

Environmental, spatial and temporal
drivers of plant community
composition in British forest habitat.

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Abstract

Broadleaved forest habitat is important for a number of ecosystem functions and as a refuge for many rare plant species in human-modified landscapes. It is however, threatened by global change drivers such as deforestation and the associated fragmentation of remaining habitat areas, along with increased disturbance and exposure to nutrient inputs from surrounding intensive agriculture. This thesis uses a unique combination of data on plant species occurrence, local environmental conditions and forest spatial extent in order to investigate the ways in which species richness and functional diversity in forest communities are dependent upon local and landscape scale drivers, and to quantify the strength of these relationships. This provides novel understanding of the response of forest plants with different life history traits to the configuration and quality of available habitat, and therefore the way in which understorey assemblages are likely to alter over time following landscape change. Results highlight the importance of local environmental conditions within forest patches but also suggest that patch area and landscape connectivity have an important effect on the trait composition of communities. Preserving large, well connected areas of habitat is therefore likely to be key for the conservation of many species, particularly rarer forest specialists which often possess traits linked to low dispersal ability. Furthermore, there is evidence that species are slow to respond to changes in the spatial extent of habitat. As such, considering the history of forest patches is necessary in order to explain present day patterns in plant species occurrence and to devise effective conservation measures. This highlights the need to integrate understanding of local and landscape scale processes with temporal data

in order to properly understand the way in which forest communities are formed and to predict ongoing change under expected global change scenarios.

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Declaration

I declare that, other than where the contribution of others is specified, that this thesis is entirely my own work and has not been submitted for the award of any other degree, either at Lancaster University or elsewhere.

Adam Robert Kimberley

Statement of authorship for multi-authored chapters

Chapter 3: Identifying the trait syndromes of conservation indicator species: how distinct are British ancient woodland indicator plants from other woodland species?

Kimberley, A., Blackburn, G. A., Whyatt, J. D., Kirby, K., & Smart, S. M. (2013) Identifying the trait syndromes of conservation indicator species: how distinct are British ancient woodland indicator plants from other woodland species? Applied Vegetation Science, 16; 667-675.

The concept and methodological approach for this chapter was decided upon through a series of discussions between the authors. As the first author of the above publication, I designed and carried out the classification tree and logistic regression modelling around which the paper is centred. From the results of these statistical analyses, I then produced the draft text of the manuscript, including all tables and figures. Finally, I was responsible for co-ordinating the revision of this draft following the comments of co-authors and referees, and the eventual submission of the finished manuscript to the journal for publication.

Chapter 4: Traits of plant communities in fragmented forests: The relative influence of habitat spatial configuration and local abiotic conditions.

Kimberley, A., Blackburn, G.A., Whyatt, J.D., Smart, S.M. (2014). Traits of plant communities in fragmented forests: The relative influence of habitat spatial configuration and local abiotic conditions. Journal of Ecology. 102: 632–640.

The concept and methodological approach for this chapter was decided upon through a series of discussions between the authors. As the first author of the above

publication, I was wholly responsible for extracting the relevant explanatory variables from existing Countryside Survey and Land Cover Map datasets, as well as manipulating these into the form required for the statistical analyses. I then performed all statistical modelling (including both the WinBUGs modelling to impute missing trait values and the multimodel inference analysis). Having obtained the results of these analyses I then produced the text and figures of the paper, producing an initial draft which was modified in subsequent revisions, following additions and suggestions from the other authors and anonymous referees and submitted the revised article for publication.

Chapter 5: How well is current plant trait composition predicted by modern and historical forest spatial configuration?

Kimberley, A., Blackburn, G.A., Whyatt, J.D., Smart, S.M. (2015). How well is current plant trait composition predicted by modern and historical forest spatial configuration? Ecography. In press.

The concept and methodological approach for this chapter was decided upon through a series of discussions between the authors. As first author of the above publication, I was solely responsible for obtaining the data used from the various sources and carrying out all statistical modelling. I then produced a draft manuscript based upon the results obtained, including all figures. Following this, I was responsible for coordinating the revision of this draft version in response to comments and suggestions from both co-authors and referees and the final submission of the manuscript for publication.

Chapter 6: Forest change in the Anthropocene: Do we need to combine habitat suitability and landscape connectivity to model understorey biodiversity?

Kimberley, A., Blackburn, G.A., Whyatt, J.D., Smart, S.M. (2015). Forest change in the Anthropocene: Do we need to combine habitat suitability and landscape connectivity to model understorey biodiversity? To be submitted to Ecology Letters.

The concept and methodological approach for this chapter was decided upon through a series of discussions between the authors. As first author of the above manuscript, I was responsible for extracting the observed species richness information and land cover data from Countryside Survey datasets and performing the connectivity and habitat suitability modelling. Using the information obtained, I then performed the subsequent statistical analysis and produced the figures and text of a draft manuscript based upon the results of this modelling. This draft was then revised in response to comments from all co-authors.

I confirm that the above information on the authorship of these chapters and the contribution of Adam Kimberley is accurate.

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1. Introduction

1.1. Thesis aims and structure

The spatial arrangement of forest within the landscape is thought to act as an important constraint on the composition of plant communities, filtering out species with unfavourable life history traits (Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Fischer & Lindenmayer 2007). Different spatial factors are often highly interrelated however, and their effects generally considered secondary to the strong influence of local conditions such as light availability and soil fertility. Detailed data on vegetation composition and environmental conditions, sampled across a gradient of forest types and levels of forest fragmentation, are therefore needed to properly establish the effects of forest configuration on plant communities (Ewers & Didham 2006; Smith et al. 2009). Hence, knowledge of the relative effects of forest condition and spatial arrangement is still incomplete, with few studies investigating the partial effects of important factors such as patch size and landscape connectivity on biodiversity and trait composition after fully accounting for important local variables (Humphrey et al. 2015).

This thesis addresses this knowledge gap by incorporating information on local environmental factors and forest patch age into analyses investigating the way understorey communities in areas of broadleaved forest are affected by variation in habitat spatial configuration. The unique datasets used, comprising detailed field data captured across a wide geographic range, allowed the effects of different local and landscape scale drivers on understorey community composition to be quantified, in addition to the ways in which these processes are modified by forest age and

changes in spatial extent over time. This provides novel understanding of the way in which species with different traits respond to their local patch environment and the land use composition of the surrounding landscape; knowledge which is important to help identify species which are most likely to be threatened by ongoing changes in land use and forest quality, and to create conservation measures which are effective in maintaining biodiversity (Opdam & Wascher 2004; Foley et al. 2005; Turner et al. 2013; Mitchell et al. 2014).

This thesis consists of seven chapters (plus appendices). In chapter 1, the aims of the thesis are outlined, along with the data sources which underpinned the analyses.

Chapter 2 provides a broad introduction to the problem of habitat loss and fragmentation and an overview of the importance of studying its influence within forest communities. This is followed by a detailed review of the existing literature surrounding forest fragmentation, the effects that this has on different plant species and existing efforts to conserve forest habitat. Following this review, four analytical chapters are presented, three of which have been published (see statement of authorship above for full references and authorship details) and a fourth which has been prepared in a style appropriate for submission to a scientific journal.

References for each of these chapters have been collated into an overall reference list which is provided at the end of the thesis.

Chapter 3 is a species-focussed study which uses classification tree analysis to determine the extent to which species which have been anecdotally, albeit expertly, classified as Ancient Woodland indicators share common traits, and to identify the trait syndromes (i.e. combinations of trait values and states) that are most common

in plants which are largely absent from secondary forest areas. This work helped provide an indication of the mechanisms which affect the occurrence of many of these individual species and the extent to which simple measures such as plant species richness were likely to obscure differential responses to forest change that could be better separated using traits. The analysis also importantly helped validate a trait-based foundation for an existing separation of plants based on rarity and conservation value given their presumed association with ancient forest. The understanding gained from this chapter was then applied to subsequent larger scale studies.

Chapters 4 and 5 investigate the trait composition of communities within forest patches. Chapter 4 compares the effects of spatial variables such as habitat amount and patch area on mean trait values with those of local environmental conditions such as shade and soil fertility. Chapter 5 investigates the potential existence of lag effects in forest habitat, attempting to quantify the levels of extinction debts and immigration credits which remain following past change in the spatial extent of forest patches. This analysis provides important evidence of lag effects in contemporary temperate forests. These effects need to be quantified in order to properly interpret the results of studies modelling present day plant composition using modern habitat extent, such as in chapter 4 here.

Finally, chapter 6 uses a recently developed measure of landscape connectivity in combination with models of species habitat suitability, to investigate the effects of forest connectivity on forest species richness and therefore the importance of considering landscape scale processes when studying forest understorey

communities. Chapter 7 then concludes the thesis, drawing together the themes investigated in earlier chapters to summarise the key findings and implications for future forest research and conservation.

1.2. Data sources

Countryside Survey (CS) is a Great Britain-wide monitoring scheme designed to provide a representative sample of the state of British countryside in all land types (Norton et al. 2012). In 2007, the most recent survey, 591 one kilometre square areas of land were surveyed. In each survey landscape, land cover was mapped and data on plant community composition and environmental conditions collected for a number of vegetation sampling plots (Figure 1.1). Those used in this thesis consisted either of area plots (200 m²), randomly located within the survey landscape or linear plots (10 m²), targeting features such as hedges, streams and road verges. In each of these plots, all plant species present were recorded by expert surveyors and the amount of shade graded on a categorical scale from one to three (unshaded, partially shaded and fully shaded). Within the area plots a 15 cm topsoil sample was taken, from which soil moisture content, pH and carbon to nitrogen ratio were later measured. The resulting spatial land cover data combined with the detailed local plant species and environmental data formed the basis of most of the analyses in this thesis. Here, the focus is on plant communities in vegetation plots that occur in “broadleaved and mixed yew woodland” as per the Broad Habitat classification used in CS 2007 (including priority habitat woodland types nested within this; see Maskell et al. (2008) for full details). This habitat is henceforth referred to as “forest” or “woodland” habitat and excludes both coniferous forest areas and forest plantations.

Although CS provides data on land cover present around vegetation sampling plots, this is constrained by the 1 km square based sampling design, with no information on forest habitat outside of this area. Furthermore, CS represents a snapshot of the landscape at a moment in time, with no forest patch history available. As a result, CS data were augmented by data from additional sources in an attempt to improve measures of forest patch size and landscape connectivity. Information on forest habitat outside of CS squares was obtained from Land Cover Map 2007 (Morton et al. 2011) and historical forest extent from digitised 1st series Ordnance Survey (OS) maps (Ordnance Survey County Series 1:10,560, 1st Edition, 1849-1899). These extra data sources provided important spatial and temporal context around vegetation sampling plots (Figure 1.2).

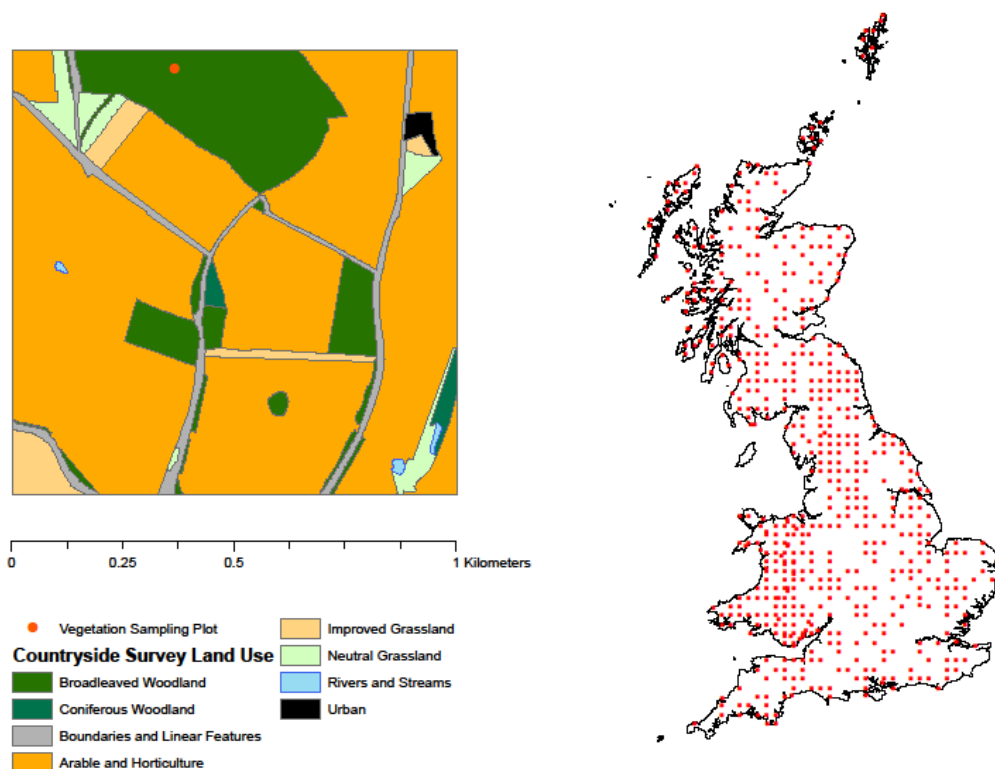


Figure 1.1 Example Countryside Survey 1 km sampling square and the distribution of Countryside Survey sampling locations across Great Britain.

The nationwide coverage of CS (Figure 1.1) meant that when these data were combined with the additional information on forest extent and history, a high quality set of variables describing forest habitat in Britain, across a wide gradient of climatic and environmental conditions and in landscapes with a range of forest cover was available. These data therefore provided an excellent opportunity to address the aim of the thesis; investigating the interacting effects of forest age, spatial configuration and local conditions on forest plant communities.

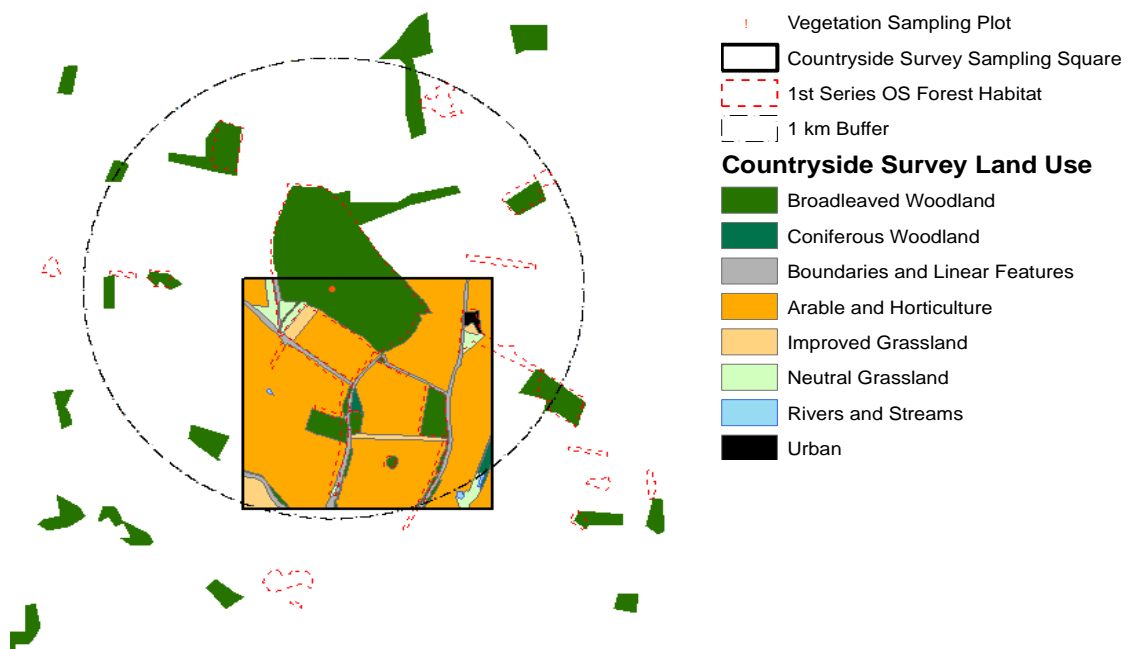


Figure 1.2 Example Countryside Survey square and additional data sources used.

2. Literature review: Spatial and temporal drivers of forest plant community composition

2.1. Introduction

2.1.1. Habitat loss and fragmentation

Land use change as a result of urbanisation and agricultural intensification has led to the loss of large areas of many habitats, as natural ecosystems are converted to urban land or to land for food production (Foley et al. 2005). This land use change inevitably results in the local extinction of any species reliant on the habitat which is lost. Furthermore, many species which occur elsewhere in the landscape may still undergo a reduction in abundance which leads to their population size dropping below the threshold required for long term persistence (Hanski et al. 1996). As such, habitat loss is considered a primary driver of ongoing biodiversity declines in a number of taxa worldwide (Dirzo & Raven 2003).

The process of habitat loss is often associated with increased fragmentation of remaining habitat area. This results in patches which are smaller, more isolated and have a higher edge to area ratio (Figure 2.1; Fahrig 1997, 2003). The consequent smaller population sizes and reduced movement between suitable habitat areas are also thought to act as an important filters for the occurrence of many species, preventing them from forming viable meta-populations and increasing their risk of local extinction (Andrén 1994; Hanski 1998; Hames & Rosenberg 2001). This is particularly the case for specialist species which rely on core habitat (Bender et al. 1998; Fischer & Lindenmayer 2007). Additionally, the reduction in landscape

connectivity following habitat loss can reduce species' ability to shift their range in response to changing climate (Travis 2003; Opdam & Wascher 2004). Thus, understanding the effects of landscape change on different groups of species is important to minimise the further loss of important species and functional diversity (Ewers & Didham 2006).

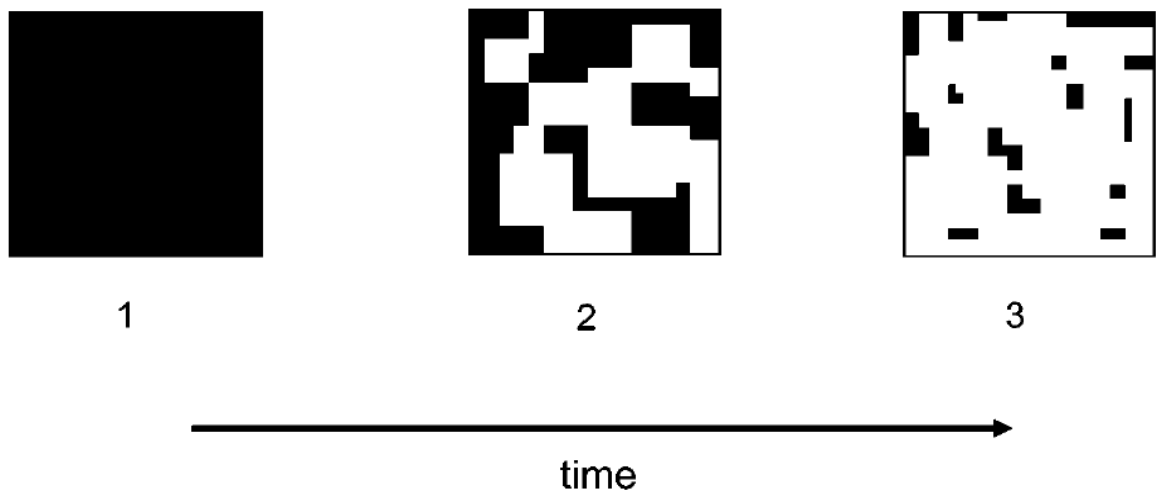


Figure 2.1 From (Fahrig 2003); the process of habitat loss and fragmentation, whereby “a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original” (Wilcove et al. 1986).

2.1.2. Forest habitat

Broadleaved forest habitats, and particularly ancient forest areas (forest which has been continuously wooded since at least 1600), are of high conservation importance due to their ability to sustain many rare and specialised plants (Peterken & Game 1984; Goldberg et al. 2007). A number of these species are almost totally restricted to ancient forest in parts of their range (Peterken et al. 1974; Honnay et al. 1998; Verheyen et al. 2003). Forests are also highly valued due to the variety of different services for which they are responsible; providing wood for fuel and materials, mediating crop production and pest regulation in surrounding agricultural land and

contributing to soil and water quality (Forestry Commission 2003; Quine et al. 2011; Mitchell et al. 2014). Loss of forest can also impact on pollinator networks which are important for many plant species (Taki et al. 2007).

The conversion of natural ecosystems to agricultural land has led to the clearance of large areas of ancient semi-natural forest habitat across Europe and North America over the last 1000 years (Rackham 1990; Williams 2003; Kolk & Naaf 2015). The amount of temperate forest habitat worldwide is estimated to have decreased by 315 million hectares between 1700 and 1920 (Williams 2003). This history of forest clearance means that much remaining forest consists of small patches embedded in a matrix of fairly intensive agriculture, particularly in lowland areas (Williams 2003).

The loss and fragmentation of ancient forest habitat, along with historical management practices, are likely to have resulted in significant and ongoing changes to the composition of understorey communities (Vellend 2003; Flinn & Vellend 2005; Hermy & Verheyen 2007). Hence, the protection of remaining forest habitat has been a primary focus of recent conservation strategy (Forestry Commission 2003).

