantation thinning on ecosystem functioning, quality and quantity of timber in both conifers and hardwoods and timber price (Seiwa et al. 2012).

5.5.2 Effects of stand age on biodiversity in planted and secondary forests

Conventional plantation management in Japan has used a rotation age of between 40 and 60 years (Masaki et al. 2006). However, extended rotation ages > 70 years are becoming increasingly widespread, as a way of hedging against fluctuations in the price of timber with a larger and more valuable stock (Masaki et al. 2006; Nagaike 2012). This review has shown that the richness and abundance of many taxonomic groups increases with planted stand age (Figure 5.3). These increases are likely attributable to the combined effects of time favouring colonisation by dispersal-limited species, and structural diversification as the forest ages (Norden and Appelqvist, 2001). The richness of some taxonomic groups, including ground layer plants and soil and terricolous invertebrates, declined with stand age, however. With different taxonomic groups exhibiting contrasting species richness levels in different successional stages, our results support calls for young forest stands to be included in plantation forest mosaics for invertebrate and ground layer plant conservation (de Warnaffe & Lebrun, 2004).

Richness and abundance relationships with stand age revealed little difference between the biodiversity value of 50 year- and 70-year old plantations. Indeed, for birds and insects, the species composition of younger planted stands reached equivalence to overmature stands after around 50 years (Figure 5.4). Extending the rotation length from the conventional age of 40-60 years to >70 years may therefore not offer a win-win for economic return and biodiversity conservation. However, it is important to understand patterns of biodiversity variation beyond 70 years, as a high proportion of planted stands are likely to remain unmanaged in Japan. It is likely that biodiversity relationships with stand age may change as plantation forests enter a later successional phase of canopy break up (Humphrey et al, 2003), from which ground-layer plants can benefit (Duguid and Aston, 2014). As the majority of plantations were established during the post-war housing boom in the 1950s-80s, few studies exist on plantations older than 70 years. We retrieved one that studied *Chamaecyparis obtusa* plantations from 20-250 years old. Susuki et al. (2005) found that stands > 200 years old had different species compositions than stands < 100 years old, and had developed multi-layered canopies, with broadleaved species occupying the lower canopy. The authors state that canopy openings were a product of both past logging events and natural stand dynamics, and suggest that even much older planted forests stands may require thinning. Yamaura et al. (2008) sampled larch plantations of a range of ages up to >100 years old in and found stand height (a proxy for age), larch snags (which increase in abundance with age) positively affected the abundance of multiple bird groups including flycatchers, stem probers and tree creepers. Another strong motivation for maintaining aged forests is the large amounts of stored carbon contained by them (Yamaura, 2012).

The concept of traditional satoyama management figures prominently in popular and media discourse concerning the conservation of nature in Japan (Knight, 2010). The

Satoyama Initiative, launched concurrently with the Strategic Plan for Biodiversity in 2010, aims to restore satoyama owed to perceived benefits for biodiversity and ecosystem service delivery (Takeuchi, 2010). We have shown that species richness and abundance relationships with stand age varied according to taxonomic group in secondary forests (Figure 5.5). Flying invertebrates and ground-layer plants benefited from more open, early-successional conditions and tended to decline with stand age while the abundance and richness of birds and soil invertebrates increased with stand age (Figure 5.5). Traditional satoyama management is therefore not necessarily the panacea for biodiversity conservation that it is promoted as (Indrawan et al. 2014). Late successional secondary forests are needed to support mature forest-specialists; in a study of the drivers of bird assemblage composition in satoyama landscapes, Yamaura et al. (2007) showed the occurrence of mature forest users inhabiting broadleaved forests was affected by stand height only. They suggest that increasing forest height through extended rotation would effectively conserve mature forest users.

5.5.3 Effects of contemporary satoyama management on biodiversity

In many places, contemporary management of satoyama forest differs from that of the traditional management regime that predominated in Japan's pre-developmental era. Indeed, the previous primary function of satoyama was for production (Indrawan et al., 2014), whilst recreation, cultural heritage and biodiversity conservation are more recent priorities (Tsuchiya et al., 2014). Undergrowth clearance is typically performed by local voluntary community groups, in response to encouragement and subsidisation by local prefectural governments across Japan (Tsuchiya et al., 2014). Periodic removal of the understorey is thought to increase ground layer plant species diversity by increasing the amount of light reaching the forest floor (Figure 5.8).

Figure 5.8 Undergrowth from secondary broadleaved forests that have been abandoned (left) and that have had the understorey removed (right) in Yanbaru, Okinawa. From Ito et al. (2000).

This review has highlighted a lack of studies investigating the impact of undergrowth clearance in secondary forests. The majority of studies came from a single site in Okinawa. Moreover, four out of five of the observations were on soil dwelling invertebrates with the remaining study on flying invertebrates. Random-effects meta-analysis demonstrated that species richness declined with undergrowth clearance, whilst abundance showed a tendency to increase. Whilst data were not available for compositional analysis, Ito (2003) attributed these patterns to compositional differences between cleared and uncleared secondary forest stands, whereby large numbers of a few generalist species occur in forest stands that were cleared of undergrowth (Ito, 2003). Furthermore, rare, endemic species were negatively impacted by undergrowth clearance, whilst widespread species were not (Ito and Aoki, 1999; Ito et al. 2000). Due to the low number of studies on undergrowth clearance, their geographic bias to southern Japan and taxonomic focus on soil invertebrates, our understanding of the impact of this management intervention is therefore limited in taxonomic focus and geographic extent. Despite these limitations, it is clear that a conflict exists between the objectives of undergrowth clearance (recreational and aesthetic appeal) and biodiversity conservation, at least for soil invertebrates. It is likely that this management intervention will negatively affect other forest specialist groups: Heyman (2010) found that complete undergrowth clearance of urban forests in Sweden negatively affected breeding bird density, possible due to the removal of suitable habitat for foraging and protection (Heyman, 2010). It is likely that open habitat species may benefit undergrowth clearance.

5.5.4 Effects of patch area on species richness

Species richness of forest specialists exhibited strongly positive relationships with forest patch size (Figure 5.7). This is likely due to larger patches typically having lower extinction rates and higher immigration rates than small patches, as predicted by island biogeography (MacArthur and Wilson 1967) and meta-population theory (Hanski and Gyllenberg 1997). Furthermore, patch area may act as a surrogate for patch characteristics, with larger forest patches containing a wider range of habitat conditions and providing more opportunities for niche segregation (Jamoneau et al. 2011).

Non-forest specialist communities had no relationship to patch size, and groups of all species comprising specialists and non-specialists had an intermediate relationship overall (Figure 5.7). This finding agrees with recent empirical and modelling studies from other regions (Bender and Fahrig, 2005; Guldemond and van Aarde, 2010) demonstrating that patch size is often more important for forest-dependent species than for generalist species. Indeed, the dichotomy between patch and matrix habitats breaks down for groups that also inhabit matrix habitat (Soga and Koike, 2013). There was high heterogeneity among effect sizes in the response of richness to patch size for non-forest specialists (Figure 5.7); however sample size was too low to examine the influence of moderators such as matrix quality, stand structure and taxonomic group that might explain effect size heterogeneity. Whilst most observations tended to be negative, Soga and Koike (2013) found that generalist butterfly species richness correlated positively with patch area, which disagrees with findings from previous studies investigating generalist-forest area relationships (Guldemond and van Aarde, 2010). The authors attribute this finding to the fact that the matrix habitat surrounding the forest patches in their study was completely urbanised, and uninhabitable for even generalist butterflies due to increased air and soil pollution. In studies where forest patches were parts of satoyama landscapes, weaker to negative relationships are likely to exist for generalist species, due to the fact that boundaries between patch and matrix are obscured for high matrix-tolerant species in satoyama landscapes (Soga and Koike, 2013). It is therefore crucially important to maintain large patches of forest in highly urbanised landscapes in Japan. Furthermore, the majority of studies included in this review treated ‘forest’ as a uniform land use, but Yamaura et al. (2007) demonstrated that the effects of surrounding forest areas on bird occurrence are greater for mature forest bird species users inhabiting plantations than for those inhabiting broadleaved forests. The configuration and type of forest are therefore important considerations that must be made when managing forest landscapes; Yamaura et al. (2007) assert the importance of maintaining broadleaved forests near to plantation patches for conserving the species reliant on mature forest in plantations.

5.5.5 Study limitations

In our analysis of stand-age biodiversity relationships, low sample sizes for some taxonomic groups led to low precision in effect sizes (Figures 4 and 5). Furthermore, whilst it is known that functional groups within broad taxonomic groupings are likely to vary in their responses to forest management impacts (Spake et al. 2015), low sample sizes forced their grouping into broad taxonomic groups. This may obscure differences in responses of some groups within these broad groupings that may be important to ecosystem functioning. Most studies contributed more than one observation to our analyses, for example several taxonomic groups and management intensity levels or age classes were included in the same study. Whilst the incorporation of an appropriate random-effects structure into models can overcome problems of non-independence (Mengersen et al. 2013) the data are still biased geographically. For example, four out of five effect sizes characterising the impact of undergrowth clearance were from the same network of study sites in Okinawa, subtropical Japan. The use of meta-analysis allows us to test whether there is a clear effect of forest management on biodiversity when examined over a broad region, a valuable exercise regardless of inter-study differences. However, if the majority of studies come from the same study region, characterised by particular soil conditions and land use histories, there may be limited scope for generalising to the rest of the nation. There is therefore an urgent need for more studies investigating the impact of undergrowth clearance on biodiversity, a management intervention widely practised by local volunteer groups across Japan (Tsuchiya et al. 2014).

5.6 Conclusions

The future management of Japan’s vast forest area is currently being discussed. Our meta-analysis of a relatively large set of published studies investigating particular management interventions proposed in Japan’s National Biodiversity Strategy shows that management can enhance the species richness and abundance of particular taxonomic groups. Plantation thinning can significantly increase plant and invertebrate species richness and abundance, but repeated thinning treatments may be required to sustain this positive effect. Young planted forest stands differ in species composition to older planted forests stands, suggesting that a range of forest ages should be present in production landscapes to maximise beta diversity. However, we found that plantation rotation age extension from 40-60 years to >70 years does not bring additional biodiversity benefits, although much longer rotation ages have not been studied. The revival of traditional satoyama management through secondary forest clearcutting may benefit certain taxonomic groups, but the species richness of many taxonomic groups increase with stand age. We reveal a knowledge gap with regards to studies on undergrowth clearance.

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5.7 Co-author contribution

Contributor	Contribution to this research
RS	Formulated research questions, performed systematic review of and data extraction from relevant English papers, performed meta-analysis using data from English and Japanese papers and wrote the paper
K Kitayama	Advised on research question, methodology and write-up
SY	Will do the systematic review and data extraction of Japanese papers
YY	Advised on research question, methodology and write-up
K Kawamura	Will do the systematic review and data extraction of Japanese papers
CPD	Advised on research question, methodology and contributed to write-up

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Chapter 6: General discussion: evaluating forest management strategies for biodiversity conservation

The conservation and management of old-growth forests remains one of the most extensively researched topics in the modern literature on forest ecology and management (Lindenmayer, 2009). It is evident that their high structural diversity and long continuity make old-growth forests irreplaceable biodiversity resources (Curran et al., 2014, Spake et al., 2015). They are typically used as benchmarks against which to compare the effectiveness of sustainable forest management and conservation actions such as restoration (Bullock et al., 2011).

Whilst the strict protection of old-growth forests will likely remain a conservation priority throughout the world, the potential for other types of forests to support biodiversity is gaining increasing recognition (Gibson et al., 2011, Putz et al., 2012; Chapter 3). The importance of diversity is recognised in the Strategic Plan for Biodiversity, drawn up by the Convention on Biological Diversity and agreed upon by the governments of the world in Aichi, Japan 2011. Target 11 of the Strategic Plan states that by 2020, at least 17% of the areas of particular importance for biodiversity and ecosystem services are to be conserved through “ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures”. Target 7 advocates the implementation of sustainable management strategies for production forests, whilst Target 15 calls for the restoration at least 15% of degraded areas through conservation and restoration activities. If we are to reach these targets for the forest ecosystems of the world, we need a sound empirical and synthetic understanding the functioning and the relative importance of forests under varying management regimes and conservation designations. A synthetic understanding is achieved through the collation of empirical research and yields practicable generalisations for guiding forest management and conservation.

This thesis has investigated the effectiveness of conservation and sustainable management strategies for secondary forests for biodiversity conservation through a series of case studies. The case studies have ranged in both taxonomic focus and scale from a global analysis of forest restoration impacts on biodiversity (Chapter 2; Spake et al. 2015), to national scales assessing drivers of biodiversity in UK and Japanese plantation forests (Chapters 4, Spake et al. 2016, and 5) to assessing biodiversity in planted and old-growth forest stands in a UK National Park (Chapter 3; Figure 1). This chapter aims to synthesise the findings of the thesis in the context of existing forest ecology and management literature and make suggestions for future research.

6.1 Old-growth forests are irreplaceable for sustaining forest biodiversity

Chapter 2 (Spake et al. 2015) demonstrated long recovery times for planted and secondary forests to attain the species richness value of old-growth forest for certain functional groups; over a century for lichens, and almost a century for ectomycorrhizal fungi and ~60 years for saproxylic beetles (Chapter 2; Figure 2.1). These recovery times are unacceptable when considered relative to the beneficiaries' generation time (~25 years). Century-long recovery times for species richness have been found in other quantitative syntheses of stand-age biodiversity relationships across all biomes (see refs in Table 6.1). Faunal richness recovery can be relatively fast (Table 1; Dunn, 2004), but the recovery of species composition takes considerably longer in tropical secondary forests (Table 1; Chazdon, 2009). A similar pattern has been observed for tropical trees and epiphytes, which recovered richness within 50 and 100 years, respectively, but composition appeared to never recover within this time (Table 1; Martin et al. 2013). These findings suggest that the recovery of beetle, lichen and fungi composition will take considerable longer than the time predicted for richness recovery in Chapter 2.

The principal conclusion of Chapter 2, as of other quantitative syntheses of stand age-biodiversity relationships, is that old-growth forests are irreplaceable due to the long recovery times of certain (but not all) taxa essential to ecosystem functioning. The comparison to planted and secondary forests has demonstrated, however, that they support considerable levels of biodiversity (Table 6.1), highlighting their potential conservation value. The protection of old-growth forest from development through reserve creation should therefore remain a conservation priority, but planted and secondary forests of high biodiversity value should be considered too. Indeed, Chapter 3 demonstrates that overmature planted forest can eventually support ectomycorrhizal communities present in old-growth forests and argues that such forests can be used to develop ecological networks; core areas of habitat connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules (Lawton et al. 2010; Humphrey et al. 2015).

Table 6.1 Published meta-analyses of biodiversity recovery in forests that have been planted or regenerating following major disturbance.

Study	Brief descriptions of forest types	Taxonomic / functional groups	Recovery times to reference levels
Dunn (2004)	Compared mature forest controls with secondary regenerating forests in the tropics	Ants, birds and other groups	Secondary forest richness resembled that of undisturbed forest just 20–40 years after abandonment. At least for ants and birds however, recovery of species composition appears to take substantially longer.
Chazdon et al. (2009)	Compared old-growth composition with that of secondary forests regenerating naturally after significant disturbance, in tropics	Trees, seedlings, volant and non-volant fauna	Only 40% of undisturbed forest species had colonized secondary forests after 80 years of recovery
Dent and Wright (2009)	Compared old-growth controls with secondary forest regenerating from clearance (mostly for agriculture) in the tropics	Invertebrates, amphibians and reptiles, birds and mammals	The proportion of old-growth species present in old secondary forests >50 years old was high (0.80 ± 0.06)
Martin et al. (2013)	Compared undisturbed forest with secondary forests described as previously forested areas undergoing secondary succession following total or near total removal of trees in the tropics	Trees and epiphytes	Tree richness recovered within 50 years, while epiphyte richness took > 100 years. The proportion of undisturbed forest trees and epiphyte species found in secondary forests was low and changed little over time.
Curran et al. (2014)	Compared old-growth controls with planted and secondary forests stands in tropical, temperate and boreal reigons	Trees, other mainly non-woody plants, birds, mammals, herpetofauna, insects and other invertebrates	In the best case, richness converged to reference values within a century, species similarity (Sorenson) took about twice as long, and assemblage composition (Morisita-Horn) up to an order of magnitude longer (hundreds to thousands of years).
Bogdziewicz and Zwolak, (2014)	Compared unharvested or mature forest stands with clear-cuts up to 20 years old in Europe	Small mammals	Generalist species increase in abundance after clear-cutting. No relationship with time since cutting, as stands up to 20 years were only studied.
Spake et al. (2015); Chapter 2	Old-growth controls compared with planted or secondary forest stands regenerating form major disturbance in temperate and boreal regions	Beetles, lichens and fungi	The recovery of richness to old-growth levels for epiphytic lichens, mycorrhizal fungi and saproxylic beetles took 180, 90 and 60 years, respectively. Non-saproxylic beetles declined with stand age and deadwood and litter fungi showed no relationship.