The decline in forest cover in some areas has been reversed in recent years due to management policies incentivising forest creation and the regrowth of forest habitat on abandoned agricultural land (Foster et al. 1998; Forestry Commission 2003; Flinn & Vellend 2005; Quine et al. 2011). The percentage cover of woodland habitat in the UK for example has recovered to 8.7% (in 2009) from a low of 5.1% in 1924, although this is still well below the estimated figure of 15% in the 11th Century (Quine et al. 2011). The ecological benefits of secondary forest habitat and the timescales over which these are likely to become apparent remain unclear however, with abiotic

conditions and community composition often taking many years to recover following agricultural activity (Koerner et al. 1997; Dupouey et al. 2002; Vellend 2003; Flinn & Vellend 2005; Brunet et al. 2012). Investigating the ways in which the amount, configuration and history of forest patches act to filter plant species pools in both old and recently established forest habitat is therefore essential in order to gain understanding of the effects of habitat loss and fragmentation, and to predict future trends in forest plant composition under different management scenarios.

2.1.3. Biotic homogenization

Land use change does not affect all species to the same extent; the life history traits that different plants possess are important determinants of their response to habitat loss and fragmentation (Henle et al. 2004). Specialist species and those with limited population sizes or dispersal ability are more strongly affected because they are likely to be less capable of surviving in or dispersing across landscapes dominated by unfavourable habitat types (Devictor, Julliard & Jiguet 2008). Ruderal species which produce many small seeds with low terminal velocity, and possess high relative growth rates and high seedbank persistence, can respond more rapidly to landscape change and are able to quickly colonise new forest edges and areas of secondary woodland (Tabarelli et al. 1999; Brunet 2007). Hence more generalist species may even be positively affected by the increased heterogeneity and disturbance created in smaller patches by landscape change (Liira et al. 2014).

Over time, species which do not possess traits which are conducive to survival in highly fragmented habitat are likely to be lost from communities in small, isolated forest patches (Kolb & Diekmann 2005; Ozinga et al. 2009). Species with lower

dispersal ability and no tolerance for grazing are expected to decline in abundance, while later flowering, persistent species increase (Naaf & Wulf 2011). In such situations plant communities become dominated by “winners”, as “losers” are lost from habitats (Naaf & Wulf 2011), culminating in a degree of biotic homogenisation (McKinney & Lockwood 1999; Devictor et al. 2008). Evidence suggests that while plant communities are expected to become more functionally similar through this process, species richness is likely to remain constant or even increase, dependent on local abiotic conditions (Fukami et al. 2005; Smart et al. 2006). Understanding the way habitat loss and fragmentation affect species with differing life history characteristics is therefore important provide insight into which species which are most vulnerable to ongoing land use change.

2.2. Effects of habitat spatial configuration on forest plant species

2.2.1. Forest patch area

The composition of forest understorey plant communities is thought to be closely linked to the area of forest patches. A number of studies have found higher total species richness and increased forest specialist richness in larger forest patches (Peterken & Game 1984; Grashof-Bokdam 1997; Petit et al. 2004), while the occurrence of individual species has also been shown to be positively related to increasing habitat area (Dupré & Ehrlén 2002; Jacquemyn et al. 2003). Evidence suggests however that the occurrence of high numbers of forest specialist species in large patches may be heavily dependent on the habitat in question having had time to accumulate slow colonising plants (Brunet 2007; Jacquemyn et al. 2011).

The relationship between forest patch area and biodiversity has been attributed to the fact that larger patches generally contain a wider variety of environmental conditions, and therefore a greater number of available niches (Peterken & Game 1984; Honnay et al. 1999; Honnay et al. 2005). It has therefore been suggested that habitat quality is the main driver of plant species occurrence within forest habitat, rather than patch area itself (Peterken & Game 1984; Honnay et al. 1999; Liira et al. 2014). More recent studies however have found that the occurrence of forest plants can be explained by the size of patches even after accounting for the effects of environmental conditions (Dupré & Ehrlén 2002; Jacquemyn et al. 2003). Higher forest specialist richness has also been observed in larger patches in studies using small sampling plots, in which environmental heterogeneity is unlikely to have a significant impact (Petit et al. 2004). This suggests that patch area has an additional effect on species assemblages not linked to that of local abiotic factors.

The small populations found in smaller forest patches are thought to be highly vulnerable to extinction following stochastic variability in demography and environmental conditions (Shaffer 1981; Lande 1988; Dornier & Cheptou 2012). A species which occurs in lower numbers is therefore at increased risk of a single event (e.g. disturbance) causing its local extinction. Hence, as forest patches reduce in size, such species are more likely to be lost. The small populations found in fragmented habitats are also believed to undergo a reduction in genetic variation as a result of an increase in self-fertilisation and mating with related individuals (Young et al. 1996; Gijbels et al. 2015). Such “inbreeding depression” is thought to have negative consequences for the viability of the affected population due to individuals possessing lower fitness through reductions in seed production (Jacquemyn et al.

2002). This decrease in reproductive capability is likely to limit the ability of plant species to persist long term in small patches, or to survive following environmental change (Booy et al. 2000; Dornier & Cheptou 2012; Gijbels et al. 2015). Species which rely on outbreeding through pollination are likely to be more negatively affected by this process than species that are able to reproduce clonally, whose extended generation times mean genetic diversity is retained for longer periods (Honnay & Jacquemyn 2007).

The risk of local extinction due to small population size is thought to be modified by the life history traits of species, as well as other interdependent factors like patch isolation and edge to area ratio (Henle et al. 2004; Didham et al. 2012). Species with low dispersal ability and those which are less able to persist in the soil seedbank are thought to be at greater risk from reduced patch area because they are less able to rescue small populations or colonise unoccupied habitat through immigration or via regeneration from seed (Ozinga et al. 2009; Lindborg et al. 2012). Hence, species with such characteristics should be disproportionately absent where forest patch area is low (Lindborg et al. 2012). This dominance of persistent species with high dispersal ability in small forest patches is likely to explain the low richness in forest specialist plants, which are generally thought to be characterised by low colonising ability (Verheyen et al. 2003).

While this seems to indicate that forest patch area has an effect on the ability of populations to survive, environmental variables such as soil pH, macronutrient availability and amount of shade are frequently found to have a considerably stronger effect on most species' occurrence (Dupré & Ehrlén 2002; Jacquemyn et al.

2003). This suggests that although patch area is an important factor for many species, its effect is secondary to that of the direct filter of local habitat quality. The weak signal between patch area and plant composition may in part be due to the slow loss of vulnerable species in forest fragments (Vellend et al. 2006). If area-related extinctions are still ongoing, then the relationship between patch area and forest understorey composition is likely to become stronger as species richness changes to reflect current landscape configuration (Honnay et al. 2005; Vellend et al. 2006). The importance of landscape scale patch configuration compared to patch scale environmental conditions has important conservation implications. If increased heterogeneity is the main reason for larger patches containing more forest species, then forest patches of all sizes are viable conservation targets, provided they are old enough and contain the environmental conditions which support species of interest (Honnay et al. 1999; Liira et al. 2014).

2.2.2. Patch isolation

Following the loss of forest area, remaining patches often become more isolated from neighbouring forest habitat (Fahrig 2003). This increased distance between patches reduces the probability of species dispersing from one patch to another across surrounding unfavourable land use types, and means that isolated patches are less likely to be colonised by plant species with low dispersal ability (Verheyen & Hermy 2004; Brunet 2007). Species which are less able to travel long distances across landscapes are also less capable of rescuing threatened populations in isolated patches through immigration (Johst et al. 2002; Verheyen & Hermy 2004).

At a regional scale, species often exist as meta-populations; a number of spatially distinct local populations which are linked by the movement of individuals between patches. Each local population is vulnerable to stochastic extinction over time, but species continue to persist in the landscape due to the re-colonisation of available habitat through migration from neighbouring patches (Hanski 1998). This dynamic process of extinction and re-colonisation means that as long as dispersal between patches remains possible, vulnerable “sink” populations in small or low quality habitat areas can be maintained through the arrival of dispersing individuals from nearby “source” populations (Eriksson 1996). Meta-populations therefore allow species to continue to occur in forest fragments from which they would most likely be absent without this rescuing effect. Since movement across the landscape is a key component of meta-population dynamics, greater isolation of forest patches can disrupt this process, increasing the risk of local populations becoming extinct.

The fact that many forest plants are perennial species with long generation times means that their local extinction is often delayed following environmental change because remnant populations can survive for a relatively long time in unfavourable conditions (Eriksson 1996; Hermy et al. 1999; Verheyen et al. 2003). This, coupled with the often low colonising ability of forest specialists, means that any meta-population dynamics of extinction and re-colonisation are likely to occur over a long time period in forest habitats (Verheyen et al. 2004; Vellend et al. 2006; Naaf & Kolk 2015). Hence, if the configuration of the landscape remains dynamic, source populations may be removed via the loss of old forest habitat before new or unoccupied habitat areas are colonised. Further disruption of meta-population dynamics is therefore likely where turnover of forest patches is high, particularly for

species which are very slow to move across landscapes (Johst et al. 2002; Verheyen et al. 2004).

The importance of dispersal in colonising isolated forest patches and maintaining viable meta-populations in more fragmented landscapes means that such habitat is likely to be dominated by well dispersed species (Ozinga et al. 2009). Evidence suggests that related traits such as height, seed number, seed mass and seed terminal velocity all affect the ability of plant species to persist where movement between patches is impeded (Kolb & Diekmann 2005; Schleicher et al. 2011).

Dispersal vectors, such as the ability of species to use wind or grazing animals to disperse seed, are also important determinants of local persistence in fragmented habitat (Purschke et al. 2012). Species which are dispersed by birds or other large animals are more likely to experience long distance dispersal events (Nathan et al. 2008) and are consequently more likely to persist following environmental change such as habitat fragmentation or climate change, provided the dispersal vector in question is not similarly negatively affected. There is evidence however that the dispersal vector which a species is capable of using is only one of a number of important life history traits determining species' ability to survive, alongside factors such as species' seed longevity and ability to grow under high nutrient conditions (Soons & Ozinga 2005).

The level of isolation of forest patches is best considered as the amount of reachable habitat within the surrounding landscape, which has been shown to be a more reliable measure of isolation than other metrics based upon distance between patches (Bender et al. 2003). The amount of reachable habitat is likely to depend

upon both the amount and configuration of habitat resources, in addition to the ability of species to exist in surrounding habitats and the number of connecting elements such as corridors of habitat which occur (Henle et al. 2004). These factors all contribute to the level of overall landscape connectivity, which determines the extent to which species can access suitable habitat areas and therefore their capacity to withstand the loss of habitat area or the degradation of patch quality through continued immigration from less affected patches.

2.2.3. Landscape connectivity

Connectivity is defined as the extent to which a landscape facilitates the movement of species amongst habitat resources (Taylor et al. 1993). High levels of connectivity reduce the level of isolation of patches because species are more able to disperse to suitable habitat areas (Taylor et al. 1993; Staddon et al. 2010). Connectivity is therefore an important factor in the response of species to habitat fragmentation and changing climate, meaning accurate measures are required to help guide conservation decisions (Travis 2003; Pascual-Hortal & Saura 2008; Saura et al. 2014). However, measures of landscape connectivity which are based on simple metrics such as number of patches or number of links between patches, often produce misleading results. Where a single large patch is broken into a number of smaller patches covering a lower area for example, these measures increase, despite the amount of available habitat decreasing (Pascual-Hortal & Saura 2006). Measures of connectivity which apply the concept of habitat availability, by which connectivity is considered as the area of reachable habitat within a landscape (thus including the area of habitat patches themselves), are therefore thought to provide a more robust

and realistic assessments of connectivity (Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007; Saura & Torné 2009).

The amount of connectivity within a landscape can be increased through the creation of connecting elements such as corridors of habitat between patches. Such corridors provide paths through the surrounding matrix and have been shown to increase plant species richness in experimentally manipulated systems (Tewksbury et al. 2002; Damschen et al. 2006;). These corridors are particularly effective for wind dispersed seeds where they are oriented such that the prevailing wind travels along the long axis of the corridor (Damschen & Baker 2014). Hedgerows could potentially act as connecting elements between forest patches; with evidence to suggest that some forest species do occur in these linear features, particularly in close proximity to forest patches (Corbit et al. 1999; Davies & Pullin 2007; Wehling & Diekmann 2009). This is unlikely to be effective in increasing connectivity for most core forest specialist plants however, due to the unfavourable edge-like conditions present (McCollin et al. 2000; Smart et al. 2001). The occurrence of hedgerows and lines of trees in surrounding areas of open habitat might even reduce long distance wind dispersal events by interfering with air flows across the landscape (Heydel et al. 2014).

The creation of corridors of forest habitat which are wide enough to include the core forest needed by forest specialist species is likely to be difficult to achieve in practice in agricultural landscapes, due to the disruption that would be caused to surrounding cropland. As such, expanding existing patches may be a more viable approach to increasing connectivity (Peterken 2000). Increased connectivity through

higher patch area is also thought to be of greater benefit for very poor dispersers, for whom links would not exist between even relatively nearby patches if they are separated by hostile land use types (Saura & Rubio 2010). Since many forest specialist species are thought to possess low dispersal ability, they are therefore unlikely to benefit from corridors and links between habitat patches (Wulf 1997; Hermy et al. 1999; Peterken 2000).

The amount of reachable habitat within a landscape is dependent on both the structural composition of the landscape and on species' dispersal abilities and habitat preferences. As such it varies according to the characteristics of the organism considered (Saura & Torné 2009). Connectivity is generally higher for species which are capable of dispersing long distances and are able to reach all suitable habitat within a landscape, either directly or via other habitat patches as stepping stones (Saura & Rubio 2010). The extent to which species can survive in less suitable habitat is also an important determinant of landscape connectivity for species. Intensive arable land can change environmental conditions at forest edges, potentially reducing the amount of available habitat for highly specialised core forest species (Willi et al. 2005; Watts & Handley 2010;). These species are sensitive to the higher disturbance and soil fertility found in more intensively managed habitats.

Maintaining the presence of hedgerows and less intensive land use types in the wider landscape may therefore act to soften the matrix, potentially increasing the connectivity of the landscape for forest species both by reducing the area of edge-like habitat and creating links between patches (Donald & Evans 2006; Fischer et al. 2008). Buffering high value habitat with less intensive land use may therefore be an effective way to conserve forest plant diversity (Thorell & Götmark 2005).

2.2.4. Edge effects

The environment within a forest patch is seldom uniform; soil conditions, disturbance, the density of vegetation and the influence of species from surrounding habitats have all been shown to differ towards forest edges compared to core habitat areas (Murcia 1995; Kennedy & Pitman 2004; Willi et al. 2005). The openness at forest edges also means communities are exposed to greater light availability, air and soil temperatures and wind speed than forest interiors (Gehlhausen et al. 2000). As forest patches lose area, the amount of edge habitat often increases, at the expense of the area of core forest habitat (Laurance & Yensen 1991; Smith et al. 2009). Studies vary in their estimates of the distance edge effects extend into forest patches, but some have observed edge effects over 100 metres from the forest edge, depending on the variable in question and the aspect of the edge, with South or West facing edge habitats extending further into the forest interior (Gehlhausen et al. 2000). In temperate forests however, edge effects rarely extend more than 50 metres into habitat patches (Honnay, Verheyen & Hermy 2002). The variation between environmental conditions at forest edges compared to interior habitat is also reflected in the species composition, with many forest specialist species incapable of surviving in the more fertile, better lit conditions found at forest edges (Pellissier et al. 2013).

Species dependent upon the interior of forest patches tend to possess traits linked to higher shade tolerance and lower dispersal ability such as slow growth and heavy, fast falling seeds (Hermy et al. 1999). Edge species on the other hand are more likely to reflect the surrounding habitat matrix, with traits associated with better lit and more disturbed conditions (Willi et al. 2005). In the more fertile, better lit conditions

near forest edges, weedy, fast growing species are able to outcompete the shade tolerant forest interior specialist species (Gehlhausen et al. 2000; Laliberté et al. 2012). As such, forest specialist species which are dependent on the shaded, undisturbed conditions of forest interiors should be missing from most forest edge habitat (Murcia 1995; Hermy et al. 1999). In reality there is evidence to suggest that forest specialists are not suppressed at forest edges (Harper et al. 2005), provided these are long-established rural edges consisting of well-defined hedges and banks rather than urban edges (Vallet et al. 2010). In long-established forest patches therefore, forest edges may appear to be resistant to invasion from weedy plant species (Honnay, Verheyen & Hermy 2002). Where forest habitats are surrounded by intensive agricultural land however, forest edges are increasingly dominated by species usually found in more fertile habitats (Chabrerie et al. 2013). Maintaining a high proportion of core forest area relative to edge is therefore important for forest specialist plants in agricultural landscapes.

2.2.5. Interdependence of spatial variables

Investigating the effects of different aspects of habitat fragmentation is difficult, because patch size, isolation and edge length are often strongly correlated with each other as well as habitat amount at the landscape scale (Fahrig 2003; Fahrig 1997; Smith et al. 2009). It is therefore important to minimise the confounding correlation between these variables when attempting to compare their effects on plant species. Studies have used a number of methods to attempt to separate the effects of different aspects of habitat loss and fragmentation, such as residual regression, model selection and variance partitioning procedures (Smith et al. 2009). A comparison of these statistical methods found however that correlations between

explanatory variables can lead to a systematic bias in the estimation of their effects. Provided efforts were made to limit correlation between spatial variables and that results were interpreted with caution, standardised partial regression coefficients were found to represent the most reliable way of assessing the effects of habitat fragmentation on measures of biodiversity and community composition (Smith et al. 2009).

Although separating the individual effects of habitat loss and habitat fragmentation is important to help develop management strategies which address the most influential elements of habitat configuration, the interdependence of the different processes and the way this affects species must also be considered. The influence of habitat loss is likely to be modified by the degree of landscape fragmentation present rather than acting independently of it, with the effects of reductions in forest area exacerbated by high levels of fragmentation or mitigated by favourable configurations of remaining habitat (Didham et al. 2012). The inter-correlated effects of habitat loss and habitat fragmentation therefore cannot reliably be attributed to either factor individually. For example, studies suggest that the degree of habitat fragmentation controls the amount of habitat at which a critical extinction threshold occurs (Fahrig 2002). When habitat amount falls below this threshold, species extinction is thought to rapidly increase. Landscapes where habitat occurs in large, closely linked patches are capable of withstanding greater levels of habitat loss without loss of biodiversity than landscapes with small, isolated habitat patches. This interdependence between spatial variables must therefore be considered in order to achieve a proper understanding of the mechanisms by which different aspects of landscape configuration influence biodiversity (Didham et al. 2012).

2.3. Time lags in species response to landscape change

2.3.1. Extinction debts

Many species are slow to respond to the loss and fragmentation of their habitat, with present day community composition showing a stronger relationship with historical landscape structure than modern (Vellend et al. 2006; Ellis & Coppins 2007; Metzger et al. 2009). Perennial plants and species with persistent seedbanks often exist in remnant populations within modified landscapes due to their low rates of population turnover and ability to maintain small populations (Eriksson 1996; Maurer et al. 2003; Lindborg 2007). This results in the formation of extinction debts following habitat loss, where species take time to be lost from patches even where their eventual local extinction is inevitable (Tilman et al. 1994; Kuussaari et al. 2009). Over time however, the species richness of fragmented habitat will fall to the level predicted by the change that has occurred. Such extinction debts in forest plants have been observed for over 100 years following landscape change (Vellend et al. 2006; Krauss et al. 2010). Current conservation measures which protect small patches of ancient forest which have more recently lost area may therefore be overvaluing such habitat, since species are likely to be lost from these patches without further management effort (Berglund & Jonsson 2005).

Species thought most likely to show an extinction debt are those which are long lived, slow colonisers (Ewers & Didham 2006; Kuussaari et al. 2009). This suggests that landscapes with highly fragmented forest habitat are likely to become dominated by weedy generalist species as extinction debts in these species are paid (Santos et al. 2008; Lopes et al. 2009). Taking into account historical habitat

configuration is therefore essential to avoid underestimating the extent to which vulnerable plant species are threatened by habitat loss and fragmentation (Hanski & Ovaskainen 2002; Lindborg & Eriksson 2004).

Hylander & Ehrlén (2013) propose three alternative mechanisms by which extinction debts are created. Habitat degradation through environmental change may render patches of habitat unsuitable in the long term, but the loss of species may not be immediate where the vulnerable species are long lived, leading to remnant populations and extinction debts (Eriksson 1996; Lindborg 2007; Kopecky et al. 2013). Alternatively, the loss of habitat area and resulting reduction in population sizes may increase the vulnerability of species to stochastic events, again however the population may persist for some time before random extinction occurs (Dullinger et al. 2012). Finally, at a larger scale, the loss of landscape connectivity and consequent disruption of meta-population dynamics may leave populations without the necessary immigration from neighbouring patches to save them from extinction, even without any loss of habitat area or quality (Hanski 1998; Hylander & Ehrlén 2013). If the loss and fragmentation of habitat is drastic enough, it could eventually result in the extinction of the entire regional meta-population (Hanski et al. 1996). In theory, each of these processes could occur in habitat independently of the others. The extent to which existing extinction debts are dependent on each of these hierarchical processes is likely to influence the appropriate type of conservation measures to apply to aid threatened species (Hylander & Ehrlén 2013). This may involve attempting to restore habitat quality (Vild et al. 2013), increasing patch area or improving landscape scale connectivity.