The quantitative syntheses of stand-age biodiversity relationships discussed thus far have focussed on the recovery of forest communities following major, stand-replacing disturbances including clear-cutting and fire. Whilst disturbances of this magnitude are widespread, a comparatively new paradigm of forest management is gaining momentum: retention forestry. A practice fundamental to retention forestry is the retention of single trees and/or intact forest patches on site during harvest, thereby reducing the contrast between clearcuts and natural forests (Figure 6.1).The aim is to achieve a level of continuity in forest structure and complexity that more closely resembles the effects of natural disturbance, thereby conserving forest biodiversity and sustaining ecological functions (Gustafsson et al. 2012, Fedrowtiz et al. 2014). A quantitative synthesis has demonstrated that both forest specialists and open-habitat species benefit from retention cutting, relative to clear-cut and un-harvested controls, respectively (Figure 6.1; Fedrowitz et al. 2015). Furthermore, species richness recovered faster with time-since-harvest in retention cuts than clear-cuts, although the meta-analysis included few investigations of retention cuts >20 years old, indicating that more data are needed to draw firm conclusions (Fedrowitz et al. 2015).

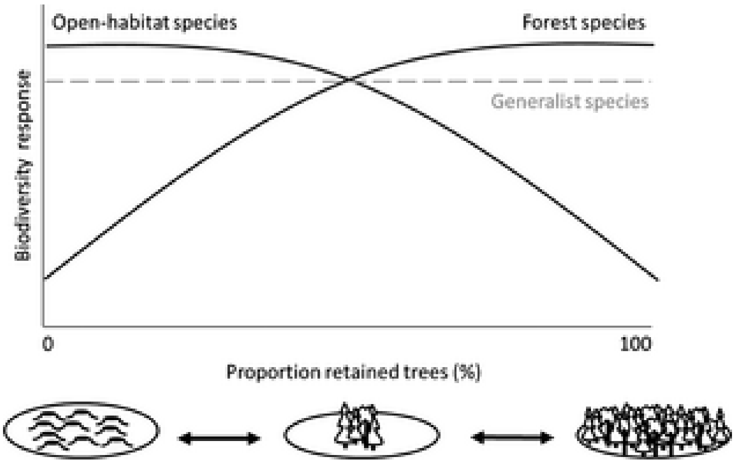

Figure 6.1 Expected biodiversity responses (species richness and abundance) for different ecological groups of taxa (forest specialists, open-habitat specialists, generalists) to tree retention in the gradient from clearcut to forest. Response curves are schematically drawn; different shapes are possible. In the meta-analysis, retention was compared to two kinds of external controls: clear-cuts and forest (arrows). From Fedrowitz et al. (2014).

To manage forest effectively for multiple use values, there is a need to simultaneously quantify values of multiple services, not just biodiversity, with stand age. Of particular concern is carbon storage because forests store more carbon globally than the atmosphere (Pan et al., 2011), and appropriate management of these carbon stores will be necessary to mitigate global climate change (Chisholm et al., 2013). A pan-global synthesis of peer-reviewed estimates of carbon pools in forests across the world has demonstrated that age-related trends in carbon cycling and storage are apparent in temperate, boreal and tropical biomes (Pregitzer and Euskirchen , 2004). Indeed, Martin et al. (2013) found carbon pools in the form of above-ground biomass accumulate more quickly than biodiversity in tropical secondary forest and suggested that these differing recovery rates should be acknowledged by policies targeting the recovery of both biodiversity and carbon in tropical forests. In terms of cultural use values of forests, uneven-aged semi-natural stands are thought to have a higher aesthetic value than younger even-aged planted stands, with temporal models of perceived scenic beauty showing a monotonically increasing relationship with time since harvest (Gobster, 1996).

6.2 Implications of thesis research for forest management and conservation in the UK, including the New Forest National Park

In the UK, ancient woodland is widely understood to be an area that has been wooded continuously since at least 1600 A.D. (1750 in Scotland; Goldberg et al. 2007). This definition includes ancient semi-natural woodland (ASNW), sites composed of native trees and shrubs, and plantations on ancient woodland sites (PAWS), that contain evidence of former ancient woodland, but have subsequently been planted with coniferous or broadleaved trees since the First and Second World Wars. ASNW are semi-natural, in that they have been selectively felled for timber in the past, but allowed to regenerate naturally, without any major tree removal since the mid-20th century (Peterken, 1977). PAWS are often less biodiverse than ASNW, but can retain some features of ancient woods (Kirby, 1988; Ferris and Simmons, 2000). The threshold date of 1600 that distinguishes ASNW from ‘recent woodland’, *sensu* Peterken (1977) differentiates their origin. Pre-17th century tree planting was normally associated with fruit trees rather than timber trees, such that plantations barely existed before this time (Rackham, 1980; Peterken, 1996; Rackham, 2006; Arden 2009); “if a woodland has not been planted in the last 400 years, it has probably never been planted” (Peterken 1996). Many ASNW sites are descendants of primary woodland (Goldberg et al. 2007). In The New Forest National Park, pollen records of many ASNW sites suggest a degree of continuity between ancient woods and the wildwood (Dimbleby 1955; 1962; Grant, 2005).

It is generally accepted that ancient woods (forest >400 years old), are more species-rich than recent woods for many taxonomic groups (Peterken, 1996, Atkinson and Townsend, 2011; but see Chapter 3). Despite this recognition, conservation designations applied to ancient woodlands in the UK are indirect (e.g. Sites of Special Scientific Interest (SSSIs) or Special Areas of Conservation (SACs)) and many ancient woodlands have no formal protection measure at all. This represents a missed opportunity, as historical records and maps can often establish woodland ages with certainty. Those protection mechanisms that do exist suffer from loopholes that allow ancient woodland to be destroyed or severely damaged (Tickell and Thackray, 2000): when planning permission is granted for development, felling or clearing trees (and sometimes entire wooded areas) is exempt from forestry controls (Tickell and Thackray, 2000). ASNW continues to be lost despite BAP targets to maintain current area; over 300 ha of ancient woodland were recorded as lost between 2001 and 2011 (Woodland Trust, 2011). Further loss of ancient woodland is a particularly pressing concern in the UK. In 2011, the UK government set in motion a process to establish a formal biodiversity offsetting programme in England, as an attempt to tackle biodiversity loss as a result of development (Lockhart, 2015). Biodiversity offsets are actions that create comparable and/or additional biodiversity gains to compensate for losses caused by development (Bull et al., 2013). Offsets have been used for the past four decades around the globe but have had limited success (Bull et al., 2013), due to the existence of time lags between the implementation of offset schemes and the accrual of their intended benefits; Chapter 2 demonstrates that it takes over a century for lichen and almost a century for ectomycorrhizal fungi in planted and secondary forest to reach species richness equivalence to old-growth forest. The actual quantification of biodiversity recovery with stand age should provide more impetus for governmental action to conserve UK ancient forest, than qualitative descriptions of old-growth value.

Chapter 3 investigated the relative biodiversity value of overmature planted broadleaved forest (average age 180 years) and ancient old-growth forest stands (>1000 years of continuity) in the New Forest National Park for ectomycorrhizal fungi (EMF). The investigation found similar richness and composition of EMF in both forest types (Figures 3.1 & 3.2), suggesting that setting aside overmature planted forest is an effective means of conserving EMF communities associated with ancient forests, given temporal continuity in the order of a century. Whilst this is the first study to investigate the importance of ecological continuity for EMF, similar studies have been done for other taxonomic groups. Carpenter et al. (2012) sampled soil, leaf litter and ground macrofauna from ancient and overmature planted forest stands across the New Forest, including many of the forest stands sampled for EMF in Chapter 3, and found that species richness of soil macrofauna did not differ between the ancient and planted forest stands. Species composition was also relatively similar, with a Sorensen index of 0.71 (Carpenter et al. 2012). Similar evidence suggests the same situation for ground flora (Tubbs, 2001). Epiphytic lichen communities, however, differ between overmature and ancient broadleaved stands in the New Forest (Wolsley and Sanderson, unpublished data). Sanderson (1966) showed that 18th century broadleaved plantations that contain fragments of 'pre-inclosure woodland', ancient woodland that existed before plantation formation, hosted considerably richer epiphytic lichen communities than 19th century plantations.

With many taxonomic groups exhibiting similar biodiversity levels in 19th century plantations and ancient old-growth forest stands (with the exception of epiphytic lichens), it is clear that these plantation represent an opportunity to expand networks of old-growth forests in historically deforested and fragmented regions such as the UK. The 19th plantations are currently not managed for timber and the New Forest Design Plan emphasises a policy of non-intervention within them. Furthermore, the majority of the 19th century plantations lie within the New Forest Special Area of Conservation (SAC), Special Protection Area for birds (SPA), RAMSAR and New Forest Site of Special Scientific Interest (SSSI). The SAC management plan also advocates their maintenance but also proposes restoration measures such as facilitating regeneration through protection from over-grazing. Whilst no formal protection measure specific to the ancient old-growth and overmature 19th century broadleaved plantations exists, the future of these forests looks secure via their protection within the National Park (Carpenter et al. 2012). There is promise, therefore, that the New Forest National Park will not lose its biodiversity hotspot status to development.

Despite being secure from development, a number of threats to the maintenance of broadleaved overmature and ancient forest stands have been identified in the National Park. These include over-grazing by high deer and pony densities, climate change, and the complex interactions of these factors (Tubbs, 2001; Carpenter et al. 2012; Martin et al. 2015). The current ASNW structure of the New Forest has been shaped by traditional tree management and past grazing pressures (Grant & Edwards 2008). Beech (*Fagus sylvatica*) arrived in southern Britain by 6000 cal years B.P., and has become a significant component of UK woodlands only in the past few hundred years (Grant and Edwards, 2008). Its expansion was likely initiated by the adoption of wood pasture (Edwards & Grant 2011, Grant & Edwards 2008), and pannage by domestic pigs that favours beech through ground disturbance, necessary for beech seed establishment (Edwards & Grant 2011). Selective removal of oak (*Quercus robur*) from the Forest for naval construction (Flower, 1980; Tubbs, 2001) will also have accelerated beech expansion. Beech is more sensitive to drought and windthrow than oak (Peterken et al. 2012). The current ASNW age structure reflects past fluctuations in grazing pressures and many stands exhibit distinct age classes (*sensu* Peterken & Tubbs 1965): i) the ‘A’ generation containing pollards dating from the 18th century, ii) ‘B’ generation trees established after the Deer Removal Act of 1851, and iii) ‘C’ generation trees originating from a period of reduced grazing pressure due to enclosure between 1935-1955 (Peterken &Tubbs 1965; Grant & Edwards 2008). Today, grazing pressure is higher than ever and is limiting regeneration within the ASNW stands (Grant and Edwards, 2009; Newton, 2010). Furthermore, the expansion of coniferous plantations and farmland throughout the New Forest landscape has led to the isolation of various ASNW woodlands, and a consequent increasing dominance by a single generation of trees and lack of suitable propagules for regeneration (Grant and Edwards 2008). The loss of large, old trees combined with limited regeneration is a major threat to the maintenance of the New Forests ASNWs and their high biodiversity. With basal area being a key driver of EMF richness, for example (Chapter 3; Figure 3.1), continued dieback within the New Forest’s ASNW stands will likely reduce EMF diversity within these stands. Conservation measures designed to sustain basal area and encourage regeneration within set-asides and ancient stands are thus direly needed to sustain the biodiversity of the New Forest’s woodlands.

6.3 Controversies and ambiguities in forest ecology research

Here I highlight several challenges to empirical and synthetic research (the meta-analysis of individual studies) that impede our understanding of the ecological impacts of forest management interventions.

6.3.1 Simple pseudoreplication in empirical research

Hurlbert’s (1984) seminal paper bought to light the issue of pseudoreplication, the lack of independence across replicates. Many forms exist (Figure 6.2), the most common being simple pseudoreplication (Heffner et al., 1996), in which multiple samples from a single contiguous treatment unit are analysed as if they were independent replicates that were interspersed with control replicates (Figure 6.2.B-1). In forest management studies, this can occur when researchers define a hypothesis and collect what they deem to be independent samples from two populations they wish to compare, when in reality the samples are not independent because, for example, each sample is collected from a single contiguous forest patch. To counter simple pseudoreplication, randomised block or systematic designs (Fisher, 1925) offer a tool to ensure that treatment units are interspersed rather than segregated; replication increases the precision of the estimate and randomisation reduces possible bias from other sources of spatial variation.

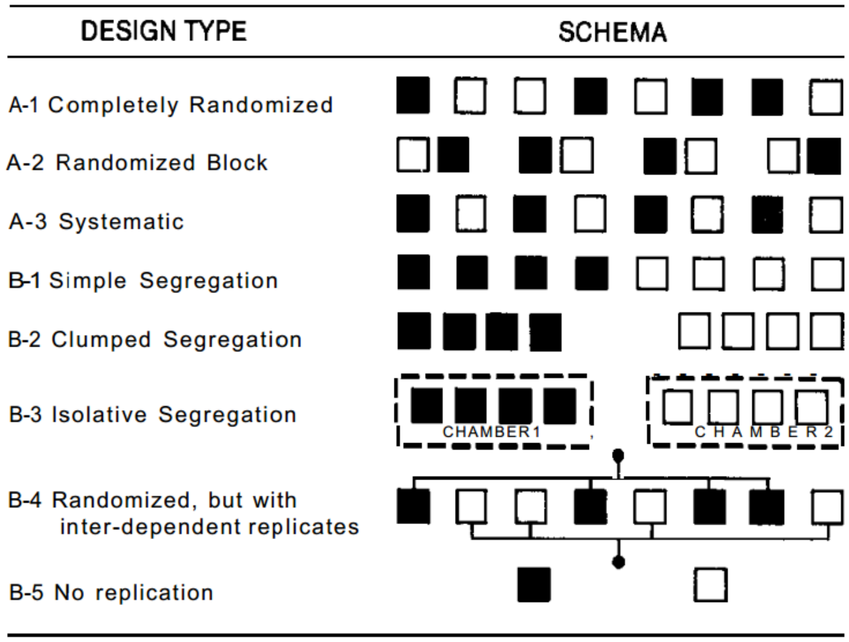

Figure 6.2 Schematic representation of various acceptable modes (A) of interspersing replicates (boxes) of two treatments (shaded, unshaded) and various ways (B) in which the principle of interspersion can be violated. From Hurlbert (1984).

Differences between control and treatment replicates that are simply segregated cannot be unambiguously distinguished from other sources of spatial variation. The inability to disentangle these factors can result in spurious detection of apparent treatment effects or concealment of a real treatment effect (Ramage et al., 2013). Despite the widespread recognition of the problems associated with pseudoreplication, it still features prominently in peer-reviewed ecological studies; Ramage et al. (2013) reviewed recent studies of the effects of logging on biodiversity in tropical forests (n = 77) and found that 68% of the studies were definitively pseudoreplicated, only 7% were definitively free of pseudoreplication, and the remaining proportion could not be clearly categorised due to poor reporting standards of study designs. It is clear that pseudoreplication remains widespread outside of the tropics also (Spake et al. 2015; Chapter 2). Reasons for this include logistical constraints associated with time, cost and study site accessibility

(Ficetola et al., 2008), and the desire to detect significant (albeit spurious) treatment effects, incentivised by publishing pressures (Ramage et al., 2013). Moreover, simple segregation may arise simply because control and treatment stands are not spatially interspersed across a landscape, a common situation when, for example, old-growth control replicates are located within a single contiguous reserve, or only a single restored treatment forest is available due to the great expense of forest restoration.

6.3.2 Simple pseudoreplication in synthetic research

The number of published meta-analyses in forest biodiversity research has increased greatly over the last decade, keeping pace with empircal research in this field (Figure 6.3). Meta-analyses yield generalisations of practical value when they summarise the magnitude and direction of effect sizes that measure the impact of a forest management practise on biodiversity and they attribute variation in these effect sizes to meaningful covariates. Such generalisations can significantly advance the field of applied conservation science. However, potential problems exist in the forest biodiversity meta-analysis literature, relating to the inclusion of studies with pseudoreplicated study designs and uncommon control conditions.