Research into extinction debts within forest understorey communities has found that they are largely paid 160 years after landscape change (Kolk & Naaf 2015), however the speed at which communities respond can depend on both landscape composition and the life history traits of the threatened organisms (Kuussaari et al. 2009). Evidence suggests for example that debts are paid off more quickly in landscapes which have very little remaining habitat (Cousins 2009). Habitat within such landscapes is more likely to be well below the extinction threshold - the amount and connectivity of habitat required for long term persistence - leading to rapid extinction of vulnerable species. In landscapes where habitat amount and landscape connectivity are close to the extinction threshold however, meta-populations can remain present for long periods before their eventual local extinction (Hanski & Ovaskainen 2002; Helm et al. 2006). The time taken for any species to be lost from fragmented habitat however suggests that there may be time to develop and implement effective conservation measures to preserve many vulnerable species (Lee & Thompson 2005; Quine & Watts 2009).

2.3.2. Immigration credits

Delays in the response of plant species to landscape change also apply to the creation of new forest habitat. Where secondary forest habitat grows on former agricultural land, differences in the composition of the forest understorey community between ancient and secondary forest are marked (Peterken & Game 1984; De Frenne et al. 2011). Many species which are found in ancient forest habitat are almost entirely absent from secondary forest patches (Wulf 1997; Schmidt et al. 2014). This suggests the existence of “immigration credits” in such habitat, with many species slow to colonise newly created forest patches (Jackson & Sax 2010).

The most important cause of existing immigration credits in forest specialist species is likely to be dispersal limitation (Hermy & Verheyen 2007; Kelemen et al. 2014). In general, species associated with ancient forest habitat are shade tolerant species with large seeds, which do not form persistent seedbanks and reproduce clonally (Hermy et al. 1999; Verheyen et al. 2003). As such, these species possess low dispersal ability and are poor colonisers of new habitat. They are therefore less likely to cross unfavourable matrix types to reach newly created forest habitat which is isolated from ancient forest source populations (Hermy & Verheyen 2007; Brunet et al. 2011). This is likely to be an important driver of immigration credits, since the slow colonisation of forest specialist plants means that any secondary forest patch will take time to accumulate the same richness of forest specialist species found in ancient woodland habitat (Brunet et al. 2011; Naaf & Kolk 2015).

Colonisation of secondary forest habitat by ancient forest species is considerably higher in landscapes with greater amounts of forest habitat present (Honnay et al. 2002; De Frenne et al. 2011). This may particularly be the case where secondary forest habitat is located in close proximity to ancient forest habitat, where richness of forest specialist species approaches the richness of ancient forest habitat after around 80 years (Brunet 2007). Young forest patches which are highly isolated from ancient forest habitat therefore mostly accumulate species adapted for effective dispersal (Brunet 2007; Brunet et al. 2012). This is likely to result in decreased richness of forest specialist species and functional heterogeneity in isolated secondary woodland, making such patches ineffective as reservoirs for vulnerable species (Brunet et al. 2011). Increasing the connectivity between ancient forest

habitat and secondary forest is therefore likely to improve the rate at which new forest patches gain slow colonising ancient forest plant species.

Ancient forest species are shade tolerant, generally preferring forest areas with intermediate pH, fertility and moisture content (Hermy et al. 1999). These local conditions have been shown to vary greatly between recent and ancient forest habitat (Honnay et al. 1999b), with secondary forest grown on former agricultural land retaining many of the abiotic conditions of the former land use (Koerner et al. 1997; Baeten et al. 2011). Soil properties of secondary forest for example differ from primary forest habitat, possessing higher pH and concentrations of nitrogen and phosphorus than old growth forest (Koerner et al. 1997). Where open land has been reconverted to forest therefore, the legacy effects of human activity on environmental conditions leads to distinctive patterns of species richness and composition (Dupouey et al. 2002; Vellend et al. 2007). In some areas where secondary forest habitat is sited on former agricultural land this is the case even after many centuries of continuous forest cover, suggesting that recruitment limitation caused by unsuitable conditions in secondary forests may act as a permanent barrier to many forest specialist species (Dupouey et al. 2002; Flinn & Vellend 2005).

Studies have attempted to test the extent of recruitment limitation in secondary forest by investigating the performance of slow colonising forest species following experimental introduction (Ehrlén & Eriksson 2000; Endels et al. 2004; Graae et al. 2004). In most cases ancient forest plants with low colonisation ability were able to survive in recently established forest habitat, in some cases even appearing to perform better when introduced to secondary forest than in their more usual long

established forest habitat (Donohue et al. 2000). Many of these experiments have been performed over a short period of time however, and given the long lifespan of many forest species it is possible the suppressing effects of secondary forest conditions would be observed at greater time since introduction (Endels et al. 2004). Although transplanted slow colonisers were able to grow in secondary forest habitat, the effects of more nutrient rich soils are highly species specific (Baeten et al. 2009; Baeten et al. 2010). This suggests that while recruitment limitation due to soil conditions does not create a permanent obstacle to the establishment of ancient forest species in secondary forest habitat, it can amplify the effects of already rare immigration events due to dispersal limitations for many forest plants.

2.4. Forest protection and expansion strategies

Forest conservation policy in Britain has recently highlighted the importance of protecting and expanding existing ancient forest area in order to combat the effects of the large scale loss and fragmentation of forest area which occurred across much of Britain prior to the 20th Century (Rackham 1990; Forestry Commission 2003). A number of grants are now available to landowners who are prepared to create new woodland, with the aim of increasing the amount and connectivity of habitat available to forest specialist plants (Welsh Government, 2012). The need to maintain biodiversity conservation in agricultural landscapes must be balanced against the need to meet increasing demand for land for agricultural production however, therefore understanding the likely impacts of different strategies is of high importance (Fischer et al. 2008).

Two contrasting approaches to landscape scale conservation management have been proposed. In “land sparing” situations, agricultural land is optimised for production and consists mainly of large, intensively farmed fields low in heterogeneity and biodiversity (Fischer et al. 2008; Phalan et al. 2011)(Figure 2.2). Biodiversity is conserved in such landscapes in nature reserves which are separate from the agricultural land. This approach has the greatest benefit to species which are incapable of surviving in even a low-intensity agricultural matrix (Green et al. 2005) since the more productive high intensity farmland in theory allows a larger area of high quality habitat reserve to be maintained. This is likely to be of benefit to forest specialist species which require large areas of core forest habitat to sustain viable populations (Petit et al. 2004; Lindborg et al. 2012). Since the fertiliser application and irrigation practices involved in intensive farming often result in areas of the surrounding landscape being affected however, the area “spared” may not be as large as intended while community assembly in newly restored forest will have to contend with abiotic legacy effects such as high residual fertility. Indeed edge effects from surrounding agriculture may result in much of the forest habitat becoming dominated by weedy, generalist plants (Tabarelli et al. 1999; Matson & Vitousek 2006; Chabrierie et al. 2013) and where those remaining forests are embedded in an even more hostile matrix of surrounding habitat.

Landscapes following a “land sharing” (or wildlife friendly farming) approach tend to be more heterogeneous than their land sparing counterparts, with patches of semi-natural vegetation embedded within the agricultural matrix (Fischer et al. 2008) (Figure 2.2). A greater range of crops, smaller fields and retained individual trees and hedgerows within fields all contribute to this higher spatial heterogeneity. Global

declines in these wildlife friendly farming methods are thought to be linked to reductions in biodiversity across many taxa (Donald et al. 2001). The conservation value of such landscapes comes at a cost of decreased agricultural yield however (Donald et al. 2001; Green et al. 2005), affecting resource production and forcing farmers adopting such strategies to rely on external grants to remain economically viable. Furthermore for a lower yield per unit area of farmland more land must be farmed to meet resource needs, reducing the amount of habitat available to species most sensitive to even minor human intervention (Green et al. 2005).

In reality most existing landscapes are likely to be somewhere in between the extreme land sparing and land sharing situations while the continuum is in itself

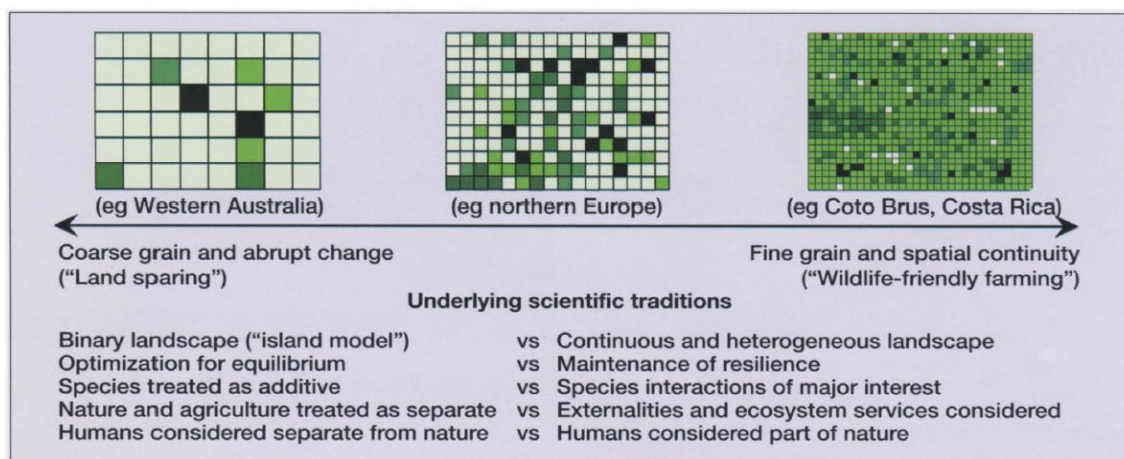


Figure 2.2. Conceptual model of the different ways in which biodiversity conservation and agricultural land can be combined within a landscape. Darker shades of green represent higher conservation value land (reproduced from Fischer et al. (2008)).

scale-dependent. The conservation strategy which is most appropriate is likely to depend both on the species being targeted and the existing composition of the landscape. Forest specialist plants may well benefit most from the formation of large habitat reserves, set aside from agricultural land, because such plants tend to be shade-tolerant species which do not compete well with ruderal species in fertile landscapes or where habitat is grown on former agricultural land (De Frenne et al.

2011; Laliberté et al. 2012). Such habitat reserves are likely to be particularly effective where the conserved forest reserve includes areas of ancient forest habitat (Peterken & Game 1984; Goldberg et al. 2007). Creating protected forest habitat areas by increasing forest area on non-agricultural land to achieve this however is likely to have a number of negative impacts on important species of other semi-natural habitat types.

The expansion of forest habitat at field margins and around stream-sides may provide connecting habitat which increases the ability of species to disperse across a landscape (Saura et al. 2014). In landscapes with larger amounts of forest, newly created forest habitat is more likely to provide links between existing habitat areas, even where not directly connected (Peterken 2000). As such the creation of “stepping stone” habitat is likely to be more beneficial in landscapes with a moderate amount of existing forest habitat. Increased abundance of hedges and semi-natural vegetation in a land-sharing type landscape is likely to protect forest habitat from negative edge effects and provide additional habitat for more generalist forest species, although it is unlikely to be of significant benefit to many ancient forest species however, unless they are capable of occurring outside of ancient forest habitat (McCollin et al. 2000; Thorell & Götmark 2005).

2.5. Summary

A number of factors, both at the patch and landscape scale, are thought to be important drivers of forest species richness and composition. Local environmental conditions are thought to act as a primary set of filters on species occurrence, while larger scale drivers like the area and isolation of habitat patches are also important determinants of forest plant composition (Dupré & Ehrlén 2002; Fahrig 2003; Jacquemyn et al. 2003; Corney et al. 2006; Lindborg et al. 2012). The strength with which these processes act upon species is thought to depend on their traits, potentially creating communities which are more functionally similar as forest habitat becomes more fragmented (Henle et al. 2004; Vellend et al. 2007). Species with traits conferring low dispersal and persistence ability are thought to be most strongly affected by the spatial configuration of habitat (Henle et al. 2004; Lindborg 2007; Ozinga et al. 2009). Since forest plant species are often long-lived with poor colonising capacity however (Hermy et al. 1999; Maurer et al. 2003), changes in community composition take place over long time scales. This means that the effects of the age, history and configuration of forest habitat on patterns of plant species occurrence remains unclear, with current trait and species composition more strongly correlated with past than with present patch configuration. In order to fully understand the likely impacts of the various potential management measures on forest plant communities, better understanding of the way in which the important drivers of plant species occurrence interact in different landscape contexts and in forest patches of differing ages is needed (Didham et al. 2012). As such, this thesis aims to investigate the way in which different aspects of forest spatial configuration and local environmental condition influence forest understorey species richness and

composition and, in particular, the way in which species with different life history traits respond to forest patch area and connectivity given variation in abiotic conditions and patch age. The knowledge gained from this will help to increase understanding of the way in which forest plant communities are formed and inform conservation planning, allowing more effective management measures to be created, tailored to the needs of the most vulnerable or most important species.

3. Identifying the trait syndromes of conservation indicator species: How distinct are British ancient woodland indicator plants from other woodland species?

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This chapter is a replication of a constituent paper of this research that was published in *Applied Vegetation Science*.

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Abstract

Question

Ancient woodland indicator species (AWIs) are plant species which are thought to be restricted to areas of long continuity woodland habitat. In many cases however these species have been identified on the basis of personal, to some extent, subjective experience. Do the species proposed as AWIs according to these lists have traits in common and how distinct is their trait profile from that of other woodland plant species?

Methods

We applied classification tree analysis to a plant trait database to assess the extent to which proposed AWI species can be clearly separated from other woodland plants based upon their traits. We contrasted AWI species with an objectively defined list of plants that are not considered to be AWIs but that have been commonly recorded in woodlands. We also investigate the effects of phylogeny and region specificity on species' proposed AWI status.

Results

The results provide support for the distinctiveness of plant species thought to be associated with ancient woodland; they were found to be almost exclusively short, perennial species, usually with a high seed weight. Results also indicate that rarer AWIs have a more distinguishable trait profile than more common species. No link was found between phylogeny and AWI status.

Conclusions

AWI species do have a distinguishable trait profile, despite their often partially subjective selection. The results of the classification tree analysis suggest that traits reflecting poor dispersal ability may be partly responsible for confining these species to ancient woodlands. This confirms other studies that emphasise their low ability to colonise secondary woodland sites and hence vulnerability to habitat conversion.

3.1. Introduction

Ancient woodland indicator plants (AWIs) are vascular plant species that are considered to be restricted to areas of long-established woodland habitat. Since they were first proposed as a method of assessing the conservation value of woodland in Lincolnshire by Peterken (1974), lists of plants which are considered AWIs in other regions of Europe and North America have been developed (e.g. Honnay et al. 1998, Motzkin et al. 1999, Verheyen et al. 2003).

Areas of ancient woodland, as defined by Peterken (1977), are considered a conservation priority due to their ability to sustain a large number of rare or vulnerable species that are unlikely to colonise isolated younger woodland (Peterken & Game 1984). They may also act as refuges for species dependent on habitat types associated with low farming intensity (Smart et al. 2006). As such, there have been efforts to map remaining ancient woodland habitat (Goldberg et al. 2007) and to protect some of these areas, for example in the UK through notification as Sites of Special Scientific Interest and Priority Habitats under the UK Biodiversity Action Plan (BRIG 2008). AWI species provide a useful means with which to identify ancient woodland and a simple tool to help assess woodland diversity and gauge the continuity of woodland cover, although they should be used in conjunction with historical land use data (Spencer & Kirby 1992).

Despite the conservation importance of ancient woodland and the use of indicator species in identifying such habitats, concerns remain over the way in which species have been designated as AWIs, often based upon anecdotal evidence of their association with ancient forest (Rolstad et al. 2002). Furthermore, few indicator

species are entirely restricted to ancient woodland (Wulf 2003), meaning that a subjective decision must be taken as to which species occur too frequently outside ancient woodland habitat to be considered AWIs. Too stringent a set of requirements and the resulting list of indicators will be too short to be useful, too loose a definition of an AWI and less specialised plant species may reduce the effectiveness of the indicators chosen (Rose 1999).

Here we test whether lists of species suggested as AWIs for different parts of Britain, often defined at least partly in a subjective way, do have distinctive traits such that they might be considered as a guild of woodland specialists. An objective classification tree method was used to explore differences between species that are currently proposed as AWIs compared to non-AWI species by identifying fundamental life-history traits that can be used to separate species from the two groups.

Previous studies have found differences in Ellenberg indicator values between AWI and non-AWI species, with AWIs preferring low light conditions with soils of intermediate nitrogen concentration and wetness (Hermy et al. 1999). However, these Ellenberg values do not represent morphological or behavioural traits and hence offer limited insight into the mechanisms of dispersal, establishment and persistence that define AWI species.

The distribution of species associated with ancient woodland habitat has been shown to be limited by dispersal ability and longevity (Wulf 2003; Hermy & Verheyen, 2007). Short species with heavy seeds are thought to have lower ability to colonise new habitat and adapt to land-use change (Verheyen et al. 2003; Hermy & Verheyen,

2007). Consequently we hypothesise that dispersal-related traits such as seed terminal velocity and seed weight are likely to prove important factors that can be used to group AWI species together. Due to the shade tolerance of AWI species and their association with low to moderate macro-nutrient availability, specific leaf area (SLA) was also expected to differ between AWIs and non-AWIs. While high SLA has been associated with shade tolerance (Hodgson et al 2011) it is also strongly associated with productive, human modified habitats. High SLA therefore may only be an effective predictor of AWI status after taking into account the presence of other trait states that differentiate species along the productivity and land-use intensity gradient.

When analysing the explanatory power of multiple traits across many species, it is important to consider the fact that phylogenetic relatedness may result in non-independence between species due to covariance among traits other than those included in the analysis (Felsenstein 1985). Using phylogeny as an explanatory framework reduces the likelihood of misinterpreting ecological patterns that are driven by common ancestry. AWI species may be largely restricted to certain taxonomic groups. If this is the case, the phylogeny of these species may confound any attempt to separate AWIs from non AWIs based upon specific traits. To investigate the possibility that AWI species can be differentiated as effectively by their ancestral relatedness as by the chosen traits, we performed a second, separate analysis which also attempted to split proposed AWI species from non AWIs, in this case based solely upon their phylogeny.

In Britain AWIs can be indicators of ancient woodland across the whole of their range or only considered such in certain regions, despite being distributed much more widely (Kirby 2006). For example, some species may only be classified as AWIs in relatively more intensively-managed landscapes because ancient woodlands provide the only remaining favourable niche space. The same species may however be more common in semi-natural habitats in less intensively-managed regions, and hence not considered AWIs in these regions because they are evidently not restricted to ancient woods. This wider niche breadth may therefore correspond with a trait profile less readily discriminated from other non-AWI species that occur in the same mid or early successional habitats.

We therefore hypothesise that species that are considered AWIs in only a small number of local areas despite being widely distributed across many regions have a less distinctive, more generalist set of traits than those which are AWIs across the whole of their range. This should make them harder to separate from the non-AWI species pool. Conversely, species may only be AWI in a subset of regions because they are rare. Rarer AWIs may have an even more distinctive trait profile if the reason for their rarity is the possession of specialised trait combinations that are associated with restriction to ancient woods.

In this paper we test the hypothesis that proposed AWI species can be clearly separated from non-AWI woodland species on the basis of traits linked to poor dispersal and adaptation to low light availability during the peak growing season. Having determined the trait differences between the two groups, we test two hypotheses about the trait profiles of AWI species that are indicators only in certain

regions. First, that regional AWIs are less distinguishable from non-AWIs than pan-national AWIs. Second, that those regional AWIs are more distinguishable from non-AWIs but only where they are rare across Britain. Better knowledge of the different sets of traits that are associated with AWI species should provide improved understanding of why their distribution is restricted to ancient woodland and help to develop more effective measures to identify and conserve their habitat in the future. Trait analysis might also suggest other species that might be investigated as possible ancient woodland indicators.

3.2. Material and methods

3.2.1. Classification and regression tree analysis

Classification and regression tree (CART) methods (Breiman et al. 1984) are a set of analytical techniques that can be used to explore and model large sets of data. Their ability to consider interactions between variables and to deal with missing values make them well suited for modelling complex ecological datasets (De'ath & Fabricius 2000). Here, CART analysis was performed on a database of information on the life history traits of British woodland plant species, using the "rpart" add-on (Therneau, Atkinson & Ripley 2012) in the statistical software R (R Development Core Team 2011).

CART models are built by applying a series of splits to an input dataset. At each split the data is divided into two groups based upon the value of the explanatory variable (in this case the plant trait) that results in the groups produced being as uniform as possible in terms of the response variable (here species' proposed AWI status). By applying this method to the plant species data a tree model was produced that

identifies differences between the traits of the proposed AWI species and other woodland plants (Figure 3.1). The extent to which the CART model was able to separate the AWIs from non-AWIs at each split also provided a way of assessing the strength of differences between the two groups of species for each trait, as well as the extent to which the proposed AWI species share common characteristics. In order to further investigate the way in which the tree model used the plant traits to group species as either AWI or non-AWI, the final node into which each species was classified was also extracted from the model (see Appendix 1, Table A1).

The usual procedure in CART modelling is to fit an overly large (and therefore over-fitted) tree model and then prune this back to its optimal level of complexity according to assessment of the cross-validated error (Breiman et al. 1984). Here this was achieved by carrying out 50 sets of tenfold cross-validation and taking an average of the mean cross-validated error of each sized tree, following the method recommended by De'ath & Fabricius (2000). This information was then used to determine the level of tree complexity that provided the lowest mean cross-validated error (here a tree with eight splits). The complexity parameter associated with this size of tree (0.028) was then used in *rpart* to prune the full tree to its optimal size and produce the classification tree model (Breiman et al. 1984). The control settings used for the fitting function in *rpart*; the minimum number of observations in a node before attempting a split and the minimum number of observations in a terminal node, were set at 20 and 5 respectively. Changing these settings had little effect on the pruned tree model. Surrogate variables were used where trait data were missing for a particular split, using data for other variables to estimate the missing values (Breiman et al. 1984). If all potential surrogates were

missing then species were prevented from continuing through the model rather than being sent in the majority direction (as is the default in rpart). In this case sending observations the way of the majority would have biased the model in favour of non-AWIs, particularly since AWIs had a higher proportion of missing data.

Table 3.1 Summary of input variables used to fit the classification tree model.

Trait	Variable type	Possible categories and ranges of values	No. missing values	
			AWI (n = 138)	Non-AWI (n = 423)
Maximum height	Continuous	4-5800 centimetres	0	0
Lifespan	Categorical	Perennial/biennial/ annual	0	0
Growth form	Categorical	Woody species/grass/sedge/ forb/fern/other monocotyledon	0	0
Seed weight (weight of 1000 seeds)	Continuous	0.001-12980 grams	45	66
Seed terminal velocity	Continuous	0.110-5.42 metres per second	66	151
Specific leaf area	Continuous	3.64-86.10 millimetres squared per milligram	54	35
Seed bank persistence	Categorical	Transient seeds/seeds persist for a short time/some persistent seeds/large bank of persistent seeds all year round	39	0
Dispersed by wind	Boolean	True/false	43	0
Dispersed by water	Boolean	True/false	43	0
Dispersed by animal vector	Boolean	True/false	43	0
Dispersed by human vector	Boolean	True/false	43	0

3.2.2. Testing for effects of phylogeny

In order to test for relationships between species' phylogeny and their AWI status a second CART analysis was performed. This involved using molecular phylogenetic data on the genus, family and order of 1888 British plant species, taken from PLANTATT (Hill, Preston & Roy 2004). These phylogenetic factors were used as explanatory variables in a classification tree model, which attempted to distinguish AWIs from non AWIs. The methods used to build and prune the tree model were those described in section 3.2.1. The accuracy with which this model was able to classify these species provided a way of assessing the strength with which AWI status is linked to phylogeny, and therefore whether variation in AWI status can be reliably attributed to species' traits.

3.2.3. Effects of rarity and regional AWI status

The classification tree analysis grouped proposed AWI species into one of two categories based upon their traits; either identifying them as potential AWIs or as non-AWIs. It was predicted that the probability of a proposed AWI species being identified as an AWI would increase with species' rarity, since rarer AWIs were expected to have a more distinct trait profile. However, species commonness and assignment as AWI only in local regions should reflect a more generalist trait profile therefore associated with a greater chance of being classified as a non-AWI. We used multiple logistic regression in the R package MASS (Venables & Ripley 2002) to test the hypothesis that the probability of proposed AWIs being correctly classified by the tree model was related to their rarity and the number of regions for which they are AWIs. Species' AWI status in various areas of Britain; Derbyshire,

Lincolnshire, Carmarthen, North Yorkshire, Dorset, Worcestershire, Somerset and Angus is documented in Kirby (2006) and a count of the number of these (eight) regions in which each species is considered an AWI was used in the analysis. Species' rarity was determined from PLANTATT (Hill, Preston & Roy 2004) and measured as number of occurrences in British 10 km squares in the period 1987-1999. The interaction between rarity and number of AWI regions was also included in the model. Due to the degree of inter-correlation between rarity and number of regions a type III likelihood ratio test was carried out to determine the significance of the explanatory variables. This prevented the order in which variables were entered into the model affecting the results. Out of the 138 AWI species used in the CART analysis, 108 were included in the logistic regression, leaving out 29 AWI species unclassified by the tree model due to lack of data and one species for which information on regional AWI status was not available.

3.2.4. Plant species data

The species used in the classification tree analysis included 138 that had been proposed as ancient woodland indicator plants (AWIs) in at least part of Britain, based on the list collated by Kirby (2006) and 423 other woodland species not considered ancient woodland indicators (non-AWIs) but recorded in quadrats located in woodland as part of the 2007 Countryside Survey of Great Britain (Norton et al. 2012). This approach enabled the use of randomly sampled representative data for woodlands across Britain to define a species pool of non-AWIs that nevertheless occur in woodland habitat. Crucially this reduced the extent to which differences between the traits of AWIs and non-AWIs were obscured by trait differences linked to species preferences for non-woodland habitats. The list of AWIs used was created

by combining twelve existing lists of proposed indicators across Britain drawn up by numerous authors, as described in Kirby et al. (2012). Although a number of the species on these lists were proposed as AWIs based upon independent data showing their association with ancient woodland, some have been assessed based only upon the judgement of the expert surveyors. By comparing the traits of these proposed AWIs with those of other woodland species we aim to establish whether these species do have a different set of characteristic traits and thus are a useful conservation tool.

Eleven plant traits were used to build the classification tree model (Table 3.1), representing those life history attributes considered most likely to differ between AWIs and non-AWIs. This included various dispersal related traits; seed weight, seed terminal velocity and maximum recorded species height (Soons et al. 2004, Thomson et al. 2011). A number of categorical variables were included in the model, relating to species' ability to use a number of dispersal vectors. Species could be assigned more than one dispersal vector; for example a species could be considered both wind and water dispersed. Since recent work suggests that dispersal vector variables based upon seed morphology are in fact weak predictors of the actual ability of species to disperse through the landscape (Tackenberg et al. 2003; Eycott et al. 2007) we expected that these variables would not be successful predictors of AWI status of woodland plants.

In addition to the dispersal centred traits, data on species' lifespan, seedbank persistence, growth form and specific leaf area (SLA) were also used in the classification model. SLA in particular has been shown to be a key trait in determining

plant species' resource use strategy (Westoby 1998) and is also correlated with a number of other traits such as growth rate, leaf lifespan and leaf nitrogen content (Reich et al. 1997). Together these traits therefore represented a number of the competitive and shade tolerant strategies likely to differ between AWIs and non AWI species.

The trait information was obtained from the Electronic Comparative Plant Ecology database (Grime et al. 1995), the LEDA traitbase (Kleyer et al. 2008) and other reference materials including Stace (1997) and PLANTATT (Hill et al. 2004). Where species' dispersal vectors were not available they were inferred from relevant literature and by inspection of plant parts in the illustrations of the British Flora (Ross-Craig 1948-74).

Although efforts were made to minimise gaps in the database through obtaining information from as many sources as possible, the difficulty in obtaining trait data for all species meant that a number of missing values were still present in the database (Table 1). One advantage of CART techniques is their ability to handle missing values without entirely removing incomplete records from the model; however rates of misclassification may be higher for traits with a large number of missing values such as seed terminal velocity due to the lower amount of information present.

3.3.Results

3.3.1. Trait analysis

The final classification tree model (Figure 3.1) retained six of the plant trait variables tested; seed weight, seed terminal velocity, maximum species height, lifespan,

growth form and specific leaf area. None of the four dispersal vector variables nor seedbank persistence were used by the tree model to discriminate between AWI species and non-AWIs, although the effect of these traits may be represented by some of the other variables, for example through the continuous variables describing seed characteristics.

The tree model firstly separated ferns and other monocots (59 species, largely geophytes with underground storage organs) from other growth forms. The AWI status of the former group was best reflected by their seed terminal velocity; those

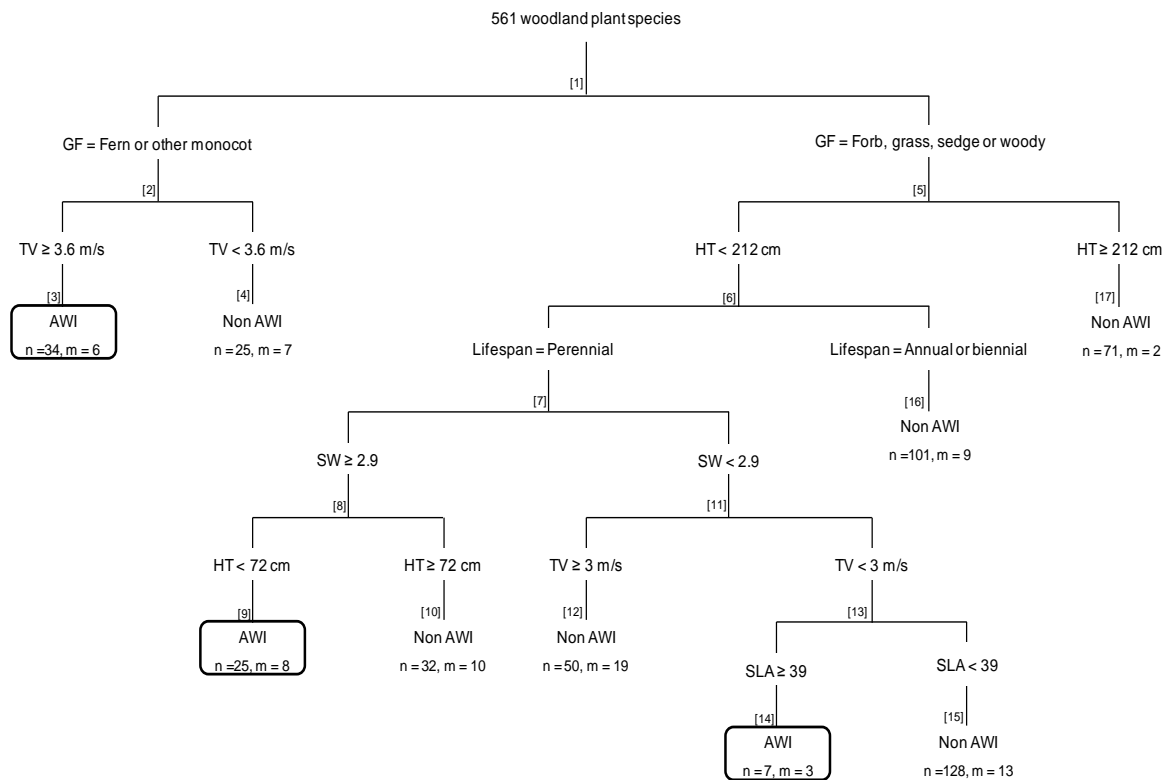


Figure 3.1 Classification tree model showing how different plant trait variables contribute to species' AWI status. Split abbreviations; GF = growth form, TV = seed terminal velocity, SLA = specific leaf area, SW = seed weight, HT = maximum height. Node labels are given in square brackets and can be cross-referenced to the species lists in the appendix (Appendix 1, Table A1). n = number of species within each terminal node, m = number of species misclassified at each terminal node.

with fast falling seeds were classified as AWIs, those with slow falling seeds as non-AWIs (Node 2, Figure 3.1). At this node only 7 proposed AWIs were classed as non-AWI species.

In other growth forms (forbs, grasses, sedges and woody species) tall species were not considered to be AWIs. Only two proposed AWI species had a maximum height of greater than or equal to 212 cm, causing them to be classified as non-AWI species according to the tree model (Figure 3.1). Among those plants shorter than 212 cm, most annual and biennial species were classified as non-AWI species, with 9 proposed AWIs terminating in this node, out of 101 species in total. Of the remaining species (perennial forbs, grasses, sedges and woody species shorter than 212 cm), species with light, slow falling seeds were not classified as AWIs unless they had an extremely large SLA. Species with heavy seeds were classified as AWIs if shorter than 72 cm but not if taller than 72cm.

88 species were not classified due to missing values; 29 AWI species and 59 non-AWIs. The traits that most clearly distinguished the two groups were height and lifespan; these two splits identifying 161 non-AWI species, while only including 11 proposed AWI species. The least certain group, node number 12 on Figure 3.1, contained species with relatively light, fast falling seeds. This group contained almost equal numbers of both proposed AWIs and non-AWIs.

3.3.2. Phylogeny and AWI status

When the genus, family and order of plant species were used to predict their AWI status, the resulting classification tree did not retain any of the three explanatory variables; an optimal tree model was returned which contained no splits. Including

the phylogenetic variables in this model only resulted in the cross-validated error of the tree increasing. This provides strong evidence that phylogeny is not an effective predictor of species AWI status.

3.3.3. Regional AWIs

Results of the logistic regression found no significant relationship between the number of regions for which a species was considered an AWI and its probability of misclassification (Chi squared = 0.0506, $p = 0.82200$). The interaction between rarity and number of regions was also non-significant (Chi squared = 1.0808, $p = 0.29853$). Rarity on its own however did have a significant effect, with rarer AWI species more likely to be correctly classified by the tree model (Chi squared = 4.4219, $p = 0.03548$).

3.4. Discussion

The results of the CART analysis largely support the hypothesis that dispersal-related traits are useful in discriminating AWIs from other plant species found in woodlands. Maximum species height, seed weight and seed terminal velocity all emerged as key correlates with AWI status. Phylogeny was found to have no influence on species' AWI status, with none of genus, family or order being able to predict species AWI status successfully. This indicates that AWIs are not confined to a particular group of related species, rather being spread across a wider range of taxa. Since none of the phylogenetic variables were capable of discriminating successfully between AWI species and non AWIs, it is unlikely that the discriminating power of the traits analysed here is confounded by the common ancestry of these species. Hence these traits seem to be those which best explain the restriction of many proposed AWI species to ancient woodlands.

Small stature, found in almost all AWI species, is associated with a number of strategies for tolerating low light throughout much of the growing season (Westoby 1998). Vernal species are constrained to complete seasonal leaf production and flowering in the narrow window between unfavourable spring temperatures and canopy leafing after which carbon fixation and biomass production is strongly light-limited (Augspurger et al. 2005). Survival for these species may therefore centre on tolerating or avoiding shade rather than growing woody biomass. Where light (or another resource) is less limiting, taller species, identified almost exclusively as non-AWIs, may have the competitive advantage.

AWI plants tend to be perennial species with heavy seeds; traits which other studies have linked to poor colonising ability (Verheyen et al. 2003). Low dispersal ability is thought under some conditions to reduce the ability of species to form viable meta-populations, leading to higher vulnerability to habitat loss and fragmentation and slower response to changes in landscape structure (Fischer & Lindenmayer 2007). The delayed response to landscape change shown by many perennial forest plants can lead to an extinction debt forming in disturbed areas, with a number of existing species destined for eventual extinction under the modified conditions (Eriksson 1996; Kuussaari et al. 2009). Many AWIs in fragmented habitat patches may therefore exist as part of such remnant populations and consequently be at risk of future extinction from such habitat.

As predicted, the dispersal vector variables were not useful in discriminating between AWIs and other woodland plants. This is likely due to the poor ability of

such categorical variables based upon seed morphology to reflect observed dispersal rates of plant species (Tackenberg 2003).

In the classification tree model, traits such as growth form, lifespan and height provided an effective initial separation between proposed AWIs and non-AWI species, suggesting that the two groups tend to have distinct values for these characteristics. Higher misclassification rates at nodes lower down in the tree model may occur because important discriminating information has not been included, either because the values for included traits are missing or because key traits have not been included. However it may also mean that what is important in determining AWI status is the interaction between the plant traits and their landscape context. For example if all that is asked of an AWI is that it occurs much less in secondary woodland than in ancient woodland this could still be consistent with a species occurring in a range of low-productivity mid-successional habitats (e.g. Motzkin et al 1999). Species that are less likely to occur in secondary woodland but can occur in other non-woodland habitats of long continuity include those in node 4, such as the fern *Oreopteris limbosperma* and the horsetails *Equisetum sylvaticum* and *E.telmateia*. These species are predicted by the tree model to be non-AWIs since they have low seed terminal velocity (Figure 3.1; Appendix 1, Table A1) and are widespread in Britain, occurring on linear features such as road verges, streamsides and hedge banks, especially in the more oceanic west and north. They are not however typical of the productive, disturbed conditions that often persist as abiotic legacy effects within secondary woodland (Gilliam 2007). These species may therefore still be valid AWIs where their relative abundance in ancient rather than secondary woodland is more important than their absolute restriction to woodland.

Other species where this applies include *Geranium sylvaticum* and *Stachys officinalis*, both of which are considered AWIs, but also occur outside the woodland environment in unimproved hay meadows, and *Cardamine amara*, *Conopodium majus*, *Hypericum tetrapterum* and *Wahlenbergia hederacea* which occur widely in non-woodland habitats but where they do occur in woodland this is more likely to be of long continuity than secondary.

A number of widespread species (for example at node 9, *Cruciata laevipes*, *Ranunculus ficaria*, *Symphytum tuberosum* and *Viola hirta*) associated with linear features were predicted to be AWI based on their trait sets. The management of such features often involves infrequent pulse disturbance such as cutting that sets back succession creating disturbance regimes and abiotic conditions that resemble those of woodland gaps. Short perennial herbs with limited seed dispersal in space or time are also characteristic of long-established meadows and pastures (Hodgson & Grime, 1990) and hence such species might be classed as having AWI type traits. Examples include *Cirsium acaule* and *Sanguisorba minor* (node 9; Appendix 1, Table A1) both short perennials of grazed calcareous grassland and best considered as outliers within the woodland species pool analysed. Adding in further traits related to shade tolerance, along with traits that could discriminate grazing tolerance might have allowed better separation of these species (Pakeman, 2004).

Preferences of some AWIs for non-woodland habitats may also mean that species are only considered indicators in regions where the non-woodland habitat in which they are found elsewhere in Britain is absent. The situation is however complicated for species such as *Hyacinthoides non-scripta* where the range of habitats they can

occupy changes geographically as a function of temperature and not necessarily habitat availability (Blackman & Rutter 1954). Moving toward the western fringes of the British Isles, mean minimum winter temperatures increase and this frost-sensitive species becomes increasingly common in mid-successional habitats.

Node 15 comprised a large, well-differentiated group of perennial herbs with light, slow falling seeds; likely to be more widely dispersed than the typical AWI (Appendix 1, Table A1). Most were predicted to be non-AWI but a subset of proposed AWIs were predicted to be non-AWI, including *Carex acutiformis*, *C. remota*, *Fragaria vesca* and *Scrophularia nodosa*. All are either grazing intolerant or not favoured by high productivity and so likely to find woodland a favourable refuge. Their wide distribution may however make them less reliable as AWIs.

Rarity was found to have a significant effect on whether or not a proposed AWI species was considered to possess AWI-like traits by the tree model. The rarity of these species may be due to highly specialised sets of traits, such as preference for high levels of shade and infrequent disturbance, which confine them to a narrow range of conditions. These species are likely to be more dependent on ancient woodland habitat and therefore more distinct from other woodland plants with a more general set of traits and consequently looser association with old growth forest.

Other characteristics may differentiate between AWIs and other woodland plants but for which trait data were not available. For example the amount of nuclear DNA that a species possesses is associated with a number of plant traits such as shade tolerance, phenology and generation time (Bennet 1987) and as such might prove

effective in distinguishing AWIs from other woodland plants. Growth rate may also be important, since plants with shade tolerant strategies have lower rates of growth (Coley 1988) thus typical AWI species may have slower growth than non-AWI plants. Inclusion of relative growth rate in the classification tree model may have been able to improve the rate of successful classification but we would expect the discriminatory power associated with this trait to have been captured by specific leaf area given the strong correlation between the two.

3.5. Conclusions

Clear trait-based patterns emerged from the CART modelling, suggesting that a distinct trait profile is associated with AWI species: despite many lists being at least partly based on subjective assessments they do appear to be a distinct guild of plants. In summary an AWI species is most likely to be a short perennial with heavy, fast falling seeds; often poorly dispersing species, not favoured by intensive disturbance regimes and high productivity. Such a step constitutes a useful generalisation that subsumes taxonomic identity and should aid further understanding of the mechanisms that confine these species to older woodlands. This knowledge may help better parameterise models of landscape connectivity for resilience mapping (e.g. Vos et al. 2008).

The functional distinctiveness of AWI species provides some support for the use of such species as a group to identify areas of conservation importance. However we also found trait-based similarities between many AWI species and non-AWIs that are found in rarer, less frequently disturbed semi-natural habitats. Some of these might

merit further investigation to see if they might also be AWI where they occur in woodland.

The strength of the association between these AWIs and ancient woodland habitat depends on landscape context. This should be considered when using the presence or absence of such indicator species to assess the conservation importance of woodland habitat. Rarer AWI species were more clearly discriminated from non-AWI woodland species on the basis of their traits and as such these species may be most reliable as indicators of ancient woodland.

4. Traits of plant communities in fragmented forests: The relative influence of habitat spatial configuration and local abiotic conditions.

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Abstract

1. The plant trait composition of forest fragments is thought to be partly determined by forest spatial properties, although the relative importance of habitat configuration and local abiotic drivers is poorly understood.
2. To address this issue, large-scale habitat extent data were combined with detailed field survey information for temperate broad-leaved deciduous forest patches to quantify the relative effects of spatial and abiotic filters on plant community mean trait values.
3. Local conditions such as shade and soil fertility had the largest effect on mean trait values, but aspects of habitat configuration also had significant partial effects on a number of traits.
4. Mean trait values within older forest patches were more strongly influenced by forest spatial configuration than in younger patches.
5. *Synthesis.* Results indicate that, in addition to the effects of greater light availability and competition in small patches and at forest edges, aspects of habitat configuration such as patch size and isolation are themselves important factors limiting the occurrence of forest specialist species. Large areas of core forest habitat contain a greater proportion of rare, poor dispersing species, although these effects were less visible in more recently established forest. This highlights the importance of maintaining existing large and old forest patches as a refuge for forest specialist plants. The results of this comparison of spatial and abiotic variables suggest that controlling the spatial properties of forest patches is likely to prove an effective way of

managing plant species diversity, provided that sites with appropriate abiotic conditions are chosen.