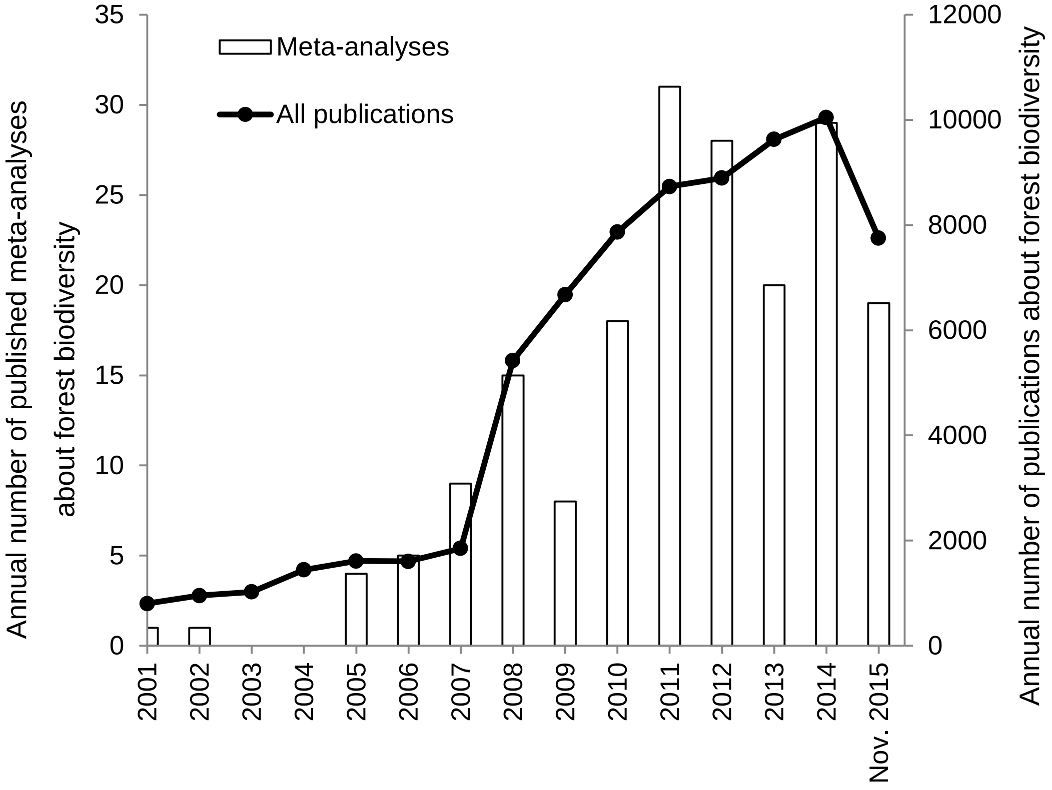

Figure 6.3 Number of articles published per year in the ISI Web of Science containing the search terms ‘forest’ and ‘biodiversity’ (black lines) and also ‘meta-analysis’ (white bars).

The issue of whether to include data from studies that are simply pseudo-replicated in meta-analyses has been discussed by several authors. Halme et al. (2010) criticise a meta-analysis by Paillet et al. (2010) for their inclusion of multiple studies with pseudoreplicated designs and argue that effect sizes from such studies are spurious and should be excluded from synthesis to prevent erroneous inference. On the other hand, several authors actually propose meta-analysis as a solution to the problem of a pseudo-replicated literature, arguing that meta-analysis is a means by which individual studies can be combined and analysed to detect consistent patterns (Hargrove and Pickering, 1992; Cottenie and De Meester 2003; Gray and Davies, 2015). Indeed, univariate directional effects, such as decreases in the species richness across a particular management intervention, are formative collectively (Ramage et al. 2014) and meta-analysis can be seen as statistical tool which effectively replicates the studied systems resulting in valid statements on the population of the type of systems involved (Cottenie and De Meester, 2003). The fact that pseudoreplicated studies are amenable to meta-analysis is of course no excuse for publication of the results of unreplicated experiments that easily could have been replicated, but it is a valuable extra argument for publishing results of studies that report on large-scale experiments that, due to the scale and the complexity of the system, were inherently difficult to replicate (Cottenie and Meester, 2003). Here I argue that the real problem concerning the inclusion of pseudoreplicated relate to how the data are actually synthesised, in terms of i) what effect size is used, and ii) the use of weighting effect sizes when pooling multiple study outcomes.

Meta-analysis expresses the outcome of multiple studies on a common scale, through the calculation of an ‘effect size’, and its corresponding variance, which represents the magnitude of a difference or the strength of a relationship (Koricheva et al. 2013). An effect size that is widely used in ecological meta-analysis is the standardised mean difference (Rosenberg et al. 2013). Standardising continuous response variables by their standard deviation supposedly allows for meaningful comparisons to be made across studies, and is most commonly estimated as Hedges’ d (Hedges and Olkin, 1995):

$$d = J \times ((\bar{x}_{control} - \bar{x}_{treatment})/sd_{pooled}),$$

where $\bar{x}_{control}$ is the mean value of control group, $\bar{x}_{treatment}$ is the mean value of the treatment group, and sd_{pooled} is the pooled standard deviation:

$$sd_{pooled} = \frac{(n_{control} - 1)(sd_{control})^2 + (n_y - 1)(sd_y)^2}{n_{control} + n_y - 2}$$

The conversion factor, *J*, corrects for small sample sizes rendering *d* an unbiased estimator of population effect size (Hedges and Olkin, 1985):

$$J = 1 - \frac{3}{4(n_{control} + n_{treatment} - 2) - 1}$$

Hedges' *d* is often chosen as an effect size measure in ecological studies as it adjusts for differences in sampling effort among studies, corrects for small sample sizes and can handle zero values for control or treatment groups (Rosenberg et al. 2013). However, the magnitude of Hedges' *d* can be difficult to interpret, and Cohen's benchmark is used as a rough estimation with mean effect sizes of $d = 0.2$ indicating a small effect, $d = 0.5$ a moderate effect and $d = 0.8$ a large effect (Koricheva, Gurevitch & Mengersen 2013). A more fundamental, and generally overlooked, consideration is that Hedges' *d* assumes that all contributing studies have the same population variation σ^2, sampled by the square of sd_{pooled}, as well as the same difference between population means $\mu_{control} - \mu_{treatment}$ sampled by $\bar{x}_{control} - \bar{x}_{treatment}$ (C. P. Doncaster, Pers. Comm.) Otherwise each contributing study will have its own true standardized difference between the means, $\delta = (\mu_1 - \mu_2)/\sigma$, estimated by a study-specific *d*, making it pointless to calculate an average *d* across studies as an overall estimate of a single δ. In general for ecological studies (as distinct from the behavioural studies that originally inspired Hedges' *d*), their spatial configuration and geographical distribution will dictate against them having a common σ^2.

A serious problem arises when using Hedges' *d* as an effect size to characterise a collection of studies that include ones that with pseudoreplicated designs. Hedges' *d* requires measures of within-group variance for its calculation, and therefore becomes inflated for pseudo-replicated studies, which typically underestimate the amount of variability of a population. Indeed, the low variation among simply pseudo-replicated replicates arises as an artefact of the study design, whereby replicates are actually interdependent samples of the same species pool (Halme et al., 2010). Effect size metrics that require within-study variability in their calculation should therefore be avoided in ecological meta-analysis.

An effect size that is being increasingly applied in ecological meta-analysis is the log response ratio (*lnR*), representing the proportional difference between control and treatment means:

$$lnR = ln(\bar{x}_{treatment}) - ln(\bar{x}_{control}).$$

Mean *lnR* effect sizes that characterise a population of studies can be back transformed to percentage differences between control and treatment groups, which can be intuitive to non-scientist policy-makers.

The problem of including pseudoreplicated studies in meta-analyses is further exacerbated when the issue of weighting is introduced. Meta-analyses may weight study-wise effect sizes in order to improve the precision of the estimate of overall mean effect and the power of tests (Gurevitch and Hedges, 1999). Effect sizes are commonly weighted by the inverse of within-group variance in order to raise the relative contributions of studies with lower unmeasured variation, on the principle that these will have higher precision (Koricheva and Gurevitch, 2014). The low effect size variance from studies that are simply pseudoreplicated will afford them a relatively high weighting in a meta-analytical model, despite their inferior study design, further inflating mean parameter estimates. In the absence of a suitable measure of within-group variation being provided by primary studies, it may be more appropriate to not weight at all, or weight by sample size on the principle that precision is supposed to increase with sample size, all else being equal. Of course, the *true* sample size should be used, i.e. the number of true replicates instead of the number of within-patch pseudoreplicates (Halme et al. 2010).

6.3.3 Old-growth controls vary amongst empirical and synthetic research

Old-growth forest is a typical reference condition utilised in forest management meta-analyses (Paillet et al. 2010; Curran et al. 2014; Martin et al. 2015; Spake et al. 2015). The definition of old-growth varies considerably across regions, but such forests tend to be native to the region, with features of maturity, old age, primitive origins or lack of disturbance by modern technology (Beadle et al., 2009). It is apparent that the concept of old-growth forest relates most typically to regions where major disturbances are stand-replacing, such as where clear-cutting or catastrophic fires predominate (Franklin et al., 1981). This observation explains why a meta-analysis that used old-growth forest as a control (Chapter 2; Spake et al. 2015), exhibited a paucity of studies from temperate Australia (Figure A.S1), where the vast majority of eucalypts which dominate the Australia's forests survive fire by resprouting from epicormic buds or lignotubers (Lindenmayer, 2009). Furthermore, Japan only contributed one study to this meta-analysis (Chpater 2; Appendix A.S1) and to another pan-global synthesis (Curran et al. 2014), explained by the sparsity of old-growth forest, with the vast majority of Japan's forests having been intensively managed in the past. Forests that have regenerated naturally following disturbance > 80 years previously comprise only 18% of total forest area (FRA, 2010). A common criticism of meta-analysis is that researchers combine different kinds of studies (‘apples and oranges’) in the same analysis, leading to summary effects that ignore important differences across studies (Borenstein et al., 2009). Many studies from Japan and Australia were therefore excluded from Chapter 2’s meta-analysis to allow for a common control across studies so that meaningful inferences could be made. Such discipline is not always practised, however; a meta-analysis by Duguid and Ashton (2013) synthesising the effects of forest management for timber on understory plant species diversity compared treatment stands with either ‘old-growth’ or ‘mature’ controls, as defined by the empirical researchers, that encompassed a very diverse range of ages, land-use and disturbance histories. Effect sizes from studies therefore represented different relationships that were not necessarily comparable. For example, some studies may have compare young plantation with control deemed as ‘old-growth’, whilst others may have compared young plantation with a control deemed an ‘overmature’ plantation. Whilst overmature plantations can support communities present in old-growth forest for some taxonomic groups (e.g. EMF, Chapter 3), many studies have shown that this is not the case for understorey plants (e.g. Peterken, 1974).

The issue of including apples and oranges in the same quantitative synthesis calls into question whether pan-global syntheses are always appropriate. The use of meta-analysis allows one to test whether there is a clear effect of a forest management intervention on biodiversity when examined over a broad region, arguably a valuable exercise regardless of inter-study differences (Duguid & Aston, 2013). However, the real utility of meta-analysis lies in the identification of factors that moderate effect sizes (Koricheva et al. 2013). Whilst mixed-effects meta-regression can be used to attribute variation in study-specific effect sizes to meaningful covariates that vary across studies and regions, not all covariates can be quantified or characterised. For example, whilst the impact of coppice abandonment on biodiversity is a global issue, it might be wrong to conduct a pan-global meta-analysis of the effects of coppice management on biodiversity; coppicing techniques vary widely across regions with regards to rotation period and selection system (Nascimbene et al., 2013) and these differences might not be amenable to be characterisation or quantification into formal covariates. It therefore seemed more appropriate to limit the meta-analysis of the effects of coppice management (‘satoyama’) on biodiversity in Japan to a nation-wide synthesis (Chapter 5).

6.3.4 The use of old-growth forest as a control in empirical and synthetic studies

Empirical studies measuring the biodiversity value of a forest under a particular management regime of interest typically measure value relative to a reference state that has attributes of an undegraded ecosystem (Bullock et al., 2011). This is typically an ‘undisturbed’, ‘natural’, ‘old-growth’ or ‘pristine’ forest. The consistent application of this benchmark should allow for comparability amongst empirical studies, and provide scope for generalisability and synthesis with regards to how forests across the world respond to management and conservation action. Furthermore, comparison with old-growth can yield important information on the ability of the disturbed/managed stands in question to support the communities of this threatened land use, which often contain rare, dispersal-limited species that require long-periods of stand continuity to colonise (Chapter 3). By using old-growth as a control in Chapter 2 to assess the relative value of planted and secondary forests, we demonstrate that old-growth, a declining and threatened land use, is an irreplaceable biodiversity resource owing to the long recovery times of certain taxonomic groups. The findings of this work both advocate their exemption from biodiversity offsetting schemes and support initiatives that protect old-growth through reserve creation.

However, the choice of an undisturbed reference may not always be appropriate; indeed the concept of ‘pristine’ forest may not hold true in an era of pervasive anthropogenic change (Ghazoul et al. 2015). Biodiversity and ecosystem service assessments must produce data relevant to decisions affecting that management regime; and it might be important to know the difference between the biodiversity value of forest under a management regime in its current state compared to a more plausible alternative one (Peh et al., 2013). The alternative state might be a description of a possible future, based on the management question of interest (Peh et al., 2013). For example, true old-growth forests, those that are several centuries old with little recent management intervention, are very rare in Japan. The term ‘old-growth’ is often applied to forests barely older than 100 years in empirical studies in Japan. It is appropriate, therefore, to consider the plausible alternative state of abandoned forests, those that are 100 years old and currently unmanaged, as control forest stands in Japanese empirical studies, as these represent a plausible alternative state to truly old-growth stands.

A second issue with the use of undisturbed old-growth forest as a reference state is the fact that these forests often include legacies of past disturbances of which we have little or no knowledge (Ghazoul et al. 2015). It is possible that old-growth stands themselves may comprise a depauperate subset of the biotic community that was once supported in the past. If this were true, it would be dangerous to generalize results of these studies to other regions where bioiversity has not been diminished in old-growth stands. This is a potential concern for the results of Chapter 3, which compared the biodiversity value of old-growth and overmature planted stands in the New Forest National Park. Indeed, potential threats to ectomycorrhizal communities in the park include nitrogen deposition, past selective tree felling and soil compaction by high herbivore densities (Newton, 2010), which might have diminished diversity in the park. However, New Forest has been designated as an Important Fungus Area by national assessment, due to its high diversity (~2,600 species of fungi across all functional groups and habitat types) have been recorded across the New Forest; Dickson & Leonard 1996), the persistence of populations of conservation concern and the presence of habitats of known mycological importance (Evans, 2001; Newton, 2010).

Even if an empirical study employs a completely randomised design (table 6.2) in which control and treatment forest stand replicates are spatially interspersed, there are still confounding effects that must be acknowledged by such studies, and by any meta-analysis that synthesises data from. For example, for studies on logging impacts on biodiversity, unlogged forest stands are usually located in steep, high elevation sites with generally less fertile soils and lower productivity than logged sites. Such differences are likely to have consequences for stand structure and biotic communities independently of logging, reducing the likelihood of detecting significant harvest impacts on biodiversity (Lindenmayer and Laurance, 2012). Furthermore, logging impacts may be cumulative, over space (Lindenmayer et al., 2011) or time (Lindenmayer and Laurance, 2012), which can be difficult to quantify. For example, low intensity selective logging can have little impact after a single cycle, but repeated logging events might exacerbate biodiversity impacts (Gibson et al., 2011, Woodcock et al., 2011, Edwards et al., 2011, Lindenmayer and Laurance, 2012). Furthermore, it might be true past management intensity in terms of the number of rotations that a stand has experienced is confounded with stand age (younger stand having a higher number of rotations), which may influence the results of meta-analyses that have summarised stand age- biodiversity relationships.

6.3.5 Methodological differences between chapters 2 and 5

Chapters 2 and 5 both used systematic review and meta-analysis to quantitatively synthesise the effects of a forest management intervention on within-sample species richness. The methodological approaches used were quite different, however. Chapter 2 adopted a militant stance towards studies with simply pseudo-replicated study designs on the principle that such studies can yield spurious differences from confounding treatment variation with random site variation, and excluded these studies from the meta-analysis. Upon reflection, this exclusion was perhaps not necessary, because the log response ratio was used as an effect size, and because an unweighted analysis was performed (see 2.8 Chapter 2 Addendum). The inflation of study-wise and population mean effect sizes that can occur as a result of low variances inherent to pseudoreplidated studies was therefore avoided (for the reasons discussed in section 6.3.2). Chapter 5 elected to include pseudoreplicated studies and to weight meta-analyses by sample size, as opposed to the inverse of sample variance, on the principle that larger sample sizes yield more precise effect sizes. Whilst greater replication can yield greater precision in effect size estimates, greater replication does not yield greater accuracy if sampling is biased, e.g. due to spatial segregation of control and treatment samples (Sokal & Rohlf, 1981; Doncaster, pers. comm). The meta-analysis in Chapter 5 may therefore have favoured precision over accuracy. However, because meta-analysis effectively replicates the studied systems, they are unlikely to exhibit a consistent bias across them in terms of the direction and magnitude of an effect. The meta-analysis in itself is likely to yield more accurate population mean effects, compared to individual component studies.