4.1. Introduction

Forests, particularly those of long continuity, are a conservation priority in many areas due to their potential to act as a refuge for rare or threatened species (Peterken & Game 1984; Wulf 1997). An assessment of the way in which the spatial configuration of these habitats affects species with different life history traits is therefore essential to allow accurate modelling of the impacts of ongoing landscape change on forest specialist plants. Urbanisation and agricultural intensification have dramatically changed landscapes worldwide, causing the fragmentation and loss of many habitat types (Foley et al. 2005). In a fragmented landscape, habitat availability is reduced for target organisms, with favourable patches generally smaller and less well connected. Consequently the populations of species which are dependent on this habitat may be smaller and at greater risk of localised extinction (Fischer & Lindenmayer 2007). Here, the effects of a number of variables describing forest configuration, condition and history upon plant community mean trait values were investigated. The aim was to quantify the partial covariance between mean trait values and forest spatial configuration given variation in patch age, soil quality and levels of shade, thus allowing the strength of the effects of both spatial properties and local abiotic conditions on mean trait values within forest patches to be compared.

Although species with particular life history traits exhibit a negative response to habitat loss and fragmentation, the occurrence of most plant species is dependent upon habitat quality rather than habitat configuration (Dupré & Ehrlén 2002). Direct

filters such as substrate pH, soil moisture and macronutrient availability within forests are strongly related to plant species occurrence (Critchley et al. 2002; Corney et al. 2006; Smart et al. 2010) and as such may be the biggest drivers of mean trait values. Light availability at ground level is also important, since a number of forest specialists possess traits such as high specific leaf area and small stature which make them well adapted to low light conditions (Hermy et al. 1999). It was therefore hypothesised that mean trait values in this study would be more strongly affected by local abiotic condition variables than forest spatial configuration.

Species that are most vulnerable to the effects of landscape fragmentation and habitat loss tend to be those that have characteristics that do not favour effective dispersal in space or time (Henle et al. 2004; Kolb & Diekmann 2005; Ockinger et al. 2010). Species with fast falling seeds and no persistent seedbank are generally less able to rescue threatened populations through immigration from nearby patches (Jacquemyn et al. 2003; Ozinga et al. 2009; Schleicher et al. 2011; Jacquemyn et al. 2012). Dispersal method is also important, with abiotically dispersed species more prone to extinction in fragmented landscapes than those which are capable of dispersing via animal vectors (Marini et al. 2012). Consequently species possessing traits such as these occur less frequently in small, isolated habitat patches, which become dominated by a higher proportion of more persistent, longer lived and better dispersed species (Kolb and Diekmann 2005; Lindborg 2007). Factors such as patch area and the amount of forest habitat in the surrounding landscape should therefore be important determinants of mean trait values within forest patches, as should distance to the nearest forest edge, since species dependent upon the interior of forest patches tend to possess traits linked to higher shade tolerance and

lower dispersal capability (Hermy et al. 1999, Pellissier et al. 2013). The presence of lag effects, which result in a lack of coupling between contemporary habitat structure and species composition (Lindborg & Eriksson 2001; Purschke et al. 2012) may however reduce the strength of this association.

Human activity has long lasting effects on abiotic conditions and therefore on patterns of species richness and composition within secondary forests (Dupouey et al. 2002; Vellend et al. 2007). As such, mean trait values within more recently established forest patches are likely to be more strongly determined by these historical environmental effects than by forest configuration, particularly where sited on former agricultural land with conditions which are unfavourable to many forest specialist species (Dupouey et al. 2002). Conversely, older patches are likely to contain a greater proportion of ancient woodland indicator species, characterised by poor competitive and colonising ability (Verheyen et al. 2003; Kimberley et al. 2013); traits which are likely to make them more vulnerable to habitat loss and fragmentation. These species should be more frequent in large patches or far from the edges of forests, but mainly in the long-established habitat in which they almost exclusively exist due to time lags caused by the slow colonisation of younger forests by ancient woodland specialists (Jacquemyn et al. 2003). For these reasons, trait values in older forests should be more dependent on habitat configuration than those in younger forests.

In summary the following hypotheses were tested;

1. Variation in abiotic conditions exerts a stronger selective filter on mean trait values than forest spatial configuration and age.

2. Relationships between forest spatial configuration, patch age and mean plant trait values in British forest patches are still detectable having accounted for variation in abiotic conditions.
3. The spatial properties of older forest patches have a stronger effect on mean trait values than those of younger patches.

4.2. Materials and methods

4.2.1. Plant trait data

Plant species occurrence data were collected in 406 randomly stratified sampling plots located in broadleaved deciduous forest habitat within 1 km² regions across Great Britain as part of the 2007 Countryside Survey (Norton et al. 2012). Mean values for a number of life history traits within each of these plots were obtained by averaging available trait data across species present. The mean trait values obtained were then used as response variables in the subsequent modelling. To allow the amount of shade present to be included as an explanatory variable without introducing circularity to the analysis, trees and shrubs were excluded from this process. Mean trait values were left un-weighted by species' abundance. This approach places each species, whether subordinate or dominant, on an equal footing and avoids confounding the results by introducing the influence of variation in cover as a result of local competitive sorting. Plant trait information was obtained from the Electronic Comparative Plant Ecology database (Grime et al. 1995), the LEDA traitbase (Kleyer et al. 2008), Stace (1997) and PLANTATT (Hill, Preston & Roy, 2004). Species' rarity was obtained from PLANTATT (Hill, Preston & Roy, 2004) as the number of occurrences in British 10 km squares in the period 1987-1999.

In total, 445 species were present across the vegetation sampling plots. The difficulties in obtaining trait data for so many species meant that data were not available for all traits for all species. The five traits tested, along with the percentage of species with missing values were; log natural seed weight (23.4%), seed terminal velocity, (35.5%), specific leaf area (10.3%), seedbank persistence (39.6%) and rarity (0.9%). Following the Bayesian approach of Thompson & McCarthy (2008), missing trait values for species were drawn randomly from a posterior statistical distribution of trait values which was created based upon the distribution of known values for other species within the same family, using a hierarchical model written in WinBUGS (Lunn et al. 2000). This approach is superior to simply imputing mean values since missing values were estimated taking into account all available information for related species.

4.2.2. Local conditions

The approach taken was to include measurement of influential abiotic conditions in the analysis but to treat them as “nuisance” covariates whose effects would be removed prior to estimating the magnitude of the effect of forest spatial configuration on mean trait values. By including both the spatial characteristics of forest patches and data on local conditions in the same analysis it was possible to evaluate the relative importance of these different sets of variables in determining the mean trait values within forest habitat.

Two types of Countryside Survey vegetation sampling plot were employed in the analysis, linear plots (10 m² in area), located parallel to forest streambanks and forest tracks, and area plots (200 m² in area), located within the wider areal extent of each

patch but not sampling a linear feature. Shade was estimated on a three point scale for all vegetation plots and plots designated unshaded, partially shaded or fully shaded by field surveyors. Within each of the area plots (n = 87) soil pH, volumetric soil moisture content and carbon to nitrogen ratio were measured based on a 15 cm topsoil sample taken at the same time as the flora was recorded in each plot. In the linear plots (n = 319) directly measured soil data were not available. Values within these plots were estimated using published equations derived from a national calibration of observed values of the three soil variables against the mean Ellenberg values of plants in 1033 plots from a stratified, random sample of the range of British vegetation types (Smart et al. 2010). The mean Ellenberg values used in these equations to generate soil variables were derived only from the trees and shrubs which were excluded from the calculation of mean trait values, thus avoiding the problem of circularity when the estimated soil variables were used to model mean trait values. In order to account for differences in response between the area and linear plots, plot type was included as a categorical explanatory variable. Climate and residual geographic variation across Britain were accounted for by the inclusion of the northing of each sample plot as a continuous explanatory variable (Corney et al. 2006).

4.2.3. Spatial woodland variables & patch age

To determine the configuration of forest patches around vegetation samples, the geo-referenced Countryside Survey plot data was overlain with forest extent data obtained from Land Cover Map (LCM) 2007 using ArcMap 10.0 software (ESRI 2011). LCM 2007 is a satellite-derived dataset containing information on the spatial extent of various habitat types across Great Britain (Morton et al. 2011). Use of this data set

enabled the spatial configuration of broadleaved forest patches in the wider landscape around vegetation plots to be assessed.

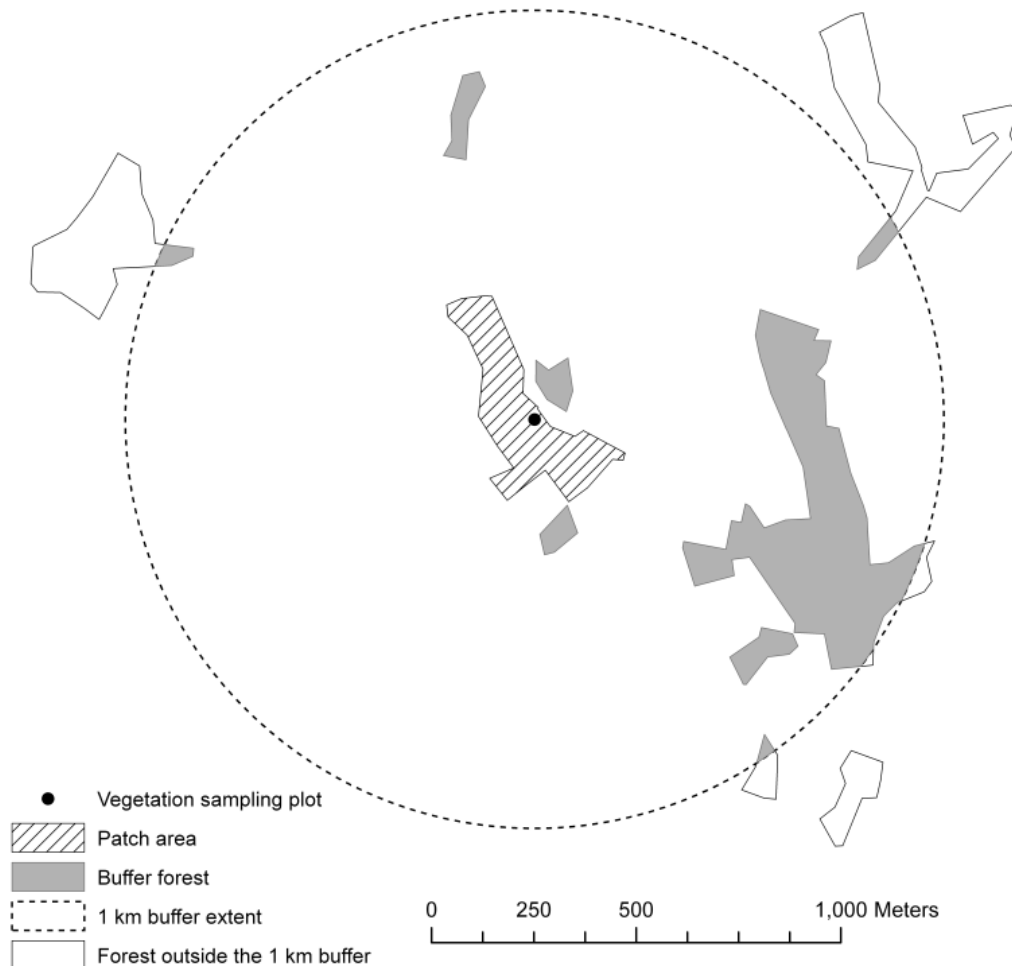


Figure 4.1 Map showing an example Countryside Survey vegetation sampling plot and surrounding Land Cover Map forest data. These data were used to calculate the various spatial metrics for the patch in which the plot occurs. The hatched area of forest habitat shows “Patch area” while the grey shaded area represents “Buffer forest”. Forest habitat outside the 1km buffer area was not considered within the Buffer forest variable, even where contiguous with patches inside the buffer.

Figure 4.1 illustrates the spatial variables obtained from the various data sources for an example Countryside Survey vegetation plot. These were “patch area” (the area of the forest patch containing the vegetation sampling plot), “distance to edge” (the Euclidean distance between each vegetation plot and the nearest point of forest

edge) and “buffer forest” (the percentage of forest habitat within a 1 km buffer area around the vegetation plot). To reflect the fact that the majority of plant species have maximum dispersal distances of less than 1 km (Thompson et al. 2011), only forest habitat within 1 km of vegetation sampling plots was considered. Forest area further than this was therefore assumed to be too far away from vegetation plots to have a significant impact on trait values and therefore not included in this statistic, even where contiguous with patches within the 1 km area. Patch area and distance to edge were both natural log transformed prior to inclusion within the modelling, to reduce the positive skew in their distributions.

Finally, the age of forest patches was estimated using First Edition Ordnance Survey maps (County Series) dated from 1849 to 1899. Presence or absence of woodland patches on these historical maps was used to divide present day woodland patches into either younger woodland (established after 1899, $n = 255$) or older woodland patches (established before 1899, $n = 151$).

4.2.4. Statistical modelling

Mean trait values within forest patches were modelled using the various local conditions and forest spatial properties described earlier. For each trait a full linear mixed effects model, containing all of the spatial and abiotic explanatory variables, was built. Interactions between forest age and patch area, buffer woodland and distance to edge were also included and all models were fitted using the Countryside Survey 1 km square identifier as a random intercept. This accounted for spatial autocorrelation caused by the presence of multiple plots within the same 1 km sampling region.

The R package MuMIn (Barton 2012) was then used to fit all subsets nested within the full model described above. Models were standardised following the procedure of Grueber et al. (2011), in order to provide effect sizes on a comparable scale. To avoid bias resulting from the low ratio of observations to parameters, models were compared using an adjusted Akaike information criterion (AICc) statistic, as recommended by Burnham and Anderson (2002). AICc is a measure of model performance which compares the maximum likelihood estimate of models, adjusted for increasing model complexity. The model with the lowest AICc value is considered the best performing model (of the set tested). All models with AICc values within 4 of the lowest value were then selected as a “confidence set”, thus including possible models possessing a considerable level of empirical support (Burnham and Anderson, 2002). These confidence sets were then used to derive relative importance values and model averaged effect sizes for each explanatory variable. Relative importance represents the probability of a variable being present in the best performing model for a particular trait, and was calculated in MuMIn using the relative Akaike weights of models within the confidence set (Burnham and Anderson 2002). Model averaged effect sizes were calculated for each explanatory variable by averaging the parameter estimates across each model in which a given variable occurred. 95% confidence intervals were also generated for these effect sizes and a significant effect of a variable is indicated where the confidence intervals do not overlap with zero (Grueber et al. 2011). The resulting statistics provide a way of assessing which spatial, age and local variables affect each trait, and the magnitude of these effects. Recent work on the same plant species pool showed that their traits helped discriminate ancient woodland specialists from other woodland species yet

segregation of species into either group was not explained at all by phylogeny (Kimberley et al. 2013). It is therefore unlikely that ancestral relatedness is responsible for artefactual correlations between traits and the explanatory variables used to quantify forest age and patch geometry. For this reason phylogeny was not included in any analyses.

4.3.Results

4.3.1. Selection probability

The relative importance values shown in Table 1 indicate the probability of each explanatory variable being selected in the best performing model (of the set tested) for each plant trait. Where a selection probability > 0.50 the variable in question is more likely to be included in the best performing model than not, and is therefore considered an important predictor. Abiotic predictors had a selection probability > 0.50 in a higher proportion of cases (20 out of 30) than the spatial/age predictors (11 out of 35) although both sets of variables were important predictors across the range of traits. This suggests that a strong local filtering effect is operating upon mean plant trait values but that forest spatial configuration is still an important driving factor.

Table 4.1 Probabilities of spatial and local abiotic explanatory variables being included in the best performing model of the model set tested for five life history traits. Variables with a selection probability of greater than 0.5 are shown in bold.

Explanatory variable	Seed weight	Seed terminal velocity	Specific leaf area	Seedbank Persistence	Rarity	Important responses
Spatial/age variables						
Distance to edge	0.53	0.77	0.40	0.34	0.52	3
Patch area	0.18	0.31	0.19	0.91	0.82	2
Buffer forest	0.21	1.00	0.19	0.44	0.28	1
Age	0.35	0.78	0.58	0.65	0.58	4
Age x Distance to edge	0.11	0.74	0.05	0.17	0.13	1
Age x Patch area	0.14	0.04	0.01	0.47	0.43	0
Age x Buffer forest	0.01	0.14	0.00	0.06	0.05	0
Abiotic variables						
Shade	1.00	1.00	0.94	1.00	1.00	5
C:N ratio	0.75	0.17	1.00	0.18	1.00	3
Soil moisture	0.58	1.00	1.00	0.19	0.47	3
Soil pH	0.20	1.00	0.50	1.00	0.72	4
Plot type	0.16	1.00	1.00	0.10	0.21	2
Northing	1.00	0.49	0.22	0.81	1.00	3

4.3.2. Model averaged effect sizes

Seed weight

Amount of shade present had the strongest effect on mean seed weight values in vegetation sampling plots, with significantly heavier seeds found in plots which were fully shaded compared to plots which were fully lit (Figure 4.2a and Table A2 in Appendix 2). Increasing northing and C: N ratio were both found to lead to a significant reduction in mean seed weight, albeit with an effect size of lesser magnitude. Despite distance to nearest edge having a high probability of inclusion in the best performing model it was only found to have a weak effect on mean seed weight values.

Seed terminal velocity

Seed terminal velocity was significantly affected by a number of the local condition variables, with amount of shade again having the strongest effect (Figure 4.2b, Appendix 2, Table A3). More shaded plots were found to contain sets of species with faster falling seeds, as were plots with a low soil moisture content and a high soil pH value. Although the local condition variables had the strongest effect on mean seed terminal velocity values, the amount of buffer forest also had a significant effect on this trait, with species with faster falling seeds found in patches with more forest habitat in the 1 km buffer area. Furthermore, the effect size observed for this spatial variable was similar in magnitude to the effects of soil moisture and soil pH. This suggests that the spatial structure of forest habitat is influencing plant species composition with a similar degree of strength to the local conditions.

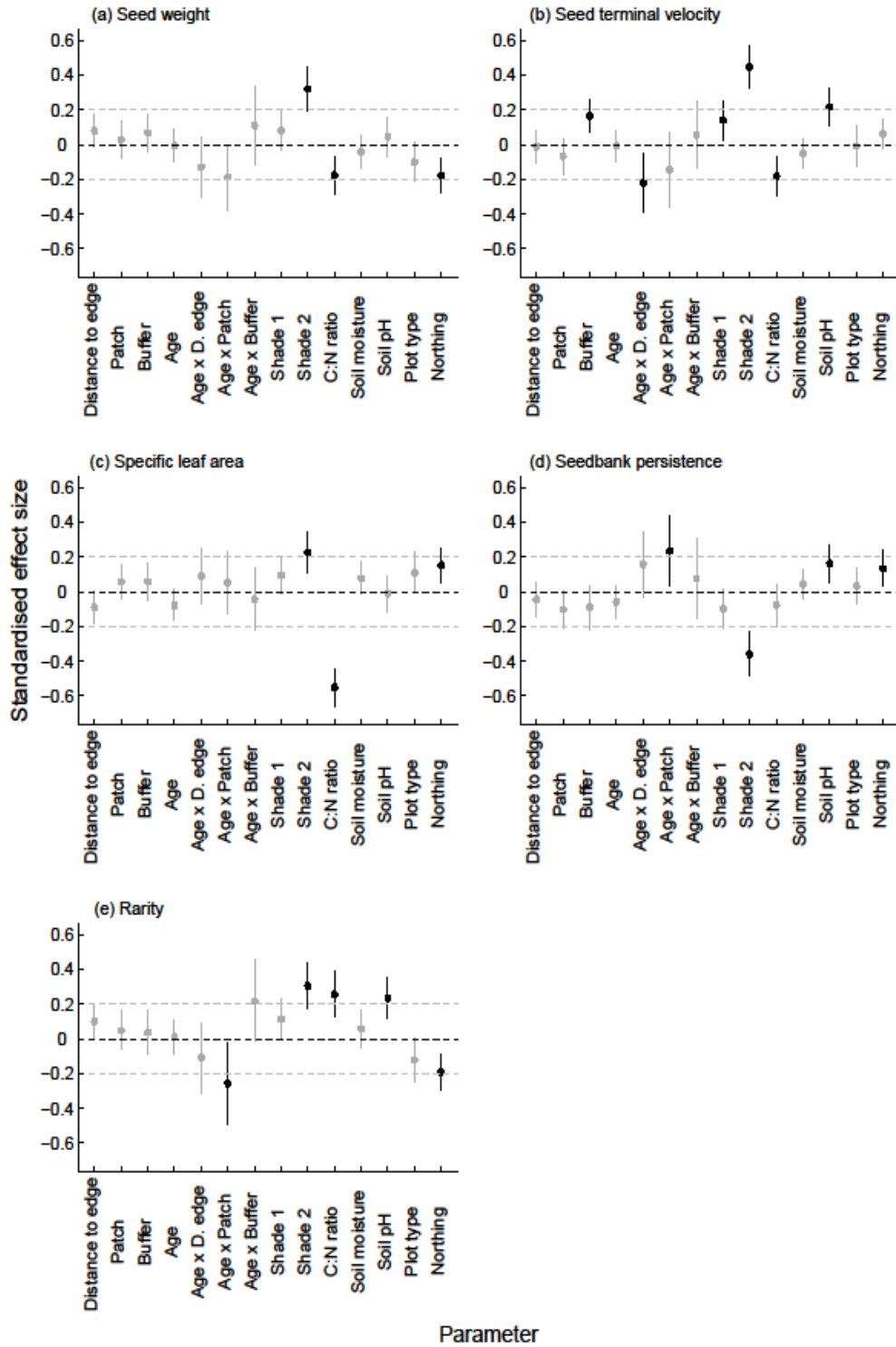


Figure 4.2 Model averaged effect sizes of 14 explanatory variables on mean trait values in forest plots. Points show the average effect size taken from multimodel inference analysis, while the error bars indicate 95 percent confidence intervals. Where the confidence intervals do not overlap zero (black points), a significant effect is indicated. The further a point is from zero, the stronger the effect. Dashed horizontal lines at +0.2 and -0.2 delimit small from medium sized effects according to Cohen (1988). Shade 1 shows the difference between unshaded and partially shaded plots, Shade 2 the difference between unshaded and fully shaded.

A significant effect was also found for the interaction between forest patch age and distance to nearest patch edge. This suggests that the influence of core forest habitat depends upon the age of the patch in question. As Figure 4.3 suggests, the relationship between mean seed terminal velocity of plots and increasing distance to the edge is slightly stronger in older habitat than in younger.

Specific leaf area

Although none of the spatial variables tested were found to influence mean specific leaf area (SLA) values within plots (Figure 4.2c and Appendix 2, Table A4), a strong relationship was identified between the levels of soil carbon present and mean SLA. Where soil C: N was high, lower SLA values were observed within plots. Increasing shade also had a significant, albeit smaller effect on this trait, with heavily shaded plots containing species with a higher mean SLA than more open plots. Mean SLA values were also higher in more northerly plots and in plots with lower soil moisture.

Seedbank persistence

The amount of shade present was found to have the strongest effect on mean seedbank persistence values, with fully-shaded plots containing species with a less persistent mean seedbank than non-shaded plots (Figure 4.2d). Weak but still significant relationships were also found between increasing soil pH and increasing Northing and higher mean seedbank persistence.

The interaction between age and patch area had a weak but non-significant (at the 95% confidence level) effect on mean seedbank persistence values within vegetation sampling plots (Figure 4.2d and Appendix 2, Table A5) suggesting that the

relationship between patch area and mean seedbank persistence may be stronger in older forests than younger forests. This is supported by Figure 4.3, where mean seedbank persistence decreases with increasing patch area in old forest patches but shows little response in younger forest patches.

Rarity

Forest patches with high levels of shade and soil C: N contained a greater proportion of rare species. Conversely, plots in the north of Britain were found to have, on average, species which are more common (Figure 4.2e and Appendix 2, Table A6). Again, the spatial variables did not have a significant effect on rarity considering all forests together, but patch area was found to have a stronger effect on mean rarity in older forests, shown by the significant effect of the interaction between patch area and patch age in Figure 4.2e. Figure 4.3 suggests that, in older forest patches, as the area of forest patches increases, the average rarity of species present increases.

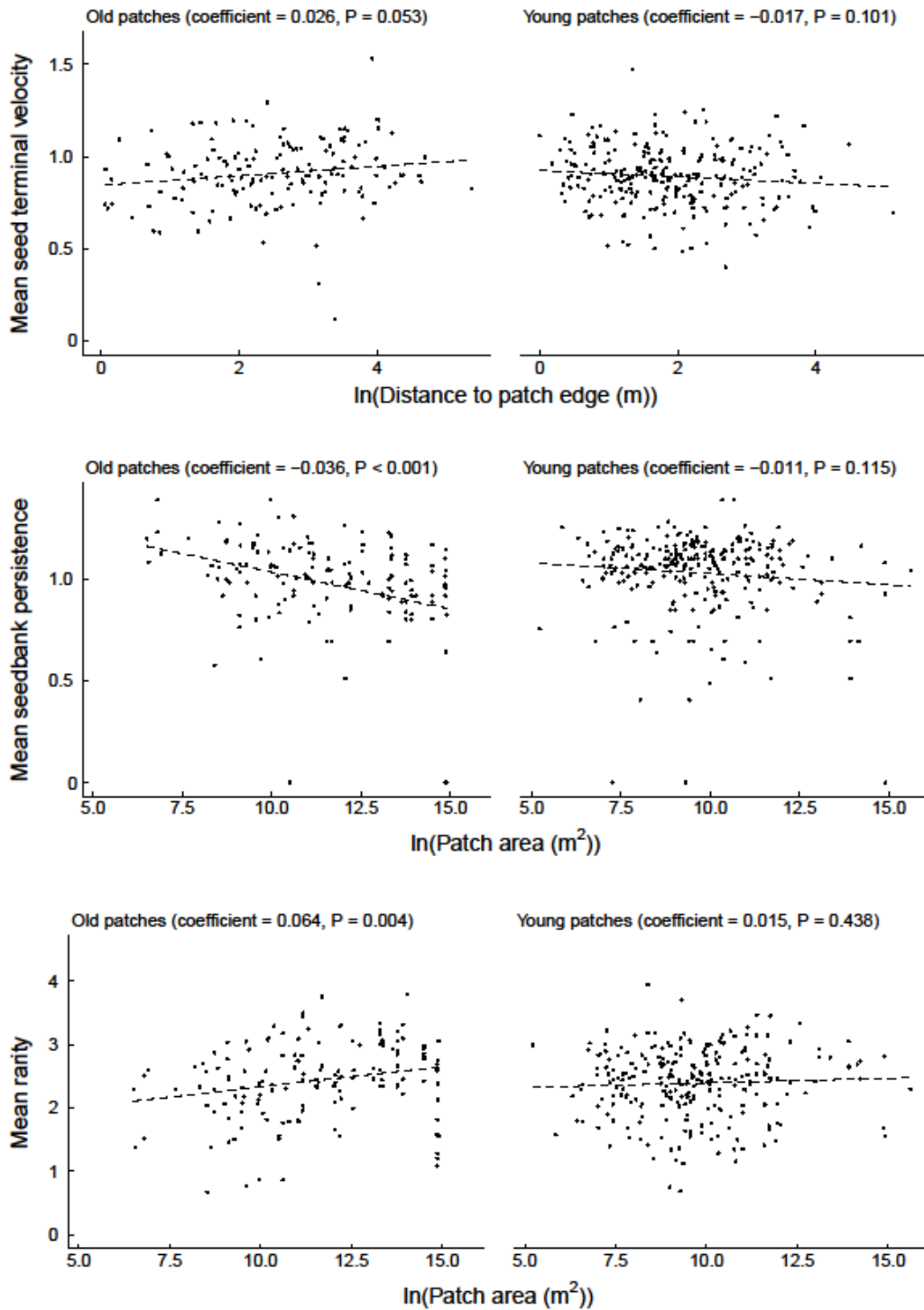


Figure 4.3 Relationships between spatial variables and mean trait values in older forest and young forest patches. Patch area and distance to patch edge were both log transformed. Dashed lines represent a linear model of trait versus spatial predictor. Regression co-efficients and p-values for these models are also displayed.

4.4.Discussion

4.4.1. Abiotic conditions

As expected, abiotic conditions within forest patches were found to be key determinants of plant species composition. Principal amongst these was the amount of shade in vegetation plots, which had the strongest effect on four of the five traits tested. These patterns likely reflect the different strategies needed to survive in relatively open woodlands compared with more dense forest habitat. For example, greater light availability has been shown to favour species possessing traits associated with a high relative growth rate, such as lower seed mass (Reich et al. 1998). Such patterns were observed in this study; well-lit forests contained species with significantly lower mean seed weights and mean seed terminal velocities compared to plots which were fully shaded. Species found in shadier patches had a less persistent seedbank on average, possibly since soil turnover is an unpredictable and rare event in forest environments. Persistent banks of buried seeds are a less common regenerative strategy in these conditions than, for example, non-flowering ramets or cohorts of persistent juveniles (Grime 2001).

The effect of increasing shade on mean SLA values supports previous work showing that, under low light conditions, shade tolerant species possess higher SLA (Hodgson et al. 2011). In temperate broadleaf forests such as those studied here, thinner leaves, and hence higher SLA, promote greater light capture for least expenditure on structural tissues which can then afford to be shed every autumn. This is in contrast to tropical forest trees where the longer growing season favours year round

photosynthesis and growth but at a cost of greater investment in structural tissue, resulting in lower SLA (Baltzer & Thomas 2010).

Increasing soil C: N ratio had the strongest effect on mean SLA values; on more productive soils (those with a low C: N ratio) mean SLA values were higher. Under these conditions high macronutrient availability can fund growth strategies that divert resources into rapidly accumulating plant biomass comprising leaves of low longevity and higher tissue nitrogen content (Ordoñez et al. 2009). This is consistent with the link between soil fertility and leaf mass per unit area revealed by the Leaf Economics Spectrum (Wright et al. 2004). Thus in temperate forests high SLA is not a reliable indicator of shade-tolerance associated with ancient forest because in some areas high SLA can also indicate the presence of nutrient-demanding generalist herbs (Hodgson et al. 2011).

Other multivariate studies have assessed the effects of spatial and abiotic factors on community composition using species occurrence data, thus only accounting for their overall effect on various different traits (Foster et al. 1998; Vellend et al. 2007). In this study mean trait values were analysed separately, allowing the differences in the way traits respond to important variables to be detected. Care must be taken when interpreting these results however, due to correlations between pairs of traits. For example, part of the observed effect of shade on seedbank persistence may be due to the close relationship between this trait and seed mass (Westoby et al. 2002) which is also linked to light availability.

4.4.2. Importance of habitat configuration

Previous studies have related changes in the composition of forest vegetation with alterations in environmental conditions and levels of disturbance following land use changes (Foster et al. 1998). Our findings confirm the links between prevailing abiotic conditions within forest patches and mean community trait values, but also indicate that forest habitat configuration has an important effect. Rare species with fast falling seeds and no persistent seedbank responded to both the area of forest patches and the amount of surrounding forest habitat, even when abiotic factors were accounted for. This suggests that such species are not restricted to large, old forest fragments solely due to the increased disturbance and competition at the edges of small or young patches, but also because aspects of landscape context such as patch size and isolation are acting as important filters on the occurrence of these species.

Conservation strategies often centre on protecting and increasing areas of existing forest habitat (e.g. Forestry Commission 2011); particularly in land sparing scenarios where large habitat reserves, separate from an agricultural matrix, are the main focus of efforts to conserve biodiversity (Phalan et al. 2011). The results of this study provide some support for such measures, since positive relationships were found between the presence of large core forest areas and the occurrence of rare, poorly dispersing species, even after accounting for abiotic environmental conditions. Increasing the size of forest patches should therefore help to promote the occurrence of many forest specialist species. The effects of patch area and buffer

forest however were often secondary to those of abiotic factors such as shade and soil C: N ratio. This suggests that the maximum benefit to these species will be obtained by focussing conservation and restoration efforts on areas where the soil and shade conditions are most favourable. Attempts to increase characteristic forest biodiversity on unfavourable sites may lead to any positive effects of extra available tree cover being negated by the stronger effects of soil fertility and light availability. In addition to the effects of forest configuration observed here, other aspects of landscape structure may also be important determinants of mean trait values. The heterogeneity of the matrix landscape around forest patches for example is likely to affect the ability of poorly dispersing species to colonise habitat patches (Matlack & Monde 2004), while large amounts of nearby woody linear features may act as a refuge for forest specialist plants, increasing resilience to patch area and isolation (Petit et al. 2004). In addition to these other important possible covariates, the high levels of noise relative to signal found in large-scale randomised survey samples such as Countryside Survey (Smart et al. 2012), may explain the small effect sizes seen here for most variables.

As hypothesised, plant community mean trait values within younger forest patches were not strongly affected by forest spatial structure, possibly due to the absence of the inefficient dispersers which are most affected by habitat structure and typify older forests (Verheyen et al. 2003; Schleicher et al. 2011). Large areas of young forest habitat may be missing many of these species, despite providing suitable habitat. This immigration credit (Jackson & Sax 2010) may result in a future change in trait composition towards one that more strongly reflects patch spatial

characteristics, as the recently established forest is gradually colonised by poorer dispersers. Any newly created habitat however is likely to take time to realise benefits to biodiversity, with studies suggesting that secondary woodlands take around 70 years to develop a similar level of species diversity to ancient forests (Flinn & Vellend 2005). Achieving this rate of community assembly also critically depends upon adjacency to existing ancient forest (Brunet et al. 2011).

Ancient forest habitat is generally thought to be of higher conservation value due to its ability to sustain a large number of rare species that are considered less capable of colonising isolated younger forest (Peterken & Game 1984). Our results suggest that this is, on average, only the case for large older patches. Smaller forests, even where they are of long continuity, are less able to support these rare species (Figure 3). Although ruderal species possessing lighter seeds and more persistent seedbanks are not characteristic of the flora of long continuity forest habitat, they were still found to dominate the flora of older yet smaller forest patches. Moreover, species with no persistent seedbank were more frequent only in forest patches which were both large and old (Figure 4.2d, Figure 4.3). Higher mean values for seed terminal velocity were also observed at greater distances to forest edge in older forests (Figure 4.2b, Figure 4.3), suggesting a clear distinction between core and periphery species. In order to obtain the conservation benefits of old growth forest, such habitat must also be large in size and contain a high proportion of core habitat. Priority should therefore be given to measures that maintain and increase the area of old growth forest habitat where the aim is to conserve rare, poorly dispersing ancient forest specialist species.

5. How well is current plant trait composition predicted by modern and historical forest spatial configuration?

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This chapter is a replication of a constituent paper of this research that was published in *Ecography*.

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Abstract

There is increasing evidence to suggest that a delayed response of many forest species to habitat loss and fragmentation leads to the development of extinction debts and immigration credits in affected forest habitat. These time lags result in plant communities which are not well predicted by present day landscape structure, reducing the accuracy of biodiversity assessments and predictions for future change. Here, species richness data and mean values for five life history characteristics within deciduous broadleaved forest habitat across Great Britain were used to quantify the degree to which aspects of present day forest plant composition are best explained by modern or historical forest patch area. Ancient forest specialist richness, mean rarity and mean seed terminal velocity were not well predicted by modern patch area, implying the existence of a degree of lag in British forest patches. Mean seedbank persistence values were more closely related to modern patch area than historical, particularly in larger patches. The variation in response for different mean trait values suggests that species respond to landscape change at different rates depending upon their combinations of different trait states. Current forest understorey communities are therefore likely to consist of a mixture of declining species whose extinction debt is still to be paid, and faster colonising immigrant species. These results indicate that without management action, rare and threatened species of plant are likely to be lost in the future as a result of changes in forest spatial configuration that have already taken place. The lag seen here for rare specialist plants suggests however that there may still be scope to protect such species before they are lost from forest patches.

5.1. Introduction

The spatial configuration of forest habitat is an important determinant of the richness and composition of forest understorey plant communities (Jacquemyn et al. 2003; Lindborg 2007; Kimberley et al. 2014). Large, well connected patches support greater numbers of rare species and species which possess low dispersal and competitive ability (Kolb and Diekmann 2005). This is particularly the case where such forests are of long continuity (Kimberley *et al.* 2014). Species with fast falling seeds and which are unable to persist within the seedbank tend to be lost from forest habitat following landscape fragmentation and habitat loss, partly because they are less able to rescue threatened populations through immigration or through regeneration from the seedbank (Ozinga et al. 2009; Jacquemyn et al. 2012; Lindborg et al, 2012).

Recent evidence suggests that the response of forest communities to landscape change is not immediate, with many species taking years to be lost from fragmented habitat or to colonise expanding forest areas. This results in the formation of “extinction debts” and “immigration credits” (Lindborg and Eriksson 2004; Metzger et al. 2009), where species assemblages remain more strongly correlated with historical landscape structure than modern habitat configurations (Kuussaari et al. 2009; Jackson and Sax 2010; Purschke et al. 2012). The consequent lack of coupling between biodiversity estimates and present day landscape configuration is likely to reduce the ability of present day forest configuration to explain and predict future patterns of plant species occurrence (Jackson and Sax 2010). This has important implications for forest conservation and management strategies which depend on accurate estimates of current biodiversity.

Although the impact of forest area, configuration and history has been investigated in previous studies (Dupré & Ehrlén, 2002; Lindborg et al, 2012), relatively little work has directly focussed on quantifying the extent of lag effects in forest habitat and determining whether they differ between plant traits in a predictable manner. Here, we combine a national scale dataset of plant species occurrence in forest patches with past and present forest extent data. We then used these data to investigate the degree to which current plant community composition is explained by historical rather than modern forest patch area.

Extinction debts are associated with species with low rates of population turnover such as those with long life spans or the ability to persist within the seedbank. Such species may remain as remnant populations for some time following unfavourable landscape change, even when their eventual local extinction is likely (Eriksson 1996; Lindborg 2007; Vellend et al. 2006). Forest habitat which has reduced in size may therefore still retain a disproportionate number of the rare, forest specialist species that survived in previously larger forest patches (Vellend et al. 2006; Kimberley et al. 2014). Conversely, immigration credits result from the slow colonisation of new forest area by poorly dispersing species (Verheyen et al. 2003; Jackson and Sax 2010). Forest patches which have been recently established or which have seen an increase in the amount of forest habitat may therefore still be dominated by better dispersing species; those with low seed weight and seed terminal velocity or seeds which persist within the seed bank, in the absence of forest specialist plants (Kimberley et al. 2014). Over time as the immigration credit is paid many of these forest specialists are likely to arrive, although the rate at which this occurs depends

upon proximity to source populations and the permeability of the intervening habitat matrix (Peterken 2000; Brunet et al. 2011).

Where extinction debts and immigration credits exist in forest patches, the proportion of species with linked traits such as high seed weight and terminal velocity and high seedbank persistence are likely to lag behind landscape change. Combinations of life history characteristics such as high seed terminal velocity and high specific leaf area are also known to differentiate slow-dispersing, shade tolerant specialists largely restricted to long-continuity, ancient woodland from forest plants that are more readily dispersed and more typical of secondary forest (Kimberley et al. 2013). Such species are also more likely to be rare. Thus ancient forest species tend to be stress tolerant and poor colonisers of new habitat (Hermy et al. 1999) and therefore may be more prone to lag behind changes in forest configuration. Since lag effects in forest plants are long lasting and have been observed more than a century after forest fragmentation (Vellend et al. 2006), we hypothesised that present day forest community mean values for these traits would be better explained by historical rather than modern forest patch area in patches which have undergone area change. In addition to the trait-based approach, the relationships between both total species richness and ancient woodland specialist richness (based on the list of ancient woodland indicators in Kirby (2006)) and modern forest spatial configuration were also analysed in order to determine whether species-based patterns could be discerned alongside trait-based relationships with historical change in landscape structure.

In summary the following hypotheses were tested:

1. Plant community traits are better predicted by historical patch area than by modern patch area within forest patches greater than 100 years old.
2. Traits associated with restriction to ancient forest habitat such as seed terminal velocity and seedbank persistence are likely to be those most strongly linked to historical forest patch area.
3. Richness of species restricted to ancient forest will be more closely related to historical forest patch area than overall species richness.

5.2. Methods

5.2.1. Survey data

Digitised First Edition Ordnance Survey County Series (OS) maps (dated between 1849 and 1899) and data from the Countryside Survey, a national ecological surveillance programme for Great Britain (Norton et al. 2012), were used to identify 82 patches of British broadleaved forest which were established prior to 1899 and that were still recorded as forest in 2007. Forest understory plant species occurrence data were then obtained for 151 vegetation sampling plots within these patches, assessed as part of Countryside Survey 2007. Two types of vegetation sampling plot were employed in the analysis; linear plots (10 m² in area), located parallel to forest streambanks and forest tracks, and area plots (200 m² in area), located within the wider areal extent of each patch but not sampling a linear feature.

5.2.2. Species and plant trait data

Plant community mean trait values for a number of life history characteristics were calculated for each plot by averaging the individual traits of all species present. These

mean values were then used as response variables in subsequent modelling. Mean trait values were left un-weighted by species abundance. This allowed both subordinate and dominant species to be considered equally, thus avoiding the confounding effect of variation in cover due to local competitive sorting. Plant trait information was obtained from the Electronic Comparative Plant Ecology database (Grime *et al.* 1995), the LEDA traitbase (Kleyer *et al.* 2008), The British Flora (Stace 1997) and PLANTATT (Hill *et al.* 2004). Species rarity was obtained from PLANTATT as the number of occurrences in British 10 km squares in the period 1987-1999.