6.4 Landscape-scale effects on stand-level biodiversity are often unaccounted for

Many empirical and synthetic studies, including those in this thesis, may not have sufficiently accounted for the importance of landscape-level factors in determining stand-level biodiversity. EMF communities require long periods of stand continuity for colonisation events to recover richness to old-growth levels (~90 years; Chapter 2; Spake et al. 2015), consistent with strong dispersal limitation. This suggests that landscape-scale factors are likely to be important in structuring EMF communities. Indeed, Peay et al. (2010) found that the EMF richness of single tree ‘islands’ scattered within a grassland matrix in California declined with increasing isolation from large patches of contiguous forests. Landscape-scale variables, such as the proportion of forest area within surrounding landscapes, were not considered as covariates in models explaining EMF variation amongst plots (Chapter 3). Nevertheless, forest blocks, each containing a pair of overmature planted and semi-natural old-growth stands (Chapter 3; Appendix B.S1) were selected to minimise variation of this nature amongst blocks, and stands within a pair were always located no more than 1-km apart. Furthermore, our minimum adequate model containing only stand-scale factors explained a relatively high amount (32%) of the variation in EMF richness among plots (Table 3.1).

The meta-analysis of biodiversity recovery in planted and secondary forests (Chapter 2; Spake et al. 2015) did not account for landscape-level variables in explaining recovery rates. This was principally due to the fact that these data were not available from empirical studies, but also because the taxonomic groups studied are typically responsive to stand-scale management interventions. However, latitude was an important determinant of biodiversity recovery (Table 2.2), where species richness differences between old-growth and planted or secondary forests were greater at lower latitudes. This latitudinal effect might represent variation in landscape configuration with latitude; spatial continuity of forest at the landscape scale is less likely to be a limiting factor for dispersal in widely forested regions such as boreal Fennoscandia, as opposed to other areas in temperate Western Europe where forests have been reduced to smaller remnants (Parviainen et al., 1999). Better reporting standards from empirical studies might allow the consideration of landscape-level variables in future synthetic studies.

The investigation of the abiotic and biotic drivers of carabid functional diversity amongst planted stands across the UK (Chapter 4) included a single landscape-level variable: the percentage of open semi-natural area including farmland, grassland and heathland within a 1-km radius of each plot. Other landscape-level variables were provided by the Forestry Commission's BAP dataset, but they were correlated; with the percentage of forest area declining with increasing open area. Whilst the percentage of open area correlated negatively with carabid body size, this variable was not a strong determinant of carabid functional diversity. Other studies have demonstrated the importance of landscape-level effects in explaining stand-level beetle composition and diversity (Barbaro et al. 2009; Duflot et al. 2014), suggesting that the better characterisation of landscape variables may have revealed their importance in explaining biodiversity variation amongst stands in Chapters 2 and 4.

6.5 Metrics used to evaluate the biodiversity value of a forest

The simplest and most widely used metric to measure biodiversity is species richness (Margurran, 2004). Chapter 2 used species richness as a biodiversity metric to judge the relative biodiversity value of old-growth reference and planted and secondary stands, a choice driven by its consistent use across empirical studies. Using species richness alone as a proxy for biodiversity can be misleading when treating it as a decision variable for setting conservation and management priorities (Lyasheva et al. 2012), as the metric takes no account of the composition of species or functional traits. Whilst Chapter 2 revealed different responses of different functional groups within broad taxonomic groups to disturbance, which vary in their roles in ecosystem functioning, insufficient data were obtained to analyse similarity in species composition amongst control and treatment stands. Compositional analysis would have been useful to explain differences in richness between control and treatment stands and inform landscape-scale management of productive forest landscape through knowledge of beta diversity.

There has been a relatively recent shift towards the use of functional diversity (FD) measures that capture the value, range or distribution of functional traits in a community (hereafter ‘functional diversity’; FD; Hooper et al., 2005, Diaz et al., 2007). It has become apparent that FD is more directly relevant to ecosystem functioning than taxonomic diversity (TD; Hooper et al. 2002; Díaz et al. 2004; Vandewalle et al. 2010). Gagic et al. (2015) compared the relative performance of a range of taxonomic and functional trait-based indices of animal diversity and showed that metrics of FD consistently provided greater explanatory power than species richness or abundance in predicting various ecosystem functions including pollination and pest control. This finding supports the notion that assessments of functional diversity, as proxies for critical ecosystem functions, are used to evaluate the success of restoration programmes (Audino et al., 2014, Aerts & Honnay, 2011).

A multitude of functional trait diversity indices exist (reviewed by Mouchet, 2010), and there is debate over which metric should be used to measure FD (Fountain-Jones, 2014). Gagic et al. (2015) found that functional divergence and functional evenness, which generally measure how niche space is filled, (as opposed to functional richness, showing how *much* niche space is filled), performed best out of all functional diversity metrics. Rao’s quadratic entropy (Rao, 1982; Botta- Dukát, 2005) was used as an FD metric in Chapter 4, due to its widespread use and proven ability to identify habitat filtering mechanisms (de Bello et al., 2009; Moretti and Legg, 2009; Aubin et al., 2013). Rao’s quadratic entropy correlates mathematically with functional divergence (*pers. obs.*; Pakeman et al. 2014; Gagic et al. 2015) and is therefore considered to be a good indicator of ecosystem function.

In addition to indicating levels of ecosystem functioning, incorporating functional traits into diversity measures is thought to increase cross-taxon congruence, as functional traits represent physical interactions with the environment (Moretti and Legg, 2009). However Chapter 4 (Spake et al. 2016) explored bivariate relationships between carabid FD and taxonomic and functional metrics of ground-layer plant FD and found no improvement on the degree of congruence from using functional metrics. The reason for this finding may simply be the fact that in this study system, plant-carabid interactions were not important in structuring carabid beetle assemblages in the first place. Pakeman and Stockan (2014) demonstrated positive correlations between measures of vegetation and carabid FD in an agricultural setting in the UK. In chapter 4, canopy cover was the most important driver of carabid FD in coniferous production forests. It might be possible that plant-carabid interactions are stronger in agricultural settings. Westgate et al. (2015) examined the degree of cross-taxon congruence across multiple taxa in relation to many factors including elevation, distance from equator. They did not investigate the influence of habitat type, however, which might have been of importance.

6.6 Parallels between forest management in the UK and Japan

Forest constitutes just 13% of land area in the UK, whilst it covers around 70% in Japan (FRA, 2010). Despite this huge difference in forest extent, certain parallels exist regarding the nations' forest management histories. Almost all of their forests have been altered by human activities in the past (Bengtsson et al. 2000; Yamaura et al. 2012), and very little old-growth forest remains. Furthermore, the UK and Japan are both nations with high proportions of planted forest relative to their total forested area, with ~80% and ~40% respectively (compared to the global average of 7%; FAO, 2010), and have similarities regarding the traditional uses of broadleaved forest resources within rural landscapes (Rackham, 2003).

Whilst Japan has satoyama forests that have been managed by clearcutting and coppicing since as early as the Jōmon period (10500–400 BC (Washitani, 2003) , the UK and many areas in Europe also have a long history of coppice management that has been traced back to the Neolithic Period (4000 - 2500 BC; Simmons , 1997). In both countries, broadleaved forests that bordered human settlements were traditionally managed for millennia by coppicing for fuelwood and food (Knight, 2010). In Japan, predominant coppice species include oak (*Quercus serrata*, *Q. acutissima*) and pine (*Pinus densiflora*), whilst in the UK, sweet chestnut (*Castanea sativa*), hazel (*Corylus avellana*), and hornbeam (*Carpinus* *betulus*), are the main coppice species, often combined with an overstorey of oak species (*Q. robur, Q. petraea*). Management of these forests in the UK, Japan and around the world largely ceased in the mid-1900s as fossil fuels become widely available (Kirby, 2000; Nagaike, 2003), leading to ageing forest mosaics in many places (Fukamachi et al. 2011). The ageing of coppice forests is regarded as a driver of biodiversity loss, particularly for early successional species, due to reduced habitat suitability for species requiring open habitats or complex low vegetation structures that are reduced under heavily shaded conditions (Benes et al. 2006; Kopecky et al. 2013).

Efforts to revive coppice management have increased over the last two decades in Japan, the UK and Europe (European Parliament, 2009; Takeuchi, 2003). There are several motives for this revival. Temperate and boreal forests are now viewed as major sources of energy (Fuller, 2013). Within the European Union, there is considerable potential for increasing forest biomass production (European Environment Agency 2006; Verkerk et al. 2011a) and all countries have renewable energy action plans. For example the Woodfuel Strategy for England aims to generate an additional two million tonnes per annum from 'under-managed woodland' by 2020 (Forestry Commission 2007). Other objectives include improving their aesthetic, cultural and biodiversity values (Knight, 2010; Indrawan, 2012). Whilst many early successional species might benefit from active coppice management, it is important to recognise that coppicing techniques vary widely with regards to rotation period and selection system, and the effects of management intensity on biodiversity are still poorly understood (Nascimbine et al. 2013). In a meta-analysis of the impact of coppice management on biodiversity in Japan (Chapter 5) it was found that biodiversity responses to clear-cutting and ageing of secondary forests were highly variable across taxonomic groups. Butterflies and moths tended to exhibit higher richness and abundance in younger secondary forest that has been clearcut recently. For ground-layer plants, another group that are thought to benefit from coppice management, effect sizes characterising species richness differences between abandoned, >100 year-old forests stands and young clear-cut were highly variable and ranged from positive to negative (Figure 5.5). This suggests that there are several factors, likely site-specific, that moderate the impact of this management intervention on biodiversity. Such factors are perhaps difficult to quantify or categorise and were therefore not modelled.

Modern approaches to forest biodiversity conservation are also similar across the UK and Japan. The EU emphasises the importance of ecological networks of protected areas connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules (Lawton et al. 2010; Humphrey et al. 2015). Japan’s National Biodiversity Strategy also recognises that restoring well-connected ecological networks is essential for implementing biodiversity conservation in urbanized lowlands of Japan, where fragmented forest remnants in the precincts of shrines and temples are scattered among residential areas, rice paddies and farmland.

It is clear that measures for protection and the level of intervention within set-aside forest varies considerably among countries. In North Europe and in some Eastern European countries, where vast areas are untouched by large-scale forestry and vegetation is shaped primarily by small scale internal dynamics, restrictive protection with little or no intervention dominates. In Central and Southern European countries however, remaining biodiversity values are legacies of past disturbance regimes that nowadays are suppressed, and active management in protected areas is emphasised (Bernes et al. 2014). The intensity of intervention varies from the removal of invasive species, blocking drainage ditches to herbivore exclusion and prescribed burning. In UK ancient woodlands that are managed for multi-use values other than production, management interventions include understorey thinning for its positive impacts on ground vegetation biodiversity and aesthetic and recreational benefits (Forestry Commission, 2010). Herbivore exclusion by temporary fencing or culling is practised in areas with high deer densities to allow for regeneration. Over-browsing by deer is also of high concern in Japan (Ohasi et al. 2014), where similar interventions are taking place. However the active management of satoyama secondary multi-use forests is more intensive than in UK ancient and set-aside woodlands. In Japan, management by local governments outside of national park areas is limited due to insufficient budgets and ecological knowledge (Tsuchiya et al., 2014, Tsuchiya et al., 2013) and local voluntary community groups have recently been recognised as playing an important role in the traditional management of satoyama landscapes. Today late successional evergreen broadleaved forests are cleared in many areas to allow for the regeneration of early successional pine species, under which species of edible mushrooms that local people are familiar with are common (K. Kitayama, pers. comm.).

The difference in management intensity in non-production forest between Japan and the UK may largely reflect differences in eastern and western perceptions of nature. Cultural studies have shown that members of Western societies tend to show preference towards pristine, untouched nature, valuing natural habitats for their intrinsic meaning, whereas members of Eastern societies have a tendency to prefer a managed look of forests and view nature and humans as part of an interlinked stewardship (Kellert 1991; Lindemann-

Matthies et al. 2013). It is clear that culture can play a major role in shaping the biodiversity and composition of ecosystems. Fukamachi et al. (2011) studied hedgerows in a suburban landscape in western Japan and found that hedgerows in areas where traditional satoyama management was still practiced by local people differed in composition than those found in areas where management had been abandoned, with the former containing a higher percentage of native species.

6.7 Conclusions

Halting biodiversity loss is one of the greatest challenges faced by humanity. The Aichi Biodiversity Targets, which were adopted at the 10th Conference of the Parties (COP) of the Convention on Biological Diversity (CBD) represent the strongest global commitment to this challenge. For forest ecosystems, which contain over 80% of global terrestrial biodiversity, halting the decline in biodiversity and ecosystem function requires their i) restoration, ii) sustainable management as multi-funcitonal ecosystems and iii) the formation of well-connected systems of protected areas. Policy governing the conservation and management of the world's forests must be informed by a rigorous and comprehensive evidence base (Pullin and Knight, 2003). Despite this now universal recognition, this is frequently not the case, even in wealthy countries (Chapter 5), and major knowlegde gaps exist in the evidence base supporting forest management (Chapters 2 and 5). This thesis has addressed several knowledge gaps that exist in the evidence base supporting forest management and conservation in temperate and boreal regions through a series of case studies. This research has shown that whilst old-growth forests, with their long temporal continuity and high structural diversity, support highly diverse biotic communities therefore warranting strict protection (Chapter 2), other forest types can support considerable biodiversity and therefore merit attention for their conservation potential (Chapter 2 and 3). Young forests that have been established through restoration, plantation or that have regenerated naturally are generally less rich than old-growth forests in many forest-dependent functional groups (Chapter 2), but they can host very different communities (Chapters 2, 4 and 5), which are more species-rich for some functional groups, particularly open-habitat specialists (Chapters 2 and 5). Landscape-scale approaches to the management of forest mosaics must therefore include both young and old-growth forest to support the maintenance of biodiversity at the landscape scale (Chapter 2 and 5), as the colonisation of young, open sites is a key process maintaining the diversity of open-habitat species in afforested areas (Chapter 2 and 5). Whilst the setting aside of old forest stands for the conservation of biodiversity that were initially established for production can be an effective means for supporting comunities associated with old-growth forest (Chapters 3 and 5), a threatened and globally declining land use, other forest types will need management intervention, such as repeated thinning, to enhance biodiversity (Chapter 5). By investigating variation in the diversity of EMF and carabid communities in forest stands that vary in environmental conditions imposed by management (Chapters 3 and 4), this research has identified appropriate management interventions within both non-production and production forests can enhance their biodiversity. However, not all forest communities will benefit from the same management intervention. For example, whilst high levels of canopy cover are beneficial for EMF richness (Chapter 3), the functional diversity of carabid communities might be compromised by management that sustains high canopy cover (Chapter 4). Management inerventions within particular forest stands will therefore need to choose the appropriate management strategy for the functional groups that require conservation attention, which itself is dependent on a range of factors including the surrounding landscape, stand management history, and the other functions and goods required from that stand.

6.8 References

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Appendices

Appendix A Supporting Information for Chapter 2

Appendix A.1 - Keywords used for search in ISI Web of Knowledge

Relevant studies were identified through computerised searches in the ISI Web of Science database. The finalised search query performed on 10 March 2015 was:

TS = (fung* OR macrofung* OR myco* OR wood-decay OR sapro* OR parasit* OR pathogenic* OR ectomycorrhiz* OR arbusc* OR endomycorrhiz* OR mycorrhiz* OR basidiomyc* OR ascomyc OR lichen* OR cyanobacteria* OR epiphyt* OR coleoptera* OR beetle OR carabid* OR saproxylic OR ground-beetle)

AND

TS = (forest* OR woodland OR wooded)

AND

TS = (richness OR divers* OR biodivers*)

AND

TS = (ancient OR old-growth OR primary OR virgin OR pristine OR mature OR remnant OR “ecological continuity” OR “habitat continuity” OR “forest continuity” OR “environmental continuity” OR “historical continuity” OR “stand age” OR “forest age” OR chronosequence OR succession* OR plantation* OR secondary OR clear-cut* OR clearcut* OR clear-fell* OR clearfell* OR afforest* OR “planted forest” OR “forest cycle” OR stand structur* OR multi-age OR “multiple aged” OR “demographic transition” OR “canopy closure” OR “stem exclusion” OR “over mature” OR “stand initiation” OR “understorey reinitiation” OR “pole stage” OR pre-thicket OR mid-rotation OR rotation)

NOT

TS = (mangrove OR bushland)

Appendix A.2 – Studies included in the analysis

Baker, S. C. 2006. A comparison of litter beetle assemblages (Coleoptera) in mature and recently clearfelled Eucalyptus obliqua forest. Australian Journal of Entomology 45:130-136.

Boudreault, C., Y. Bergeron, S. Gauthier, and P. Drapeau. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 32:1080-1093.

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Countess, R. E., B. Kendrick, and J. A. Trofymow. 1998. Macrofungal diversity in successional Douglas-fir forests. Northwest Science 72:110-112.

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

Johansson, T., J. Hjalten, J. Hilszczanski, J. Stenlid, J. P. Ball, O. Alinvi, and K. Danell. 2007. Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: Implications for conservation strategies. Forest Ecology and Management 242:496-510.

Jukes, M. R., A. J. Peace, and R. Ferris. 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.

Junninen, K., M. Simila, J. Kouki, and H. Kotiranta. 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29:75-83.

Kranabetter, J. M., J. Friesen, S. Gamiet, and P. Kroeger. 2005. Ectomycorrhizal mushroom distribution by stand age in western hemlock - lodgepole pine forests of northwestern British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35:1527-1539.

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Marmor, L., T. Torra, L. Saag, and T. Randlane. 2011. Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. Ecological Indicators 11:1270-1276.

McGeoch, M. A., M. Schroeder, B. Ekbom, and S. Larsson. 2007. Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures. Diversity and Distributions 13:418-429.

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Paquin, P. 2008. Carabid beetle (Coleoptera : Carabidae) diversity in the black spruce succession of eastern Canada. Biological Conservation 141:261-275.

Radies, D. N., and D. S. Coxson. 2004. Macrolichen colonization on 120-140 year old Tsuga heterophylla in wet temperate rainforests of central-interior British Columbia: a comparison of lichen response to even-aged versus old-growth stand structures. Lichenologist 36:235-247.

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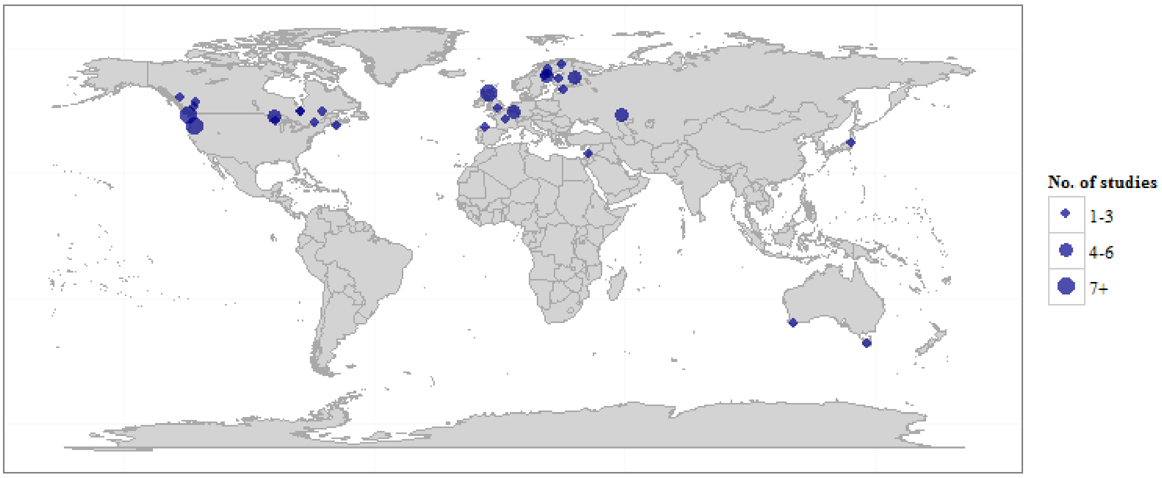
Taboada, A., D. J. Kotze, R. Tarrega, and J. M. Salgadoa. 2008. Carabids of differently aged reforested pinewoods and a natural pine forest in a historically modified landscape. Basic and Applied Ecology 9:161-171.

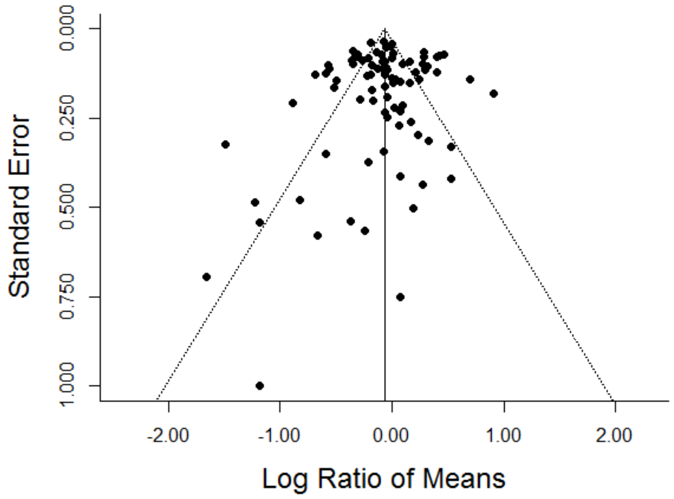
Timm, A., J. Buse, T. Dayan, W. Hardtle, T. Levanony, and T. Assmann. 2009. At the interface of historical and present-day ecology: ground beetles in woodlands and open habitats in Upper Galilee (Israel) (Coleoptera: Carabidae). Zoology in the Middle East 47:93-104.

Twieg, B. D., D. M. Durall, and S. W. Simard. 2007. Ectomycorrhizal fungal succession in mixed temperate forests. New Phytologist 176:437-447.

Appendix A.3 - Distribution of studies used in the analysis. Point size represents the number of studies per 4 degree grid cell.



Appendix A.4 - Funnel plot of the log response ratio and standard error of the entire dataset. An absence of publication bias is indicated by a symmetric funnel with larger spread at smaller sample sizes; the variation around the effect size should decrease as sample size increases.



Appendix A.5 – Rationale for unweighted regression

Here we detail issues with weighting our meta-regressions to improve precision, which may arise frequently in ecological experimental design.

In weighting by the inverse of within-group variance, the variance calculation depends on whether studies have completely randomised or matched designs (Borenstein et al. 2009; Lajeunesse 2011). Our meta-analysis included both completely randomised designs and matched designs in the form of randomised block or systematic designs sensu Hurlbert (1984). For a control group of old-growth forest and a treatment group of restored forest, the effect-size variance is estimated from group means $\overline{xi}$, standard deviations si, and sample sizes ni. The variance estimate for a completely randomised study design is: . $Var_{\ln R} = s_1^2 \big/ \left(n_1 \bar{x}_1^2\right) + s_2^2 \big/ \left(n_2 \bar{x}_2^2\right)$. The variance estimate for a matched study design requires a further subtraction from this estimate, of an amount equal to $2rs_1s_2 / \left(\bar{x}_1\bar{x}_2 n\right)$, where *r* is the coefficient of correlation between control and treatment measurements (Lajeunesse 2011). Randomised blocks or systematic groups that contain old-growth and secondary forest stands generally have low replication in ecological studies, due to the time and expense demanded by biodiversity surveys. Studies for our meta-analysis frequently reported replications of two and three matches (i.e. randomised blocks or systematic pairs) of old-growth and restored forests. Such low sample sizes make for nonsense estimations of r, and consequently of variances, for matched designs. In practice, incorporating these nonsense estimates for matched designs has the effect of reducing variance by orders of magnitude. Excluding studies with matched designs from the analysis, however, would greatly reduce the sample size of the meta-analysis (56 out of the 90 studies had matched study designs).

In meta-regression with weightings on sample size or variance, the presence of large-sample outliers can substantially influence parameter estimates (Fuller & Hester 1999). Discarding them from the analysis has the unsatisfactory consequence of a substantial decrease in power due to losing the studies most likely to have highest precision (Fuller & Hester 1999).

In lieu of excluding studies for want of more information on observed or expected variance, we set stringent criteria for including studies in the meta-analysis, based on the quality of their designs with respect to distinguishing treatment effects from unmeasured variation. Meta-analyses in ecology frequently use unweighted effect sizes, particularly in the absence of satisfactory measures of observed or expected variance (Benayas et al. 2009; Koricheva & Gurevitch 2014; Martin et al. 2013; Moreno-Mateos et al. 2012; Putz et al. 2012).Cardinale et al. (2006) and Marvier et al. (2007) found little difference between the results of weighted and unweighted meta-analyses. Unweighted meta-regression is often more robust, because it does not use potentially misleading estimation of error variances (Fletcher & Dixon 2012).

Appendix A references

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. Science 325:1121-1124.

Borenstein, M. B., L. V. Hedges, J. P. T. Higgins, and H. R. Rothstein 2009. Introduction to Meta-Analysis. John Wiley & Sons, Ltd, Chichester, UK.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989-992.

Fletcher, D., and P. M. Dixon. 2012. Modelling data from different sites, times or studies: weighted vs. unweighted regression. Methods in Ecology and Evolution 3:168-176.

Fuller, J. B., and K. Hester. 1999. Comparing the sample-weighted and unweighted meta-analysis: An applied perspective. Journal of Management 25:803-828.

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Lajeunesse, M. J. 2011. On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92:2049-2055.

Martin, P. A., A. C. Newton, and J. M. Bullock. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B-Biological Sciences 280.

Marvier, M., C. McCreedy, J. Regetz, and P. Kareiva. 2007. A meta-analysis of effects of Bt cotton and maize on nontarget invertebrates. Science 316:1475-1477.

Moreno-Mateos, D., M. E. Power, F. A. Comin, and R. Yockteng. 2012. Structural and Functional Loss in Restored Wetland Ecosystems. Plos Biology 10.

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Appendix B Supporting Information for Chapter 3

Appendix B1 – Locations of the seven pairs of ancient and overmature planted forest stands, and sampling design within locations

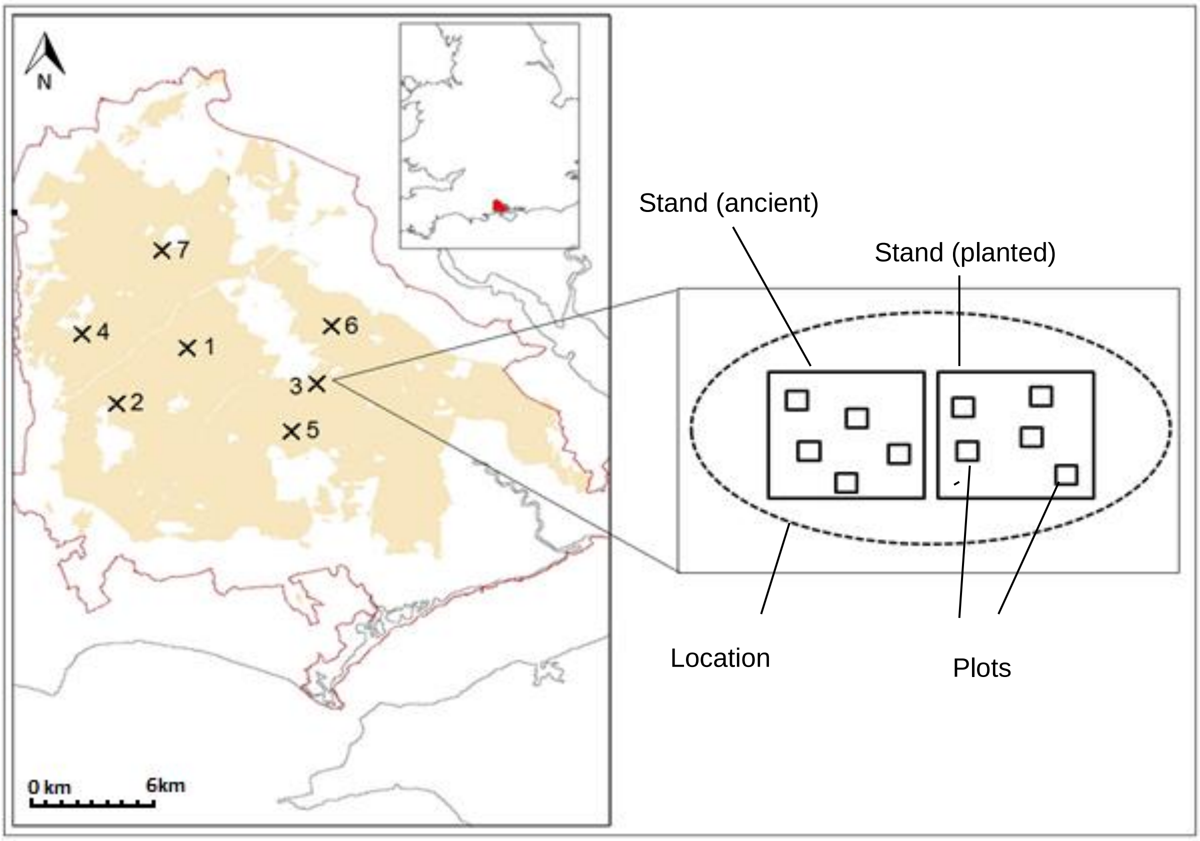

Figure B1.1. Simplified map of New Forest National Park in southern England (inset) showing the distribution of locations (×) across the forested area (coloured) and the arrangement of plots nested in stands nested in each location. Each location consisted of an ancient old-growth and a planted stand, each with five randomly stratified sampling plots, 10×10-m in size.

Appendix B

Table B1.1. Details of forest stands used in this study.

Location	Site name	Stand age / years*	Forest type[§]	Lat,Long
1	Mark Ash Wood	10^4	A	50° 52.065', -1° 39.433'
	Bolderwood Grounds	182	P	50° 52.149’, -1°39.387’
2	Berry Wood	10^3	A	50° 50.826', -1° 41.839'
	South Oakley	160	P	50° 50.671', -1° 41.558'
3	Brinken Wood	10^3	A	50° 50.796', -1° 36.217'
	Hursthill	204	P	50° 50.488', -1° 35.681'
4	Redshoot Wood	10^3	A	50° 52.516', -1° 44.097'
	Great Linford	164	P	50° 52.432', -1° 44.366'
5	Whitley Wood	10^3	A	50° 51.099', -1° 34.589'
	New Park Plantation	192	P	50° 50.771', -1° 35.318'
6	Rushpole	10^3	A	50° 53.244', -1° 33.748'
	Ironshill	192	P	50° 53.397', -1° 33.149'
7	Anses	10^3	A	50° 54.703', -1° 40.517'
	South Bentley	225	P	50° 54.867', -1° 40.206'

[§] A: ancient, P: overmature planted

*Planted forest stand ages were established from records of planting in Forestry Commission management plans. Ancient stand ages were estimated from historic maps and consultation with local experts.

NB: the ancient stand from location 2 and the planted stand at location 7 were excluded from the analysis after the PCA of soil chemistry revealed unrepresentative soil conditions within these plots in extreme outliers of EMF richness.

Details of plantation site preparation procedures in the 1800s in the New Forest National Park

When ageing a planted forest stand, it is important to consider the methods of plantation establishment. Does the disturbance involved in establishing the plantation constitute a re-setting of forest age? The answer to this depends on the species in question. From an ectomycorrhizal fungal point of view, clear-felling a forest prior to replanting involves the removal of its symbiotic host in a mutualistic relationship, in which the fungus is obligately dependent on the tree host. Clear-felling a site is a major disturbance and therefore constitutes a break in continuity, resetting the age of the forest stand for the ectomycorrhizal fungal (EMF) community. The age of a plantation therefore corresponds to the time since the site stand was replanted if the site was clear-felled.

Details relating to the procedure of inclosure formation (i.e. whether sites were completely clear-felled or not) are patchy and incomplete. There are some forestry records available, including Annual and Triennial Reports of the Comissioners of the Woods, Forests and the Land Revenues of the Crown. The general consensus is that the 19th century plantations made between 1800 and the 1850 (prior to the Deer Removal Act 1851), were clearfelled when formed as a matter of policy (Sanderson 2007). A letter addressed to the Commissioner of Woods, dated 05/12/1816, and titled “Instructions for sundry works to be executed in the New Forest” from Mr Turner, the Deputy Surveyor of the New Forest, sheds some light on the site preparation procedure following the clear-felling of a site. Mr Turner instructs:

> *“to dig a trench the ground in beds of about six feet wide each so thrown up as to leave a trench on each side for carrying off the water and leaving a space of about four and a half feet undug between each bed, to plant on the beds that one dug on trenched two rows of trees at the distance of four feet apart in a proportion of about two thirds of strong 4 or 5 year old Oak Plants and one third of Fin Sanch or other fast growing trees best calculated for shelter”.*

There is evidence of the formation of these trenches in several of the plantations in this study, including Bolderwood Grounds, Great Linford Inclosure, New Park Plantation, Ironshill Inclosure and South Oakley Inclosure. The digging of such trenches and associated upturning of the soil would constitute a major disturbance to EMF fungal communities and essentially re-set the age of the forest stand once replanting had occurred.

Appendix B2 – Details of important environmental variables measured in each plot.

Table B2.1 Stand-level environmental variables used explanatory variables in models explaining variation in EMF richness. Mean values (and SD) across five 10-m × 10-m plots are given*. See methods for variable descriptions.

Location	Forest type	Basal area / m^2	Understory richness	Canopy closure / %	Tree diversity
1	SN	102.2 (5.37)	2.80 (0.45)	84.4 (4.59)	0.73 (0.13)
	P	97.55 (14.11)	5.00 (2.12)	74.4 (9.72)	0.61 (0.35)
2	SN	111.37 (3.59)	4.20 (2.49)	86.06 (4.80)	0.43 (0.40)
	P	92.72 (7.04)	5.20 (2.95)	78.16 (9.98)	0.39 (0.22)
3	SN	98.20 (5.23)	6.00 (2.12)	72.75 (4.96)	0.16 (0.21)
	P	95.01 (6.83)	3.20 (2.17)	77.95 (5.27)	0.02 (0.03)
4	SN	114.16 (5.67)	8.6 (1.14)	83.77 (4.74)	0.42 (0.33)
	P	100.96 (7.22)	5.40 (3.13)	80.45 (3.84)	0.05(0.01)
5	SN	95.92 (10.16)	2.60 (0.89)	83.57 (6.95)	0.62 (0.24)
	P	97.22 (7.14)	5.00 (1.58)	83.15 (6.76)	0.65 (0.24)
6	SN	83.80 (10.67)	4.40 (1.52)	73.58 (8.53)	0.21 (0.15)
	P	99.39 (9.5)	4.20 (0.45)	80.90 (5.49)	0.12 (0.21)
7	SN	100.49 (15.72)	4.8 (2.17)	80.45 (11.09)	0.88 (0.22)
	P	110.21 (9.97)	2.8 (1.48)	83.57 (8.17)	0.61 (0.13)

*Basal area and tree diversity measurements are from 30-m × 30-m plots (see text).