Excluding trees and shrubs, 250 species occurred across the vegetation plots. Since trait data were not available for all traits for all species, an approach was taken to minimise this problem by estimating the missing values using a Bayesian hierarchical model written in WinBUGs (Lunn *et al.* 2000), following the approach of Thompson and McCarthy (2008) as applied in Kimberley *et al.* (2014). Imputing missing values in this manner is preferable to removing them entirely, since estimated values take into account both between and within family similarity among those species with known trait values. The five traits tested, along with the percentage of species with missing values were; log natural seed weight (17.6%), seed terminal velocity (29.6%), specific leaf area (5.2%), seedbank persistence (24.8%) and rarity (0.4%). Seedbank persistence was assessed on a four point scale (1 = Transient seed, 2 = Persistent until next growing season, 3 = Small concentrations of persistent seeds, 4 = Large year round bank of persistent seeds). In addition to the mean trait values, counts of both overall plant species richness and ancient woodland indicator species richness were also obtained, using the list of indicator species in Kirby (2006).

5.2.3. Spatial data

Patch area data for forest patches around each Countryside Survey vegetation plot were derived for two periods; modern (2007) and historical (pre 1899), by overlaying forest extent data onto the geo-referenced Countryside Survey plot data using GIS techniques (ESRI, 2011). Modern forest patch area data were extracted from the satellite derived Land Cover Map 2007 (Morton et al. 2011) whilst historical patch area data were digitised from First Series OS maps. These modern and historical area data were then natural log transformed to reduce the skew in their distribution.

5.2.4. Local abiotic conditions

Local conditions within forests are also important determinants of community composition (Dupré and Ehrlén 2002; Kimberley et al. 2014). In order to obtain a more realistic estimate of the effects of modern and historical forest configuration on mean community trait values we included a number of abiotic variables measured at the same locations as the plant species composition. Shade was estimated on a three point scale for all vegetation plots and plots designated unshaded, partially shaded or fully shaded by field surveyors. Within each of the area plots (n = 46) soil pH and carbon to nitrogen ratio were measured based on a 15 cm topsoil sample taken at the same time as the flora was recorded in each plot. In the linear plots (n = 105) directly measured soil data were not available. Values within these plots were estimated using published equations derived from a national calibration of observed values of the two soil variables against the mean Ellenberg values of plants in 1033 plots from a stratified, random sample of the range of British vegetation types (Smart et al. 2010). The mean Ellenberg values used in these equations to generate soil

variables were derived only from the trees and shrubs which were excluded from the calculation of mean trait values for the herbaceous understorey (the dependent variables in the present study). This may result in a less accurate estimate of soil conditions present in vegetation plots due to the lower sample size of woody species present, however the problem of circularity when the estimated soil variables were used to model mean trait values is avoided through this method. In order to account for differences in response between the area and linear plots, plot type was included as a categorical explanatory variable. Climate and residual geographic variation across Britain were accounted for by the inclusion of the northing of each sample plot as a continuous explanatory variable (Corney et al. 2006).

5.2.5. Modelling approach

In order to determine the extent to which modern mean community trait values are better predicted by modern or historical patch area data, the spatial data from the two time periods were combined into two new variables; one describing the mean patch area and the other the change in the patch area between the historical and modern period. The amount of change observed in patch area across forest patches is shown in Appendix 3 (Fig. A1). These variables were then used as explanatory variables in models of present day mean values of life history traits and species richness data within forest habitat. Since spatial data was replicated over time but only modern plant species data were available, this modelling approach allowed the effect of modern and historical forest spatial structure to be assessed in a single model for each response variable.

Results from the models can be interpreted as follows: the relationship between trait and mean patch area indicates whether the trait in question is significantly affected by forest patch area. In cases where a significant effect exists, the parameter estimate for the change in patch area versus modern trait relationship can then be used to indicate whether the trait is better modelled using the modern or historical spatial data. Where the relationship between mean patch area and trait is positive, a value for the change in area parameter of greater than zero will indicate a community that is better predicted by the modern spatial data. If the change in area parameter is negative, the results indicate present day trait data are more strongly correlated with historical patch area (this is reversed where the relationship between mean patch area and trait is negative). Where a significant effect of mean patch area is observed but the change in patch area regression coefficient is close to zero, the results indicate an intermediate community which is equally well explained by both modern and historical spatial data, suggesting an intermediate amount of lag. Since high, low and intermediate values for this metric all indicate important results, testing for a significant difference from zero is not appropriate for the change in patch area term. Confidence intervals are therefore not shown around results for this measure (Figures 5.3 and 5.4).

Both present and past spatial data would be expected to predict plant composition equally well where the plant composition is in an intermediate state, having moved away from the historic forest configuration following landscape change but not yet well predicted by current spatial data. However modern and historical patch area would also be expected to be equivalent in their ability to predict modern trait values where only small amounts of spatial change has occurred. In order to prevent any lag

effects being obscured by a lack of change between time periods it was therefore important to ensure that the dataset was not dominated by patches which were stable in area between historical and modern data sources. To reduce this problem 40 plots, randomly selected from those present in patches which had undergone less than a 10% change in patch area, were removed from the dataset prior to the analysis. This provided a set of patches with an approximately even distribution of amount of change which could be used in subsequent modelling (Supplementary material Appendix 3, Fig. A1).

The analysis allowed the identification of traits which are similarly well predicted by both modern and historical patch area as well as permitting the amount of change between time periods to be taken into account in the analysis. Use of the mean patch area rather than the historical value avoids collinearity problems where historical patch area is correlated with the amount of change. Thus the two spatial variables used in the analysis were statistically independent.

The approach can be demonstrated using simulated examples. An artificial dataset was created with information on modern trait composition, modern patch area and historical patch area, where all patches had undergone a randomly allocated amount of change (either positive or negative). The data were constructed such that modern values for a hypothetical life history trait were strongly correlated with historical patch area but had no relationship with a modern patch area (Figure 5.1a, b). Figure 5.1 shows the result of fitting the mean patch area (Figure 5.1c) and change in patch area (Figure 5.1d) terms against the trait values. The trait values which were associated with spatial variable values in the historical data have not changed despite

these patches having undergone change. Thus the patch area has changed – high becoming low and low becoming high – but the trait values have not (Fig 5.1a). In such a situation a relationship between trait and mean spatial variable is observed (Figure 1c), and necessarily results in a strong negative correlation between change in the spatial variable and the modern trait variable (Fig 5.1d), from which the stronger relationship between trait and historical patch area can be inferred. If the historical patch area versus trait relationship had been negative then this effect would have resulted in a positive slope in Fig 1d.

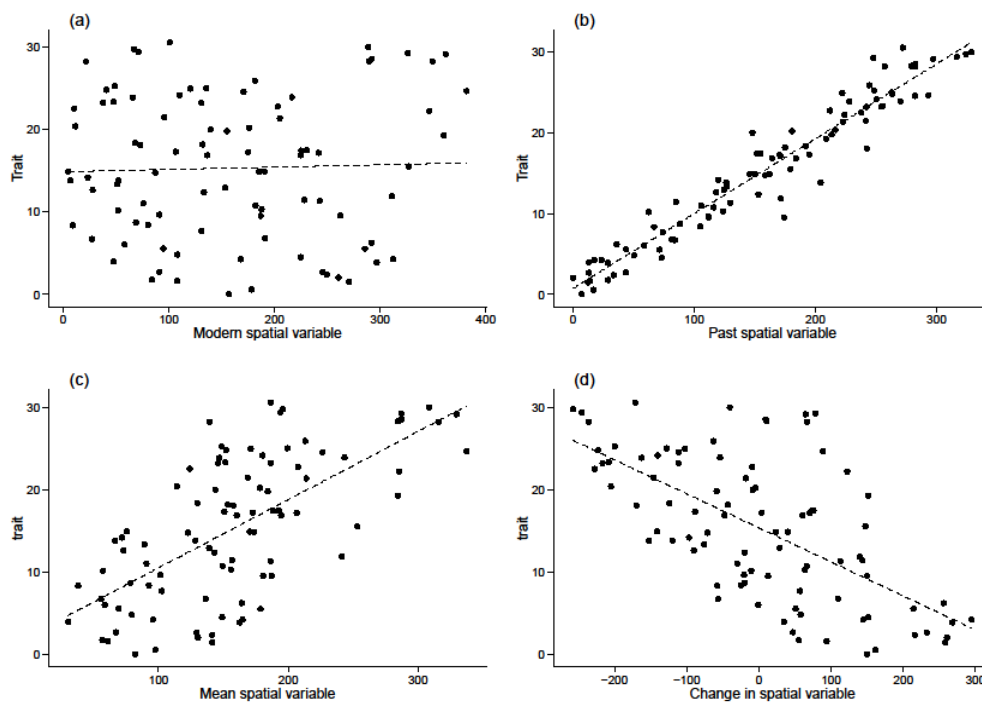


Figure 5.1 Simulated data showing the relationships between hypothetical mean trait values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across modern and historical spatial variables and (d) change between modern and historical spatial variables, where trait data is best explained by historical spatial conditions. Dashed lines show linear models between trait and each individual explanatory variable.

A further simulation shows the pattern recovered by the analysis where the same strong positive spatial-trait relationship occurs but in this case with modern patch

area. A second dataset was created; this time such that modern values for the hypothetical life history trait were strongly correlated with modern patch area but had no relationship with historical patch area (Figure 5.2a, b). The same modelling approach of fitting mean and change in patch area against trait was then applied. This again results in a relationship between trait and mean patch area (Figure 5.2c); however in this case the relationship between trait and modern patch area is revealed by the positive relationship between trait and change in patch area (Figure 5.2d).

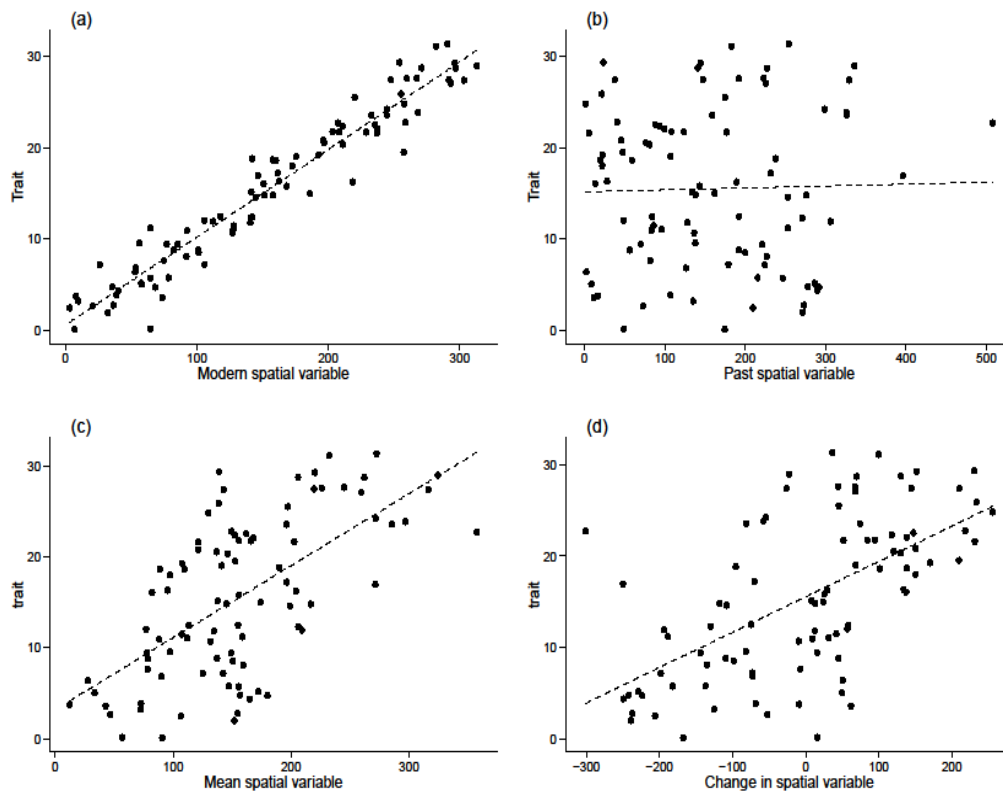


Figure 5.2 Simulated data showing the relationships between hypothetical mean trait values and (a) a modern spatial variable, (b) a historical spatial variable, (c) mean across modern and historical spatial variables and (d) change between modern and historical spatial variables, where trait data is best explained by modern spatial conditions. Dashed lines show linear models between trait and each individual explanatory variable.

The modelling approach demonstrated in the simulated examples was applied to the real data for the 111 vegetation sampling plots used. A single model was fitted for each mean plant trait, along with species richness and ancient woodland indicator richness. These models contained the mean patch area, the change in patch area and the interaction between these two variables, in addition to all local condition variables described above. The interaction term was included in each model to investigate whether patches with varying mean area differ in the extent to which modern spatial data can be used to predict trait composition. A mixed-effects modelling approach was taken, including site (Countryside Survey 1 km square) as a random intercept, using the package lme4 in the statistical software R. This accounted for the spatial autocorrelation introduced by analysing a number of vegetation sampling plots located within the same Countryside Survey sample square. Mean trait values were modelled by linear mixed effects models while generalised linear mixed effects models with a Poisson error distribution were used for species richness and ancient woodland indicator richness models, to account for the count data response. All models were scaled and centred using the R package arm, to produce comparable regression coefficients. These allowed an estimate of the effect sizes of each spatial variable on each plant trait to be made. 95% confidence intervals around these effect sizes were calculated using the bootstrap method in lme4. For linear models response values were also treated in this way to produce standardised effect sizes bounded by ± 1 . For models of count data this was not possible due to the link function used in the generalised linear models. Parameter estimates from the different model types are therefore not directly comparable. The resulting effect sizes and confidence intervals allowed the extent to

which present day mean values for different life history traits are better predicted by modern or historical forest spatial configuration to be assessed.

A number of significant effects of the abiotic variables, northing and plot type were detected, discussion of which is beyond the scope of this article. Here we focus on partial spatial relationships with trait composition having accounted for variation explained by local environmental conditions. Full modelling results are however shown in Appendix 3 (Tables A7-A13).

5.3.Results

5.3.1. Trait data

Mean patch area was a significant predictor for three of the five community mean response variables tested; seedbank persistence, seed terminal velocity and species rarity (Figure 5.3). Rarer species with faster falling seeds and less persistent seedbanks were found in patches with a high average area across the two time periods, suggesting that forest configuration has an important effect on the occurrence of species with these traits. The lag metric was close to zero for both seed terminal velocity and rarity (change in area term, Figure 5.3a,b), suggesting that both modern and historical patch area explain these traits equally well, despite the gradient of change in patch area present across the sampled woodlands. This must therefore mean that communities have not remained static and hence stayed correlated with historic patch configuration, but neither have they completely readjusted to the modern patch configuration. The lag metric for seedbank persistence however was less than zero (Figure 5.3e). Given the negative relationship between mean patch area and this trait this indicates that mean seedbank

persistence values were better predicted by the modern patch area than the historical.

The interaction between mean patch area and change in patch area had a significant negative effect on mean seed bank persistence values (Figure 5.3e). As mean patch area increases, the negative relationship between trait and change in area becomes stronger. This suggests that mean seedbank persistence was better predicted by modern patch area in forest patches with a larger mean area across the two time periods than in patches with a smaller mean area.

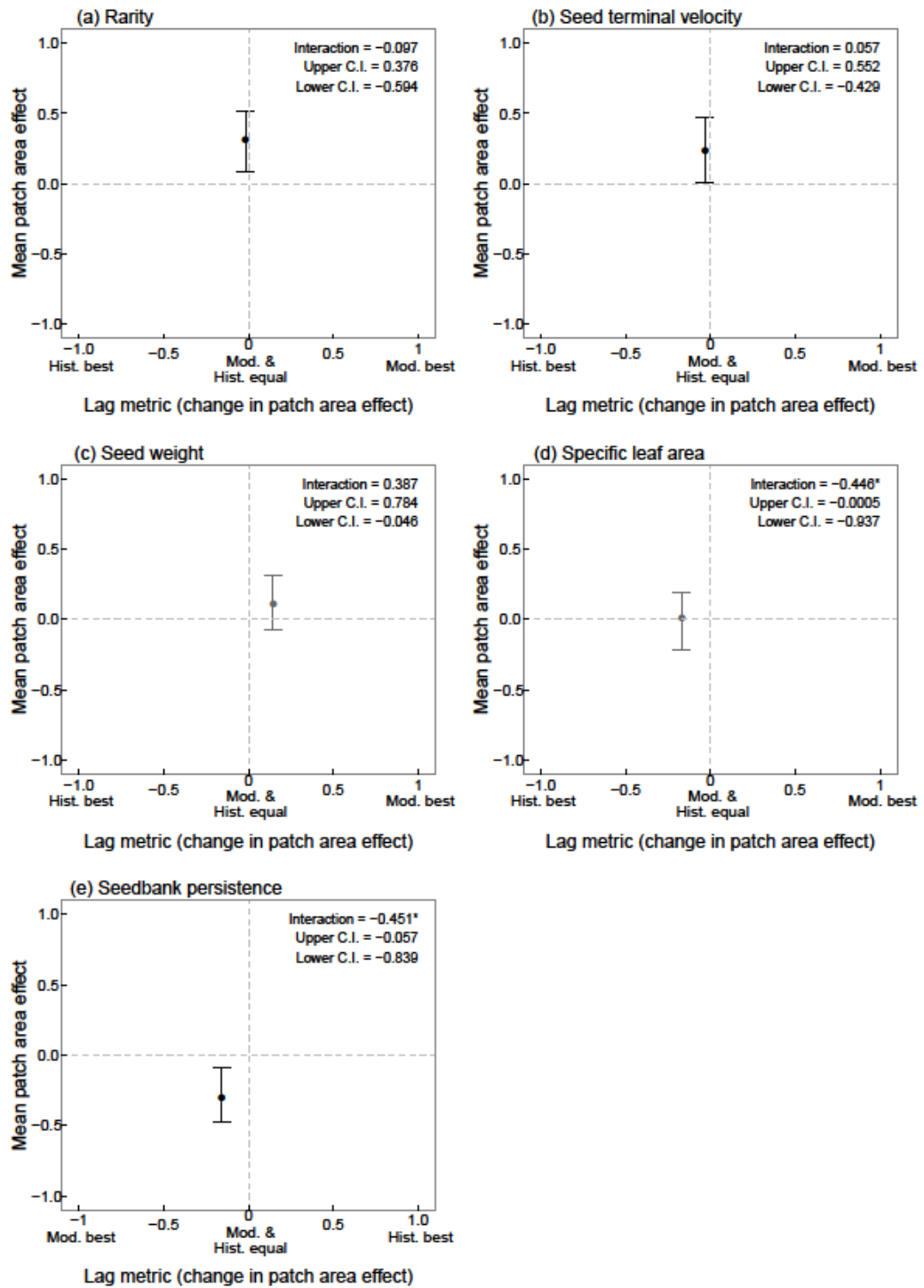


Figure 5.3 Standardised effect sizes quantifying the influence of patch area in models of five mean trait values in forest vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed confidence intervals do not overlap 0 a significant effect of patch area is indicated. The position of the point on the x axis shows the extent to which present day trait values are best predicted by historical or modern patch area. Text in the top right of each panel shows the parameter estimate and upper and lower confidence intervals for interaction terms. Parameter estimates for local abiotic variables (also included in models) are not shown here.

5.3.2. Species data

Mean patch area had a significant effect on ancient woodland indicator richness but no effect on overall species richness (Figure 5.4). This suggests that ancient forest specialists are more sensitive to patch area than other forest plants. Change in patch area had a weak negative effect on ancient woodland indicator richness, indicating that the number of ancient forest specialists is slightly better predicted by historical patch area than modern.

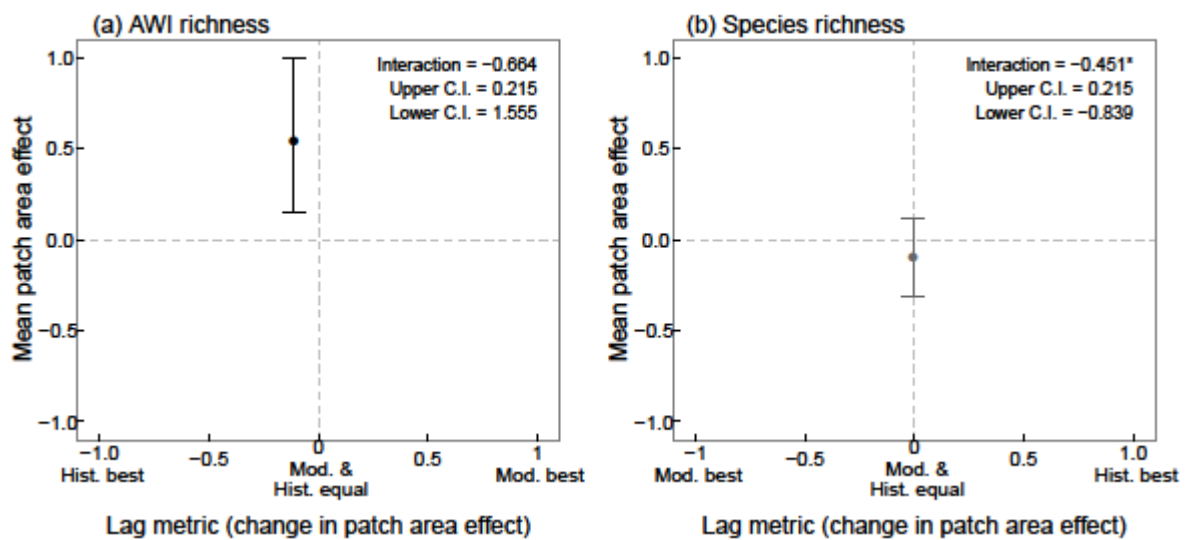


Figure 5.4 Standardised parameter estimates quantifying the influence of patch area in models of overall species richness and ancient woodland indicator (AWI) richness in forest vegetation sampling plots. Error bars represent 95% confidence intervals. Where displayed confidence intervals do not overlap 0 a significant effect of patch area is indicated. The position of the point on the x axis shows the extent to which present day trait values are best predicted by historical or modern patch area. Text in the top right of each panel shows the parameter estimate and upper and lower confidence intervals for interaction terms. Parameter estimates for local abiotic variables (also included in models) are not shown here.