Appendix B3 – Species accumulation curves at plot- and stand-levels

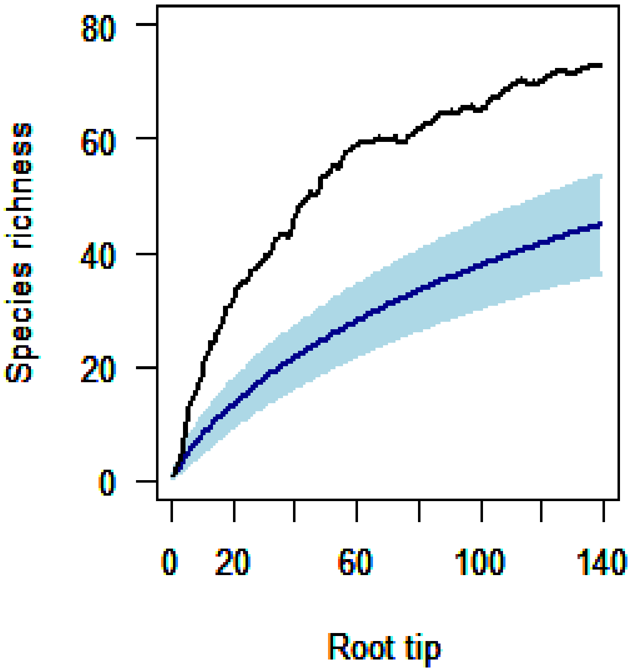

Figure B3.1. Species accumulation curves using root-tip sequence data for a planted stand (Location 1). Black = Chao1 non-parametric richness estimator; blue = mean rarefied richness (±CI) where root tips were sampled randomly without replacement using 100 permutations of the data.

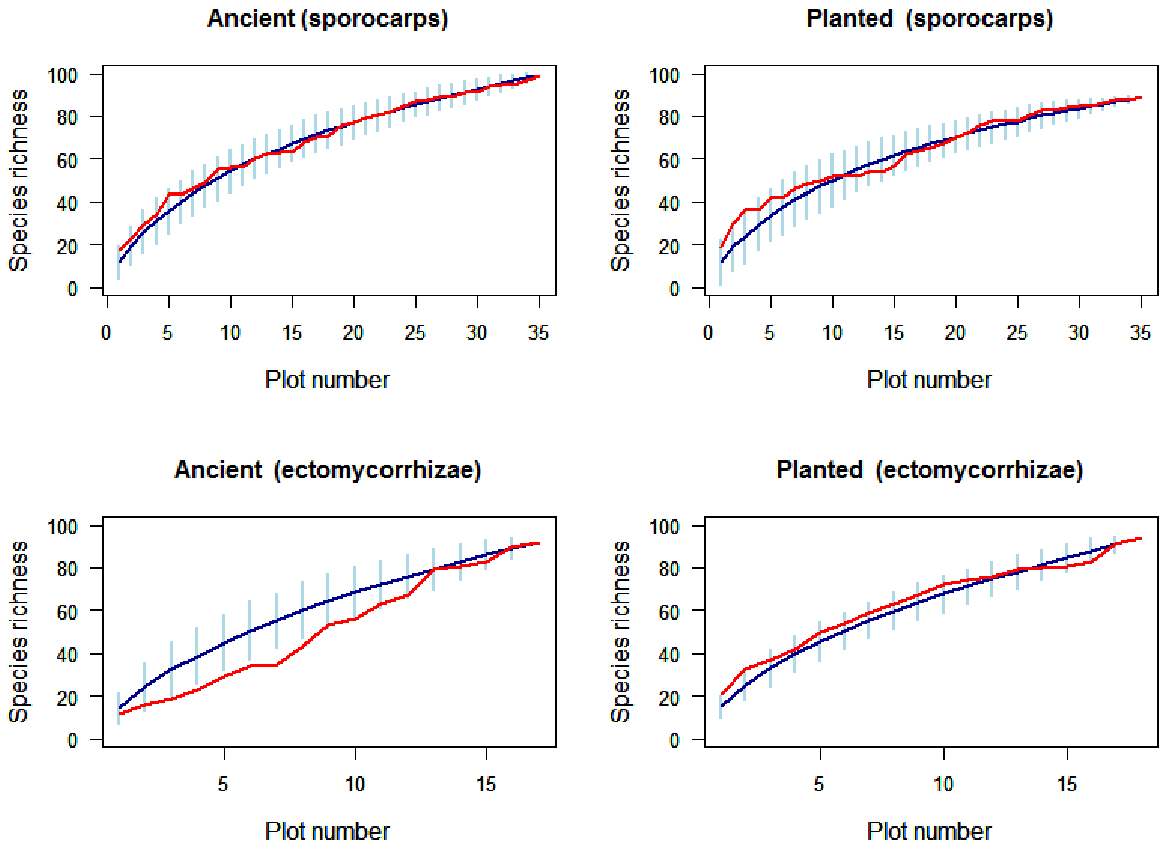

Figure A3.2. Species accumulation curves for all planted and ancient forest plots using above-ground (sporocarp) and below-ground (ectomycorrhizae) data. Blue = mean rarefied richness (±CI), with plots sampled randomly without replacement using 100 permutations of the data; red = by order of collection.

Appendix B4 – Lists of species recorded in this study and their ranked abundance distributions.

Table B4.1. The 225 species recorded as ectomycorrhizae and sporocarps in this study, with the number of plots that they were observed in.

	Number of plots that the species occurred in			
	Ancient forest		Planted forest	
Species	Ectomycorrhizae	Sporocarps	Ectomycorrhizae	Sporocarps
Amanita citrina var. alba	0	1	0	2
Amanita citrina	2	9	0	12
Amanita constricta	0	0	1	0
Amanita fulva	1	2	1	0
Amanita muscaria	0	1	0	0
Amanita phalloides	0	1	0	0
Amanita rubescens	6	7	3	11
Amanita rubescens var. annulosulphurea	0	1	0	1
Amanita vaginata	0	0	0	2
Ascomycota sp.1	1	0	0	0
Ascomycota sp.2	1	0	0	0
Ascomycota sp.3	0	0	1	0
Ascomycota sp.4	0	0	1	0
Boletus aereus	0	0	0	1
Boletus aestivalis	1	0	0	0
Boletus appendiculatus	1	0	1	0
Boletus badius	0	1	0	3
Boletus chrysenteron	0	1	0	0
Boletus edulis	0	5	1	1
Boletus erythropus	2	3	0	1
Boletus pulverentus	0	0	0	2
Cenococcum geophilum	8	0	11	0
Chaetosphaeria sp.1	0	0	1	0
Clavulina cinerea	2	0	2	0
Clavulina sp.1	0	0	1	0
Clavulina sp.2	0	0	1	0
Clavulina sp.3	1	0	0	0
Cortinarius acutus	0	2	0	2
Cortinarius alboviolaceus	0	3	0	3

Cortinarius anomalus	0	0	2	0
Cortinarius anthracinus	0	1	0	1
Cortinarius bolaris	0	0	0	1
Cortinarius brunneus	0	1	0	3
Cortinarius croceus	0	0	0	1
Cortinarius decipiens	0	9	0	5
Cortinarius delibutus	0	1	0	0
Cortinarius diasospermus	2	0	3	0
Cortinarius duracinus	0	3	0	1
Cortinarius duracinus var. raphanicus	0	0	1	0
Cortinarius elatior	0	2	0	1
Cortinarius flexipes	2	1	2	10
Cortinarius flexipes var. flabellus	0	1	0	0
Cortinarius flexipes var. inolens	0	3	0	1
Cortinarius hemitriccus	0	0	0	2
Cortinarius hinnuleus	0	0	1	1
Cortinarius incisus	1	0	0	0
Cortinarius mucifluoides	0	6	0	4
Cortinarius obtusus	0	0	1	1
Cortinarius ocroleucus	0	1	0	0
Cortinarius orellanus	0	1	0	0
Cortinarius paleaceus	0	1	0	4
Cortinarius phaeosmus	0	0	0	1
Cortinarius purpurascens	0	0	0	1
Cortinarius rigens	0	1	0	0
Cortinarius rubellus	0	0	1	0
Cortinarius sanguineus	2	4	0	8
Cortinarius sp.1	1	0	0	0
Cortinarius stillatitius	1	0	0	0
Cortinarius torvus	0	1	0	0
Cortinarius valgus	0	0	1	0
Cortinarius violaceus	0	1	0	0
Cortinarius xanthocephalus	0	1	0	0
Craterellus tubaeformis	0	2	1	3
Dermataceae sp.1	0	0	1	0

Elaphomyces muricatus	7	0	12	0
Entoloma conferendum	0	0	1	0
Exidia sp.1	2	0	2	0
Exidiopsis plumbescens	0	0	1	0
Genea hispidula	3	0	0	0
Gyroporous castaneus	0	0	0	1
Hebeloma birrus	0	5	0	5
Hebeloma crustuliniforme	0	1	0	4
hebeloma edurum	0	1	0	0
Hebeloma hiemale	0	1	0	0
Hebeloma mesophaum	0	8	0	7
Hebeloma pumilum	0	2	0	1
Hebeloma theorbrominum	0	1	0	0
Heliotales sp.1	1	0	0	0
Heliotales sp.2	0	0	1	0
Helotiaceae sp.3	0	0	1	0
Helotiales sp.4	0	0	1	0
Helotiales sp.5	1	0	0	0
Helotiales sp.6	0	0	1	0
Hyaloscyphaceae sp.1	1	0	1	0
Hydnum repandum	0	3	0	2
Hydnum rufescens	2	7	1	1
Hydnum sp.1	1	0	0	0
Hydronata tulasnei	4	0	3	0
Ilyonectria sp.1	1	0	0	0
Inocybe assimilata	1	0	0	0
Inocybe cookei	0	1	0	0
Inocybe fastigiata	0	1	0	0
Inocybe languinosa	1	0	2	0
Inocybe napipes	1	1	1	2
Inocybe pudica	0	0	0	1
Laccaria amethystina	9	22	11	29
Laccaria bicolor	0	4	0	10
Laccaria laccata	3	14	5	18
Laccaria proxima	4	3	1	6
Laccaria tortilis	0	2	0	0
Lactarius blennius	1	3	2	1

Lactarius camphoratus	5	6	7	6
Lactarius chrysorrheus	4	14	9	14
Lactarius decipiens	0	2	0	2
Lactarius evosmus	0	4	0	5
Lactarius flexuosus var roseozonatus	0	2	0	0
Lactarius fulvissiumus	0	11	0	10
Lactarius lapponicus	1	0	0	0
Lactarius quietus	16	27	18	25
Lactarius rufus	0	2	0	2
Lactarius serifluus	4	1	3	2
Lactarius sp.1	1	0	0	0
Lactarius subdulcis	5	5	0	4
Lactarius subdulcis	0	0	0	0
Lactarius subumbonatus	0	4	0	2
Lactarius tabidus	14	27	12	28
Lactarius volemus	0	2	0	0
Leccinum auranticaum	0	0	0	1
Leccinum scabrum	0	2	0	0
Leohumicola minima	0	0	1	0
Leotia lubrica	1	0	0	0
Leotiomycetes sp.1	1	0	0	0
Mortierella gemmifera	0	0	1	0
Mortierella humilis	1	0	0	0
Naucoria bohemica	0	1	0	0
Neobulgaria pura	1	0	0	0
Oidiodendron sp. 1	1	0	4	0
Oidiodendron sp.2	0	0	4	0
Oidiodendron sp.3	0	0	1	0
Pachyphloeus sp.1	0	0	1	0
Paxillus involutus	0	2	0	6
Peziza sp. 1	7	0	4	0
Pezizal sp. 2	0	0	3	0
Phialea sp.2	0	0	1	0
Phialea sp.1	1	0	0	0
Pseudocraterellus sp.1	1	0	1	0
Pseudomentella sp.2	1	0	3	0
Pseudotomentella tristis	1	0	0	0
Russula adusta	0	1	0	0

Russula aeruginea Fr.	0	1	0	1
Russula amoenolens	0	0	4	0
Russula anthracina	1	1	1	3
Russula aquosa	0	0	0	1
Russula atropurpurea	5	6	7	2
Russula betularum	0	0	0	1
Russula brunneoviolacea	0	1	2	1
Russula citrina	1	0	1	0
Russula cyanoxantha	1	7	1	7
Russula cyanoxantha forma pelteraui	0	1	0	0
Russula cyanoxantha var. variata	0	1	0	1
Russula densifola	4	6	5	4
Russula farinipes Romell.	0	5	0	3
Russula fellea	2	6	1	6
Russula fragilis	10	13	8	9
Russula graveolens	1	0	2	0
Russula heterophylla	1	0	0	0
Russula langei	0	1	0	0
Russula lutea	0	1	0	0
Russula luteotacta	0	2	0	0
Russula mairei	5	0	5	0
Russula nigricans	3	8	1	6
Russula noblis	0	9	0	9
Russula ochroleuca	9	16	13	21
Russula odorata	0	0	0	1
Russula parazurea	0	0	3	0
Russula pelargonium	0	2	0	1
Russula persicina	0	0	0	1
Russula postiana	1	0	0	0
Russula puellaris	0	0	0	1
Russula purpurobadia	0	0	0	1
Russula raoultii	0	2	0	0
Russula silvestris	1	6	8	7
Russula sp FH CLN16F1SY	0	0	1	0
Russula sp.1	0	0	1	0
Russula sp.2	0	0	1	0
Russula sp.3	1	0	0	0

Russula velenovskyi	3	0	0	0
Russula versicolor	0	2	0	1
Russula vesca	4	3	2	1
Russula violacea	0	1	0	0
Russula violeipes	0	0	1	0
Scleroderma areolatum	1	1	0	1
Scleroderma citrinum	0	5	1	6
Scleroderma verrucosum	0	1	0	0
Scopuloides hydnoides	1	0	0	0
Sebacina sp.1	1	0	1	0
Sebacina sp.2	1	0	0	0
Sebacina sp.3	1	0	0	0
Sebacina sp.4	0	0	1	0
Sistotrema sp.1	1	0	0	0
Telamonia sp.1	0	0	0	1
Thelephoraceae sp.1	4	0	4	0
Thelephoraceae sp.2	2	0	2	0
Thelophoraceae sp 2	0	0	0	0
Thelophoraceae sp.1	0	0	0	0
Tomentella botryoides	0	0	1	0
Tomentella coerulea	1	0	0	0
Tomentella sp.1	1	0	2	0
Tomentella sp.2	2	0	2	0
Tomentella sp.3	1	0	0	0
Tomentella sp.4	0	0	1	0
Tomentella stuposa	0	0	1	0
Tomentella sublilacina	5	0	8	0
Trechisporales sp.1	1	0	0	0
Trechisporales sp.2	1	0	0	0
Trechisporales sp.3	0	0	1	0
Tricholoma columbetta	1	0	0	0
Tricholoma fulva	0	1	0	0
Trichopezizella relicina	1	0	0	0
Tuber puberulum	1	0	1	0
Tylopilus felleus	1	0	0	0
Unidentified sp.1	0	1	0	3
Unidentified sp.2	1	0	1	0
Unidentified sp.3	2	0	1	0
Unidentified sp.4	1	0	0	0

Xerocomellus engeleii	0	1	0	0
Xerocomellus pruinatus	6	1	9	0
Xerocomus badius	0	0	3	0
Xerocomus chrysenteron	0	0	1	0
xerocomus ferrugineus	0	0	0	2
Xerocomus rubellus	0	0	0	1
Xerocomus sp.1	0	0	1	0
Xerocomus submentosus	0	3	0	3

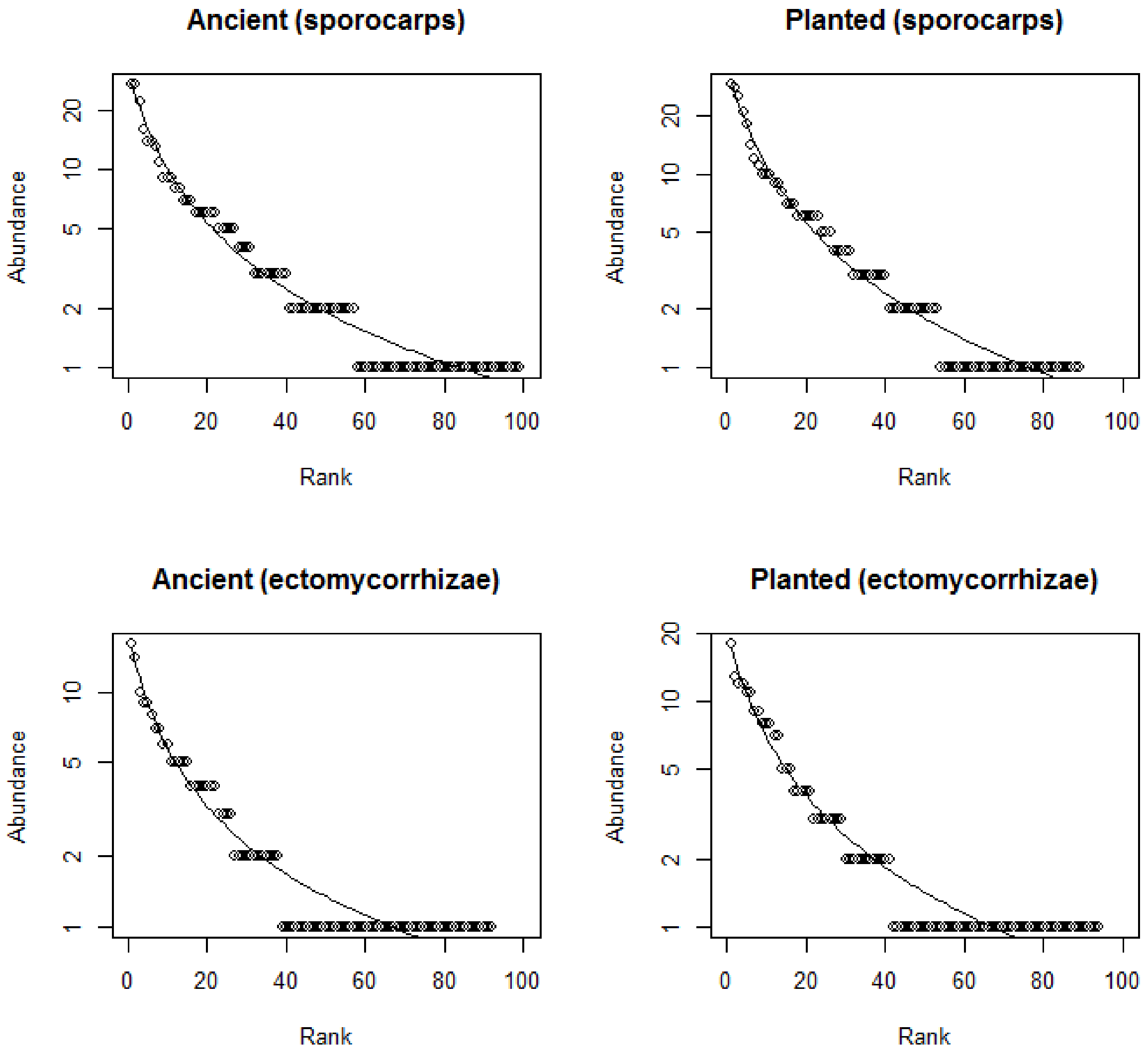

Figure B4.1. Ranked abundance distributions of species in ancient and planted forest stands as sporocarps and ectomycorrhizae. Abundance values represent the number of plots that a species occurred in. Rank abundance curves were constructed using the radfit() function of the ‘vegan’ package using the Zipf-Mandelbrot distribution (Oksanen et al. 2013).

Appendix B5 – PCA ordination of soil variables within the 14 ancient and planted forest stands.

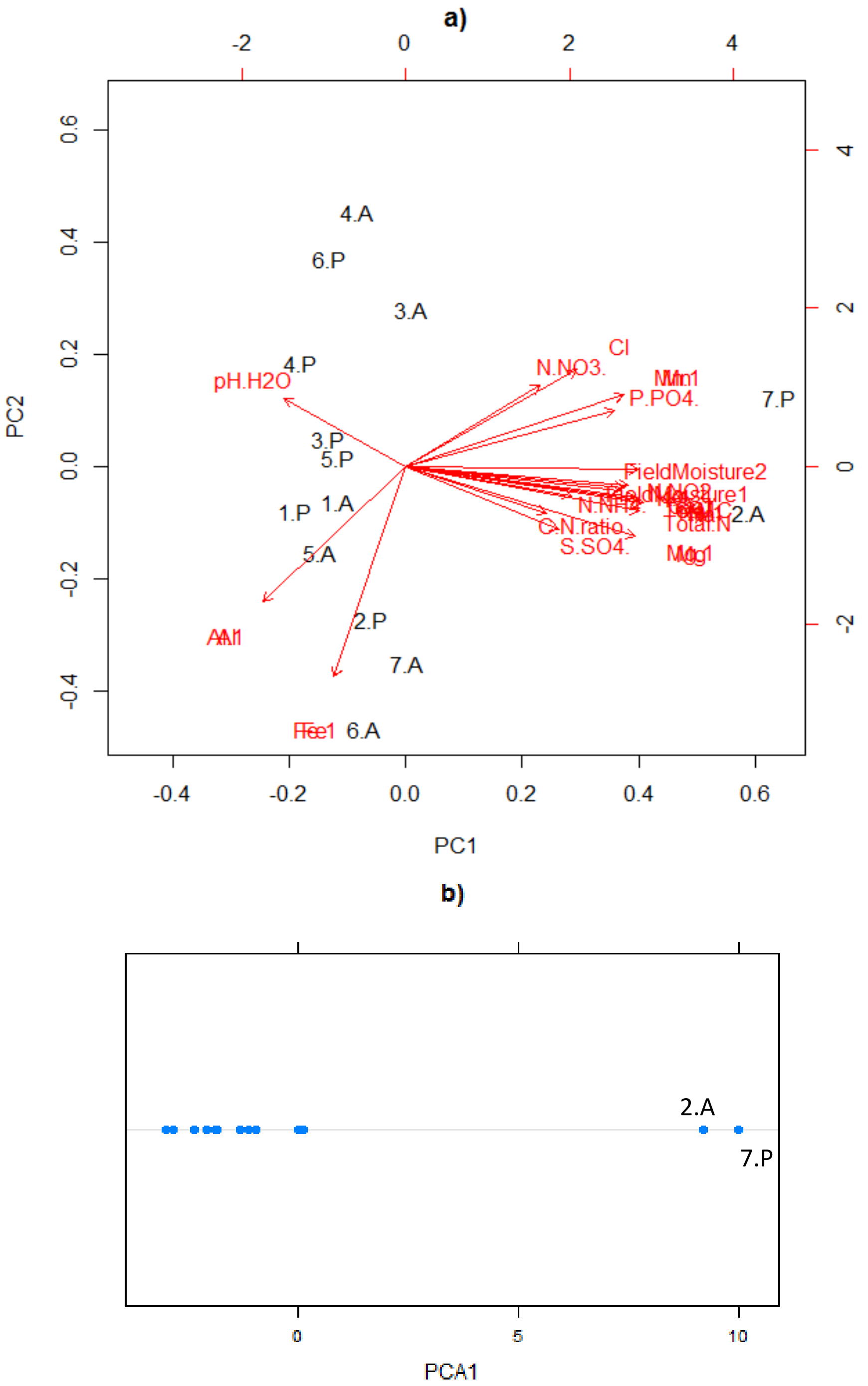

Figure B5.1. a) PCA ordination of soil variables within the 14 ancient (A) and planted (P) stands located in seven locations used in the study. b) Dotplot of forest stands across the first soil PCA axis. Stand 7.P and 1.A are very different and therefore were excluded from the analysis.

Appendix B6 – Description of PCA axes representing soil chemistry variables in forest stands included in the analysis of EMF richness variation.

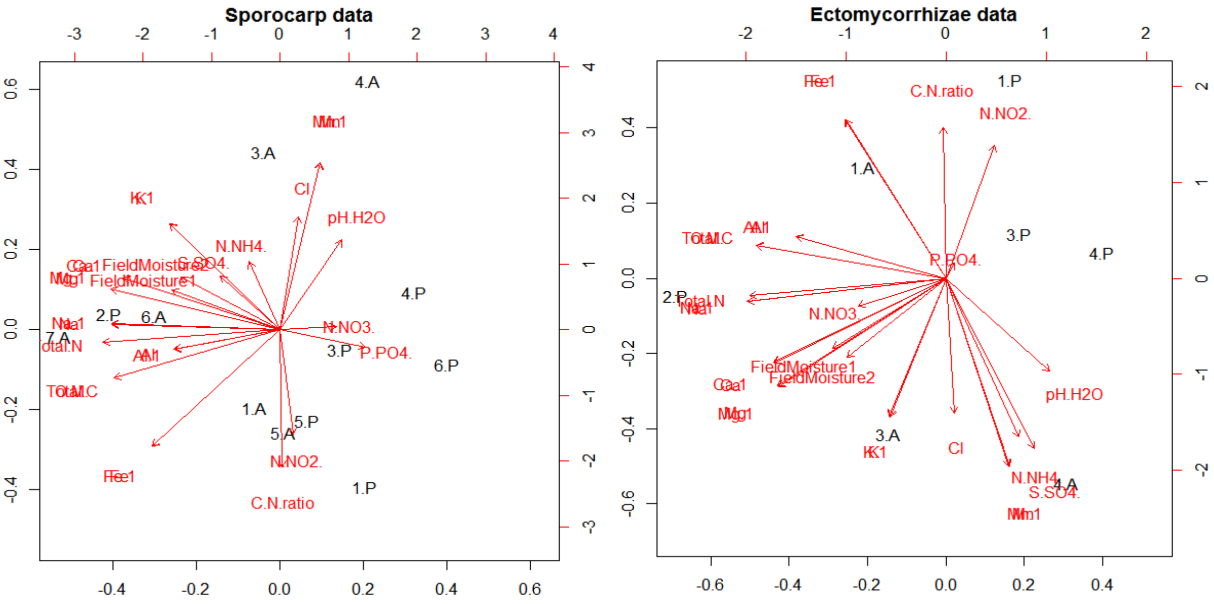

Figure B6.1. PCA ordination of soil variables used in analyses of EMF richness variation for the sporocarp and ectomycorrhizae sample datasets.

Table A6.1. Soil variable loadings on the three principle components in the forest stands used in analyses of EMF richness variation from sporocarp and ectomycorrhizae surveys. Variance values indicate the percentage of the total variance in soil properties accounted for by each principle component. The cumulative percentage of variance accounted for by the three components summed to 73% and 81% for sporocarp and ectomycorrhizae datasets, respectively.

	Sporocarp dataset			Ectomycorrhizae dataset		
Soil variable	soil1	soil2	soil3	soil1	soil2	soil3
pH	0.327	0.492	0.552	0.487	-0.457	-0.492
Field.Moisture1	-0.571	0.219	-0.160	-0.535	-0.343	-0.466
FieldMoisture2	-0.523	0.289	-0.220	-0.467	-0.388	-0.379
Total.N	-0.932	-0.069	-0.129	-0.927	-0.085	0.162
Total.C	-0.871	-0.265	-0.197	-0.897	0.162	0.084
Organic matter	-0.871	-0.265	-0.196	-0.897	0.162	0.084
C.N.ratio	0.013	-0.755	-0.105	-0.013	0.741	-0.189
Cl	0.097	0.622	-0.334	0.038	-0.664	-0.020
N.NO3.	0.296	0.017	-0.417	-0.416	-0.136	-0.060
S.SO4.	-0.317	0.296	0.785	0.416	-0.837	-0.238
P.PO4.	0.449	-0.098	-0.244	0.042	0.076	0.930
N.NO2.	0.072	-0.575	0.689	0.229	0.653	-0.593
N.NH4.	-0.162	0.373	0.651	0.344	-0.782	0.402
K	-0.582	0.580	-0.174	-0.268	-0.678	0.547
Ca	-0.823	0.285	-0.133	-0.811	-0.415	-0.241
Mg	-0.893	0.223	0.301	-0.795	-0.531	-0.084
Na	-0.887	0.028	-0.379	-0.938	-0.114	0.301
Al	-0.557	-0.108	0.695	-0.710	0.204	-0.621
Fe	-0.672	-0.641	0.073	-0.472	0.781	0.334
Mn	0.211	0.919	0.084	0.296	-0.924	-0.140
K.1	-0.579	0.583	-0.173	-0.264	-0.681	0.548
Ca	-0.823	0.284	-0.133	-0.812	-0.415	-0.241
Mg	-0.892	0.226	0.301	-0.792	-0.535	-0.089
Na	-0.887	0.033	-0.380	-0.936	-0.112	0.311
Al	-0.556	-0.109	0.696	-0.710	0.206	-0.620
Fe	-0.673	-0.640	0.070	-0.475	0.780	0.333
Mn	0.214	0.919	0.084	0.300	-0.924	-0.141
Variance / %	38.3	20.4	14.4	36.4	30.2	15.1

Table B6.2. Principle components for soil variables used in analyses

	Sporocarp dataset			Ectomycorrhizae dataset		
	soil1	soil2	soil3	soil1	soil2	soil3
1.A	-0.692	-1.602	-1.006	-1.768	2.228	-0.320
1.P	2.238	-3.192	1.055	1.342	3.994	-2.320
2.P	-4.575	0.321	-1.155	-5.728	-0.365	0.331
3.A	-0.449	3.609	-2.018	-1.235	-3.140	-0.737
3.P	1.590	-0.407	-1.699	1.547	0.894	4.155
4.A	2.330	5.061	1.274	2.538	-4.122	-1.001
4.P	3.581	0.751	0.877	3.305	0.512	-0.107
5.A	0.069	-2.093	0.566	n/a	n/a	n/a
5.P	0.722	-1.863	-0.144	n/a	n/a	n/a
6.A	-3.350	0.284	5.068	n/a	n/a	n/a
6.P	4.437	-0.715	-1.183	n/a	n/a	n/a
7.A	-5.901	-0.153	-1.633	n/a	n/a	n/a

Appendix B references

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Michin, P. R., O'hara, R. B., Simpson, P. S., Solymos, P., Stevens, H. H. & Wagner, H. H. 2013. vegan: Community Ecology Package. R package version 2.0-9. http://CRAN.R-project.org/package=vegan.

Sanderson, N. A. 2007. New Forest Inclosure habitats, habitat fragmentation and andscape history. Hampshire & Isle of Wight Wildlife Trust, Botley.

Appendix C Supporting Information for Chapter 3

Appendix C1: Correlations between taxonomic ad functional metrics of vegetation diversity with carabid functional diversity

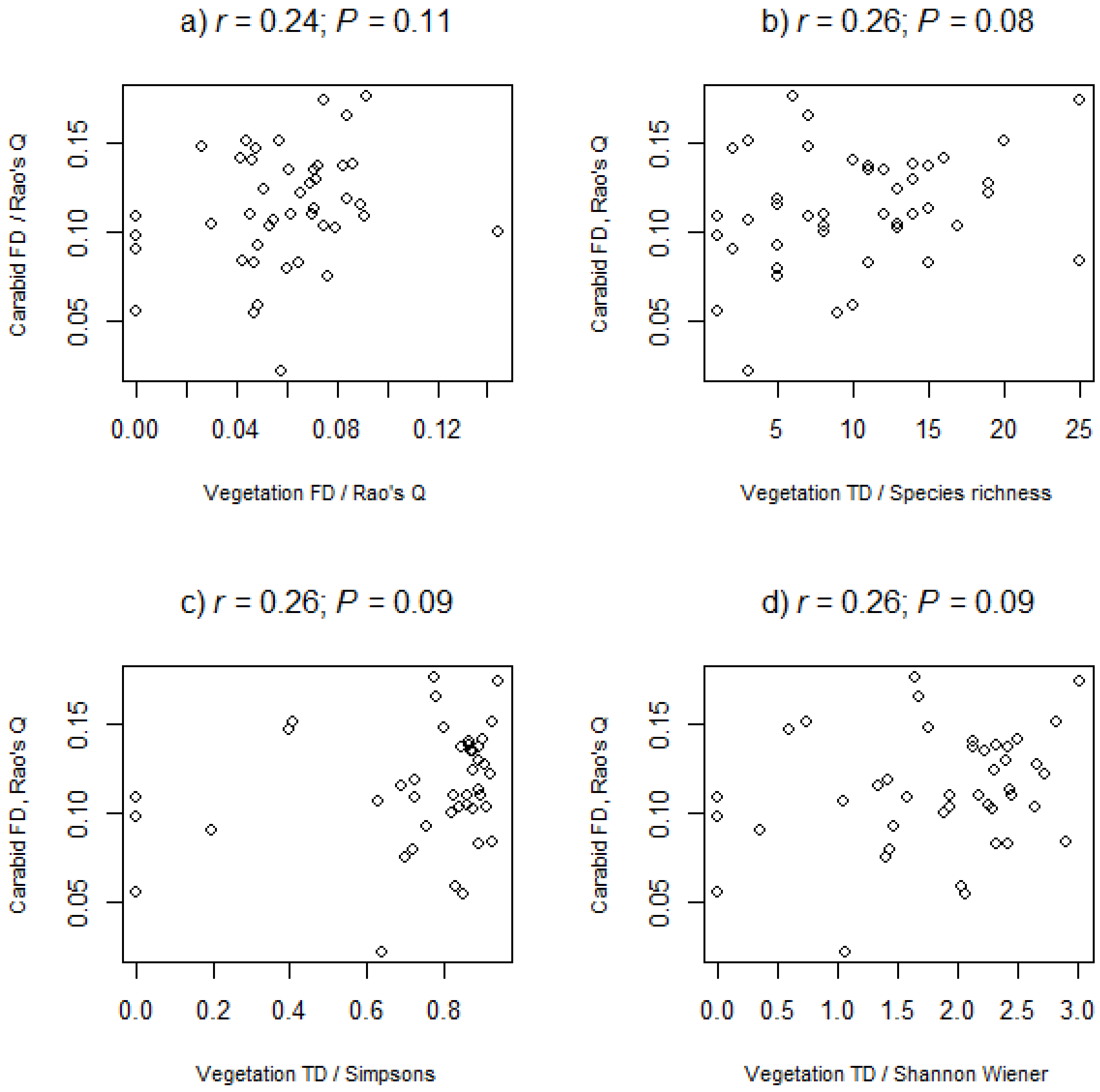

Figure C1. Bivariate relationships between carabid functional diversity (FD) and a) vegetation FD; b) vegetation species richness; c) vegetation Simpsons diversity; and d) vegetation Shannon diversity.

Appendix D Supporting Information for Chapter 5

Appendix D1 – Keywords used for search in ISI Web of Knowledge

Relevant studies were identified through computerised searches in the ISI Web of Science database. An exhaustive search for Japanese papers using words related to biodiversity and forests was done in J-Stage and Google Scholar. The finalised search query for the ISI Web of Knowledge performed on 01 July 2015 was:

CU= Japan OR South Korea
AND
TS= (biodiversity OR diversity OR richness OR abundance)
AND
TS= (forest OR coppice* OR woodland)
AND

TS=(primary OR old-growth OR oldgrowth OR “old growth” OR natural OR mature OR manag* OR clear-cut OR clearcut OR coppic* OR abandon* OR active OR passive OR restor* OR succession OR secondary OR “stand age” OR chronosequence OR plantation OR “planted forest” OR satoyama OR thinn* OR logg* OR “undergrowth removal” OR “undergrowth clearance” OR “understory removal” OR “understory clearance”)

Studies that investigated the relationship between patch size and species richness were retrieved with the following search in the ISI Web of Science, in addition to exhaustive searches in Google Scholar and J-Stage:

CU= Japan OR South Korea
AND
TS= (“species richness”)
AND
TS= (forest OR coppice* OR woodland)
AND

TS=(“patch size” OR “patch area” OR “forest area” OR “woodland area”)

Appendix D2 Calculation of the Morisita-Horn similarity index

The Morisita-Horn index accounts for the relative abundance of species and is resistant to undersampling because its value is largely determined by frequency changes in the most abundant species:

$$MOR = \frac{2\sum_{1}^{S} x_i y_i}{\left(\frac{\sum_{i}^{s} x_i^2}{\left(\sum_{i}^{s} x_i\right)^2} + \frac{\sum_{i}^{s} y_i^2}{\left(\sum_{i}^{s} y_i\right)^2}\right) + \sum_{1}^{s} x_i \sum_{1}^{s} y_i}$$

Where x_i is the abundance value of species i in the first sample and y_i is the value in the second sample. All sums are understood as i=1 to i=s (the pooled number of species across both samples).

Appendix D3 Studies used in systematic review of management impacts in biodiversity in

Studies on plantation thinning effects on biodiversity

Ehara, H., Ishii, H., Maeto, K. 2011. Ant Community Structure and Related Environmental Factors after Line Thinning in Japanese Cedar (Cryptomeria japonica) Plantations. Journal of the Japanese Forest Society, 94(1), 36-41.

Hirata, A., Sakai, T., Takahashi, K., Sato, T., Tanouchi, H., Sugita, H., Tanaka, H. 2011. Effects of management, environment and landscape conditions on establishment of hardwood seedlings and saplings in central Japanese coniferous plantations. Forest Ecology and Management, 262(7), 1280-1288.

Ishii, H. T., Maleque, M. A., Shingo, T. G. 2008. Line thinning promotes stand growth and understory diversity in Japanese cedar (Cryptomeria japonica D. Don) plantations. Journal of Forest Research, 13(1), 73-78.

Kawanishi, M., Komatsu, T., Sakio, H., Yonebayashi, C. 200). Effect of Thinning and Litter Removal on the Recovery of Riparian Vegetation in a Cryptomeria japonica Plantation. Journal of the Japanese Forest Society, 90(1), 55-60.

Kon, H., Watanabe, I., Yasaka, M. 2007. Effect of thinning on natural regeneration of broad-leaved trees in Abies sachalinensis plantations. Journal of the Japanese Forest Society,

89, 6, 395-400.

Kwon, T. S., Yang, H. M., Shin, J. H., Yi, H. B. 2010. Effects of Thinning on Abundance and Community Structure of Arthropods in a Pinus koraiensis Plantation. Korean Journal of Applied Entomology, 49(3), 187-198.

Nagai, M., Yoshida, T. 2006. Variation in understory structure and plant species diversity influenced by silvicultural treatments among 21- to 26-year-old Picea glehnii plantations. Journal of Forest Research, 11(1), 1-10.

Ohsawa, M. 2004. Species richness of Cerambycidae in larch plantations and natural broad-leaved forests of the central mountainous region of Japan. Forest Ecology and Management, 189(1-3), 375-385.

Ohsawa, M. 2005. Species richness and composition of Curculionidae (Coleoptera) in a conifer plantation, secondary forest, and old-growth forest in the central mountainous region of Japan. Ecological Research, 20(6), 632-645.

Ohsawa, M., Nagaike, T. 2007. Influence of forest types and effects of forestry activities on species richness and composition of Chrysomelidae in the central mountainous region of Japan. Biodiversity and Conservation, 15, 1179-1191.

Seiwa, K., Eto, Y., Hishita, M., Masaka, K. (2012). Effects of thinning intensity on species diversity and timber production in a conifer (Cryptomeria japonica) plantation in Japan. Journal of Forest Research, 17(6), 468-478.

Shoyama, K. (2013). Effects of thinning and excluding deer browsing on sapling establishment and growth in larch plantations. Landscape and Ecological Engineering, 9(1), 77-87.

Son, Y., Lee, Y. Y., Jun, Y. C., Kim, Z. S. (2004). Light availability and understory vegetation four years after thinning in a Larix leptolepis plantation of central Korea. Journal of Forest Research, 9(2), 133-139.

Takasaki, Y., Takenaka, C., Yoshida, T. (2010). The Effect of Thinning on the Community Structure and Densities of Soil Animals in a Chamaecyparis obstusa Plantation. Journal of the Japanese Forest Society, 92(3), 167-170.

Taki, H., Inoue, T., Tanaka, H., Makihara, H., Sueyoshi, M., Isono, M., Okabe, K. 2010. Responses of community structure, diversity, and abundance of understory plants and insect assemblages to thinning in plantations. Forest Ecology and Management, 259(3), 607-613.

Toyoshima, Y., Yamaura, Y., Yabuhara, Y., Nakamura, F. (2013). A preliminary study on the effects of line and selective thinning on bird communities in Hokkaido, northern Japan. Journal of Forestry Research, 24(3), 553-559.

Utsugi, E., Kanno, H., Ueno, N., Tomita, M., Saitoh, T., Kimura, M., Seiwa, K. 2006. Hardwood recruitment into conifer plantations in Japan: Effects of thinning and distance from neighboring hardwood forests. Forest Ecology and Management, 237(1-3), 15-28.

Zhu, J. J., Gonda, Y., Yu, L. Z., Li, F. Q., Yan, Q. L., Sun, Y. R. 2012. Regeneration of a Coastal Pine (Pinus thunbergii Parl.) Forest 11 Years after Thinning, Niigata, Japan. Plos One, 7(10).

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Hasegawa, M., Fukuyama, K., Makino, S., Okochi, I., Goto, H., Mizoguchi, T., . . . Tanaka, H. 2006. Collembolan community dynamics during deciduous forests regeneration in Japan. Pedobiologia, 50(2), 117-126.

Hasegawa, M., Okabe, K., Fukuyama, K., Makino, S., Okochi, I., Tanaka, H., . . . Sakata, T. (2013). Community structures of Mesostigmata, Prostigmata and Oribatida in broad-leaved regeneration forests and conifer plantations of various ages. Experimental and Applied Acarology, 59(4), 391-408.

Ito, S., Nakagawa, M., Buckley, G. P., & Nogami, K. 2003. Species richness in sugi (Cryptomeria japonica D. DON) plantations in southeastern Kyushu, Japan: the effects of stand type and age on understory trees and shrubs. Journal of Forest Research, 8, 49-57.

Makino, S., Goto, H., Hasegawa, M., Okabe, K., Tanaka, H., Inoue, T., & Okochi, I. 2007. Degradation of longicorn beetle (Coleoptera, Cerambycidae, Disteniidae) fauna caused by conversion from broad-leaved to man-made conifer stands of Cryptomeria japonica (Taxodiaceae) in central Japan. Ecological Research, 22(3), 372-381.

Nagaike, T., Hayashi, A., Abe, M., Arai, N. 2003. Differences in plant species diversity in Larix kaempferi plantations of different ages in central Japan. Forest Ecology and Management, 183, 177-193.

Ohsawa, M. 2005. Species richness and composition of Curculionidae (Coleoptera) in a conifer plantation, secondary forest, and old-growth forest in the central mountainous region of Japan. Ecological Research, 20(6), 632-645.

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Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T., & Makino, S. 2013. Succession Influences Wild Bees in a Temperate Forest Landscape: The Value of Early Successional Stages in Naturally Regenerated and Planted Forests. Plos One, 8(2). doi: 10.1371/journal.pone.0056678

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Toyoshima, Y., Yamaura, Y., Mitsuda, Y., Yabuhara, Y., & Nakamura, F. 2013. Reconciling wood production with bird conservation: A regional analysis using bird distribution models and forestry scenarios in Tokachi district, northern Japan. Forest Ecology and Management, 307, 54-62.

Yamashita, S., Hattori, T., & Tanaka, H. 2012. Changes in community structure of wood-inhabiting aphyllophoraceous fungi after clear-cutting in a cool temperate zone of Japan: Planted conifer forest versus broad-leaved secondary forest. Forest Ecology and Management, 283, 27-34.

Yamaura, Y., Royle, J. A., Shimada, N., Asanuma, S., Sato, T., Taki, H., & Makino, S. 2012. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodiversity and Conservation, 21(6), 1365-1380.

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Hasegawa, M., Fukuyama, K., Makino, S., Okochi, I., Tanaka, H., Okabe, K., Sakata, T. 2009. Collembolan community in broad-leaved forests and in conifer stands of Cryptomeria japonica in Central Japan. Pesquisa Agropecuaria Brasileira, 44(8), 881-890.

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Glossary of Terms

Term	Definition
Akaike's Information Criterion (AIC)	A parsimonious quantitative description of model fit by incorporating both deviance explained and number of parameters used.
Biodiversity Assessment Project (BAP)	The Forestry Commission's BAP assessed the biodiversity of multiple taxonomic groups in semi-natural and managed production forests at various stages of the forest cycle across the UK.
Biodiversity offsets	There are two major types of biodiversity offsets: 'restoration offsets' aim to generate new habitat in an 'offset site' to compensate the development-driven loss of habitat in the 'impact site'; 'protection offsets' involve protecting existing biodiversity from further threats such as deforestation
Chronosequence	A set of sites formed from the same parent material or substrate that differ in the time since they were formed
Ecological networks	Landscape management strategy that aims to mitigate against biodiversity loss in fragmented landscapes through a suite of core areas of habitat connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules.
Ecosystem service	Ecosystem services are the direct and indirect contributions of ecosystems to human well-being, and are classified according to four categories: supporting, regulating, provisioning and cultural services.
Ectomycorrhizal fungi (EMF)	A functional group of fungi that form mutualistic associations with most economically and ecologically important temperate tree species.
Fixed effects	Factors whose levels are experimentally determined or whose interest lies in the specific effects of each level, such as effects of covariates, differences among treatments and interactions.
Fourth corner analysis	Statistical procedure used to measure and test directly the correlation between the variations in species traits and the environmental variables.
Functional diversity (FD)	Quantitative measures that use multivariate methods to integrate multiple functional traits into a single continuous trait diversity index. These measures capture the value, range or distribution of functional traits in a community.
Functional trait	The morphological, anatomical, biochemical, physiological or phonological traits of a species that influence its ability to acquire resources, disperse, reproduce and persist in the environment.
Generalised linear model	Statistical models that assume errors from the exponential family; predicted values are determined by discrete and continuous predictor variables and by the link function (e.g. logistic regression, Poisson regression).
Indicator Species Analysis (ISA)	A technique used to identify species unique to the different community types, habitat conditions, or environmental changes. Indicator values represent the strength of an association and encompass two probabilities: (i) the probability that a species belongs to the sample of an environmental condition of interest (specificity), and (ii) the probability of finding the species in samples belonging to the environmental condition (sensitivity). Indicator values range from 0 (no indication) to 1 (maximum indication).
Linear mixed model	Statistical models that assume normally distributed errors and also include both fixed and random effects.

Link function	A continuous function that defines the response of variables to predictors in a generalized linear model, such as logit and probit links. Applying the link function makes the expected value of the response linear and the expected variances homogeneous.
Maximum likelihood (ML)	A statistical framework that finds the parameters of a model that maximizes the probability of the observed data (the likelihood).
Meta-analysis	Statistical tool for summarising the results of multiple studies on the same topic.
Model selection	A series of approaches to determining the best of a set of candidate statistical models. Information-theoretic approaches based on AIC, which also allow model averaging, are generally preferred to older methods such as stepwise regression.
Non-metric multidimensional scaling (NMDS)	Ordination technique that permits the visualisation of species composition across assemblages, through reflecting similarities (or dissimilarities) between assemblages.
Principal Components Analysis (PCA)	A multivariate statistical technique that uses orthogonal transformation to convert a set of correlated variables into a set of orthogonal, uncorrelated axes called principal components.
Pseudoreplication	When multiple samples from a single contiguous treatment unit are analysed as if they were independent replicates that were interspersed with control replicates.
Random effects	Factors whose levels are sampled from a larger population, or whose interest lies in the variation among them rather than the specific effects of each level.
Rao’s quadratic entropy (FD_Q)	A multi-trait FD metric that describes the variation of species trait composition within the community. It sums pairwise distances between species in a community weighted by their relative abundances. $FD_Q = \sum_{i=1}^{N}\sum_{j=1}^{N} d_{ij} p_i p_j$, where N is the number of species in a plot, d_{ij} is the difference in trait values between the ith and jth species; p_i and p_j are the proportions of the ith and jth species.
Restricted maximum likelihood (REML)	An alternative to ML that estimates the random-effect parameters (i.e. standard deviations) averaged over the values of the fixed-effect parameters; REML estimates.
	of standard deviations are generally less biased than corresponding
	ML estimates.
Saproxylic	A functional grouping of taxa of species that depend on deadwood during some part of their life cycle.
Satoyama	A management that predominated during Japan’s pre-development era, in which broad-leaved forests were clear-cut as coppices to provide a source of raw materials, such as charcoal, over cycles of 15 to 30 years. More recently, the term now referes to whole landscapes that comprise mosaics of thee forests in addition to other habitats including plantations, rivers, residential areas and rice paddies.
Scaling	Scaling of explanatory variables prior to statistical models improves the interpretability of regression coefficients. It typically involves centring and scaling. Centring is the subtraction of the sample mean from all of the input variable values, leading to a mean of the centred variable equal to zero, and all of the units on the original scale. Standardisation often refers to dividing the input variables by their sample standard deviations.
Similarity (species composition)	A measure of how similar two communities are in species composition.

Sporocarp	Above-ground reproductive structure of a fungus.
Species diversity	A measure of biodiversity that incorporates both the numbers of species present and the dominance or evenness of species in relation to one another. Common metrics include the Shannon-Wiener and Simpson diversity indices.
Species richness	A measure of biodiversity that is simply the number of species found in a sample.
Succession	The change in species composition and/or structure over time following either a severe disturbance that removes most organic matter (primary succession) or a less severe disturbance where some biological legacy remains (secondary succession). Biomass, nutrient availability and vegetation stature can either increase (progressive succession) or decrease (retrogressive succession.
Sustainable Forest Management (SFM)	Paradigm of forest management strategies that aim to achieve compatibility between timber production and the provision of ecosystem services including the maintenance of biodiversity.
Systematic review	A recognised standard for accessing, appraising and collating robust scientific data. The synthesis of data collated using systematic review can be done narratively, or quantitatively using meta-analysis