5.4. Discussion

The important effects of forest spatial configuration on understorey plant composition within forest patches were confirmed by the relationships identified here between mean patch area and three of the five mean community values tested here. The strength with which different traits could be predicted by modern rather than historical forest patch area varied, indicating that while some species may be quickly lost from fragmented habitat, many are likely to persist for some time following landscape change. Such variation in response to changes in habitat fragmentation has important consequences for conservation planning because it suggests that there may be a window of time in which to introduce measures to help vulnerable species (Wearn et al. 2012).

The analytical approach taken here allowed intermediate situations to be identified, where a mean trait value is affected by patch area but the trait is equally well predicted by both modern and historical forest extent. Results suggest that this is the current case for both rarity and seed terminal velocity, implying the existence of weak time lags for these characteristics. This supports previous studies which have found that plant communities take time to respond following landscape change (Lindborg and Eriksson 2004; Metzger et al. 2009; Saar et al. 2012). Rare species and those with heavy, fast falling seeds are likely to be less able to disperse effectively and rescue threatened populations through immigration (Kolb & Diekmann; 2005). Many such species are therefore unlikely to be able to persist long-term following the loss of forest patch area. Since many rare, forest specialist plants are perennial species however (Kimberley et al; 2013), they may survive in remnant populations for some time following landscape change (Eriksson 1996). The slow loss of species

with these characteristics may explain why mean seed terminal velocity and rarity were equally well predicted by modern and historical patch area. This is further evidenced by the fact that ancient woodland indicator richness within forest patches was more closely related to historical patch area than modern. Hence there is likely to be a disproportionate drop in the occurrence of these vulnerable plant species in the future as existing extinction debts are paid in patches which have decreased in area. In many cases these species are also likely to be slow to colonise forest patches which have increased in size, particularly in isolated patches (Brunet 2011). Hence maintaining large areas of older forest is important to avoid the loss of populations of rare or poorly dispersing ancient woodland specialist plants (Kimberley et al. 2013).

Although existing time lags are likely to lead to ongoing change in forest community composition, if the amount of change in forest extent between time periods is small the degree of future change in plant composition is also likely to be limited, even where this change takes some time to occur. It is therefore also important to consider the amount of change which occurred between time periods when interpreting these results. It is likely that a large alteration in patch size is needed to produce a significant, long lasting time lag. Here only a weak lag was identified for mean rarity and seed terminal velocity, possibly due to a modest amount of change between historical and modern patch area for many patches. Further application of this method to forests which have undergone more substantial or very recent changes in area may reveal whether this is indeed the case. If so, the greatest benefit of increasing forest patch area may be seen in patches which have recently undergone a large reduction in area. The time lag identified here for rarity and seed

terminal velocity may also be weak due to the difference in species richness and composition between area and linear plots used in this analysis. If linear plots contain a higher proportion of ruderal species with characteristics consistent with a more rapid response to landscape change, communities are likely to be closer to those predicted by modern forest patch area.

The variation in the degree to which modern or historical forest patch area best explains mean trait values suggests that different species are responsible for each individual trait relationship. For a species to persist but be bound for extinction it requires both strong ability to persist and weak dispersal capability. Any lag observed in patches which have lost area may be due to forest specialist species which have a particular combination of established phase traits (slow, shade-tolerant vegetative growth) and regenerative traits (poor dispersal) and therefore have the potential to persist for some time after landscape change (Saar et al. 2012; Kimberley et al. 2013). Forest specialist species without this trait combination are likely to be lost relatively quickly from fragmented patches while species with these characteristics remain until they are either out-competed by more ruderal immigrants or otherwise suffer mortality from disturbance, herbivory or disease (Grime 2001; Jackson & Sax 2010). On the other hand immigrant species must be both rapidly dispersed and shade-tolerant slow growers to truly survive in undisturbed forest understorey. For example ruderal species with high investment in many small seeds with low terminal velocity, high relative growth rates and high seedbank persistence can respond more rapidly to landscape change, quickly colonising new forest edges, new small areas of secondary woodland including previously larger patches which have lost forest area (Tabarelli et al. 1999).

What we see integrated into the mean trait values is likely to be the trait-controlled sum of the dynamics of fast-responding species more rapidly dispersed in time (through persistent seedbanks) and space (through light, slower falling seeds) arriving at different rates from surrounding habitats, coexisting with extinction debt species that are better fitted to historical spatial configurations and hence are likely to decline further. These two processes may occur at different rates however, with extinction debts in forest understorey plants being paid sooner (after around 160 years) (Kolk & Naaf 2015) than immigration credits (which can remain for much longer) (Naaf & Kolk 2015). If extinction debts in forest patches which have lost area have largely been paid in this analysis, this may partly explain why only weak lags were identified here for mean seed terminal velocity and rarity.

Mean seedbank persistence values lag less behind changes in patch area than mean seed terminal velocity and rarity, particularly in large forest patches. High seedbank persistence allows species to regenerate vulnerable or locally extinct populations from the soil seedbank. The absence of such persistent species in larger forest patches (Kimberley et al. 2014) may result in a community which is faster to respond to changing patch area because more species present in the vegetation possess no persistent seedbank. Such species are likely to be quickly lost when habitat area is reduced. The species present above-ground are also often poorly correlated with the species present in the seedbank (Bossuyt et al. 2002). Many species present in forest seedbanks may therefore be rapidly growing species and widely dispersed which are absent from the above-ground vegetation but likely to appear and thrive following disturbance to the soil or canopy (Bossuyt et al. 2002). When forest patches lose area or are newly disturbed they may swiftly gain these ruderal species from the existing

seedbank, reducing the lag for this trait (Smart et al. 2014). In smaller patches this effect may be weaker due to a higher original proportion of species with a persistent seedbank (Kimberley et al. 2014). This suggests that large patches are likely to be quickest to pay their extinction debts when they are reduced in size and further confirms the fact that species which are particularly dependent on large, core areas of habitat may be first to become extinct following the loss and fragmentation of forest habitat. The creation of small patches of new forest is therefore likely to be of less benefit than extending existing forest habitat (Peterken 2000).

One limitation of analysing the data in this way is that there is no way of knowing when changes in spatial properties between the two time periods have occurred. Interpretation of the results must therefore be done with care, since modern forest configuration would be expected to have a stronger effect than historical if most of the spatial change was longer ago. The large number of data points from across a wide geographic area used here however ensured that a realistic assessment of current patterns in British forests could be made. Furthermore, because the same forest habitats were analysed for all traits tested, comparisons of the relative strength with which modern forest configuration affects different mean trait values are still valid. Mean trait values were analysed separately to allow differences in the response of traits to important variables to be detected. As such however, the inter-correlation between pairs of traits must be taken into account. For example, part of the observed effect of patch area on seedbank persistence may be due to the close relationship between this trait and seed mass (Westoby et al. 2002). Correlations between mean trait values are shown in Appendix 3 (Fig. A3).

Although only forest patch area was tested here, this variable is often correlated with a number of other forest configuration variables such as the amount of forest present in the landscape or the amount of core forest habitat (Fahrig 2003). In reality, time lags in forest habitat are likely to depend on interactions between the size of patches, the amount of nearby forest (particularly that of long continuity) and the amount of edge habitat present. For example, newly created forest patches within a short distance of ancient forest habitat have been shown to accumulate forest specialist species more quickly (Brunet et al. 2011), while young forest patches which are highly isolated from ancient forest habitat mostly accumulate species adapted for effective dispersal which tend not to be ancient woodland specialists (Brunet 2007). Hedges and other semi-natural habitat types also have some ability to act as a refuge for forest specialist species (McCollin et al. 2000, Smart et al. 2001), potentially enabling such species to persist for longer, and therefore exhibit a stronger lag effect, in landscapes where such features are common. The landscape context of changing forest habitat is therefore also likely to be an important determinant of the extent to which time lags develop. High intensity agriculture in neighbouring land use has been shown to reduce the ability of forest specialist species to exist near forest edge habitat (Chabrierie et al. 2013). Where forest patches are surrounded by intensive agricultural land, forest edge is likely to be quickly colonised and dominated by weedy generalist species with higher seedbank persistence (Willi et al. 2005). Where forest edge is buffered by less intensive land uses however, stronger lags may be occurring as forest specialist species take longer to be out-competed by immigrants. Hence, some forest specialist species may still be able to persist even in small patches or at forest edges, so long as they are already

established before fragmentation and that the forest patch is appropriately surrounded by non-intensive land. Buffering forest habitat with less intensive habitat types and linear refuges may therefore allow many vulnerable forest species to persist following landscape change, but this issue requires further research.

In future, as existing immigration credits and extinction debts are paid, forest species composition is likely to shift towards present day patterns of habitat configuration, with fragmented forest likely to lose shade tolerant, poor dispersers and gain populations of immigrant species. Likewise forest patches which are increasing in size will begin to recruit suitable populations of forest plants and lose species more fitted to smaller patches with a high edge to area ratio. The fact that mean rarity and seed terminal velocity were equally strongly affected by modern and historical forest configuration in long established British forest patches highlights the importance of accounting for historical forest spatial configuration when modelling patterns of plant species occurrence (Ewers et al. 2013). Failure to do so risks both underestimating the strength with which forest configuration affects species and failing to identify species which are at risk of local extinction (Helm et al. 2006). However extinction debts in particular do present an opportunity to initiate measures to prevent the loss of threatened species (Kuussaari et al. 2009) and the time lag identified here for rare species and inefficient dispersers suggests that many vulnerable species could benefit from well targeted management action.

6. Forest change in the Anthropocene: Do we need to combine habitat suitability and landscape connectivity to model understorey biodiversity?

Adam Kimberley, G. Alan Blackburn, J. Duncan Whyatt & Simon M. Smart

Abstract

The ability to accurately model the distribution of forest understorey biodiversity under different conditions is essential in order to understand the effect of ongoing environment change on forest communities. Despite this, the extent to which landscape scale factors such as habitat connectivity and matrix hostility are necessary to predict forest species assemblages is not well known. Here we use species niche models and graph-theory based connectivity models in order to answer the question; is observed species richness better predicted by jointly modelling landscape connectivity and the effects of abiotic conditions as filters on local forest species pools? A significant effect of connectivity was found, with landscapes with higher overall connectivity containing fewer species, likely due to the dominance of a small number of forest specialist plants in large forest areas. The spatial configuration of forest habitat was also important, with landscapes where connectivity is largely provided by within patch movement containing fewer species than landscapes where higher levels of movement between patches was possible. Furthermore, the composition of surrounding land cover was found to have a significant effect on understorey communities, with patches adjacent to arable land or improved grassland significantly less species rich than those in landscapes dominated by less intensive land cover types. This highlights the important influence

of landscape composition and the configuration of available habitat on forest plant diversity in agricultural landscapes and suggests that these factors must be considered alongside local environmental conditions when attempting to manage biodiversity or predict future plant distributions.

6.1. Introduction

Ongoing global change drivers such as the loss of semi-natural habitat and the intensification of agricultural land have had a large impact on species across a range of taxa (Foley et al. 2005). Forest plants, many of which contribute to important ecosystem functions, are likely to be particularly affected due to their inability to survive in highly human-modified landscapes (Peterken & Game 1984; Mitchell et al. 2014). The ability to accurately model the effects of these changes is essential in order to predict the ways in which future forest communities are likely to respond to anthropogenic activity and to design effective measures to prevent the loss of important forest biodiversity (Guillera-Arroita et al. 2015; Hayward et al. 2015).

Species niche models are able to produce predictions of biodiversity within forest patches by estimating the likelihood of occurrence for different plants based on prevailing environmental conditions (Smart et al. 2010; Guisan et al. 2013; Guillera-Arroita et al. 2015). Hence, such models have been proposed as valuable tools for conservation decision making, assisting both in identifying areas in need of management intervention and assessing the likely outcome of different potential actions (Franklin 2013; Guisan et al. 2013). Since local abiotic factors such as light availability and soil macronutrient availability are strong drivers of forest understorey composition, estimates of forest species occurrence derived from these methods should correlate strongly with observed patterns (Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Kimberley et al. 2014; Smart et al. 2014). Where this is the case, niche models are likely to be appropriate and provide a useful way of predicting changes in biodiversity. Evidence suggests however that in addition to the filtering effect of local environmental factors, habitat spatial configuration also influences the extent to

which species are able to occur within areas of forest habitat (Ehrlén & Eriksson 2000; Schleicher et al. 2011; Kimberley et al. 2014). Specialist forest plants in particular are thought to be limited by their ability to disperse across landscapes, and are therefore found more frequently in areas of high landscape connectivity (Hanski 1998; Petit et al. 2004; Honnay et al. 2005; Brunet 2007; Kimberley et al. 2014; Liira et al. 2014). Ensuring that each species niche model usefully represents dispersal processes requires accurate but generalised estimates of species-specific dispersal rates. The cost of gathering such information often means that only a limited number of species may be covered (Boulangéat et al. 2012). Hence colonization dynamics are generally absent from species niche models which instead focus on estimating the suitability of habitat patches given local conditions rather than predicting patch occupancy. Including dispersal within species niche models for these habitats would be likely to increase their usefulness as tools for estimating the impacts of scenarios of global change but only if enough species can be modelled with sufficient accuracy and generality. Approaches which combine habitat suitability with measures of landscape scale habitat configuration may therefore potentially generate more accurate models of biodiversity and species composition (Stewart-Koster et al. 2015; Humphrey et al. 2015; Guisan & Thuiller 2005).

Despite this, a lack of understanding remains over the way in which landscape scale variables such as habitat connectivity and the composition of the surrounding non-habitat matrix influence forest communities in agricultural landscapes. Addressing this knowledge gap is therefore seen as a key priority for conservation research (Humphrey et al. 2015). Here, we test the ability of ecological models related to processes at both local and landscape scales to explain patterns in understory

biodiversity in broadleaved forest habitat in Great Britain. The aim was to investigate the extent to which aspects of forest connectivity influences plant communities in highly fragmented forest habitat, and therefore the importance of considering related variables as components of biodiversity modelling strategies (Figure 6.1).

Landscape connectivity, defined as the degree to which a landscape facilitates the movement of individuals between habitat resources, influences the extent to which species are able to colonise available habitat and rescue threatened populations through immigration (Taylor et al. 1993). High levels of connectivity are therefore important to allow species to form viable meta-populations and to shift their ranges in response to changes in climate or other environmental conditions (Staddon et al. 2010; Saura et al. 2014). Connectivity can be described both within patches (intra-patch connectivity) due to the area of habitat they comprise and between patches (inter-patch connectivity) through links that exist amongst patches which are close enough for individuals to disperse from one to another, either directly or via intermediate steps (Pascual-Hortal & Saura 2006). Species with very low dispersal ability, such as many forest specialist plants which often possess large, fast falling seeds and no specialised dispersal vector, are unable to move even relatively short distances between patches and are therefore heavily reliant on the intra-patch connectivity provided by large areas of contiguous habitat (Hermy et al. 1999; Verheyen et al. 2003; Saura & Rubio 2010; Kimberley et al. 2013). Consequently, both total connectivity and the extent to which this is a result of within versus between patch connectivity are likely to act as important filters on observed species richness which are not represented in the output of species niche models.

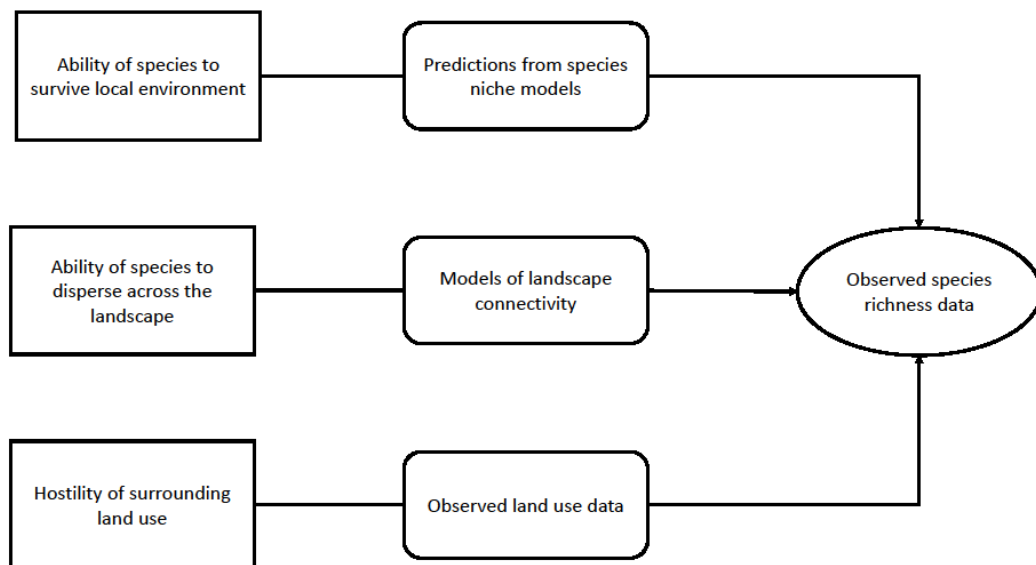


Figure 6.1 Hypothesised drivers of forest species occurrence and methods used here to quantify these effects in models of understorey biodiversity.

Previous studies have shown that where forest habitat is surrounded by intensive agriculture, the infiltration of fertilisers applied to adjacent farmland results in higher concentrations of nitrogen and phosphorous (Willi et al. 2005; Didham et al. 2015). This leads to a decrease in species richness, as communities become dominated by ruderal species favoured in the more fertile conditions that are created (Chabrierie et al. 2013; Didham et al. 2015). The presence of intensively farmed land around forest habitat may also reduce the ability of forest specialist plants to move through the matrix via stepping stones of suitable semi-natural habitat or connecting elements such as hedgerows (Donald & Evans 2006; Davies & Pullin 2007). The matrix surrounding forest patches is also therefore expected to be an important determinant of the biodiversity of forest understorey communities.

Hence, we aim to test three main hypotheses;

1. Species niche models based on local environmental conditions can be used to produce estimates of forest biodiversity that correlate strongly with observed species richness.
2. After accounting for local abiotic conditions using species niche models, the inclusion of landscape connectivity significantly improves prediction of observed understorey species composition.
3. The hostility of the surrounding matrix is also an important factor in determining observed species richness.

6.2. Methods

6.2.1. Species richness data

Understorey plant species occurrence data were obtained for 1589 vegetation plots occurring within forest habitat in 341 1 km² sampling landscapes recorded as part of Countryside Survey 2007; a national ecological surveillance programme that represents the habitats and landscapes of Great Britain based on stratified, random sampling (Norton et al. 2012). All vascular plant species were counted either in linear plots (10 m² in area), located parallel to forest stream-sides and forest tracks, or area plots (200 m² in area), within the wider areal extent of each forest patch. The species richness of forest habitat was assessed at the landscape scale as a count of the number of unique non-tree or shrub species present across all forest vegetation plots within each sampling landscape. Woody species were used to estimate some of the local environmental conditions within forest patches (see section 6.2.3 below), therefore they were excluded from the species richness measure to avoid circularity

in subsequent modelling. In total, 503 non-woody species were identified across the sampled squares.

6.2.2. Forest connectivity

Connectivity modelling was performed using the package Conefor Sensinode (Saura & Torné 2009). This is a software tool for measuring landscape connectivity using distances between habitat patches, based on the concept of “habitat availability”, whereby the area within patches is considered a space in which connectivity exists (Saura & Pascual-Hortal 2007). This method has been shown to provide a more robust measure of connectivity than many alternative metrics and requires relatively modest input data, as such representing a potentially valuable tool in large scale conservation modelling (Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007; Saura et al. 2011; Luque et al. 2012; Ernst 2013). Necessary data on the area of patches of broadleaved forest habitat within the sampling landscapes and the distance between habitat areas were obtained from Countryside Survey land cover data (Norton et al. 2012) using the Conefor inputs ArcGIS processing tool (Jenness 2011). Distances between patches were calculated as the minimum Euclidean distance between the edges of pairs of forest patches.

Conefor’s “probability of connectivity” metric (PC) uses species’ dispersal data to determine the amount of reachable habitat within a given landscape by calculating “the probability that two locations randomly selected within the landscape fall into habitat areas that are connected to each other” (Saura & Pascual-Hortal 2007). An additional metric can be derived from this statistic, termed “equivalent connected area” (ECA). This is defined as the size of a hypothetical single patch of habitat which

has the same connectivity as the real landscape (Saura et al. 2011). ECA can never be smaller than the smallest habitat patch within the landscape, therefore unlike PC it is not susceptible to extremely small values where the amount of habitat is small relative to the total landscape size. As such, ECA was used here to represent total landscape connectivity within surveyed landscapes.

ECA is calculated in Conefor using Equation 1, where a_i and a_j represent the area of patches i and j and P_{ij}^* gives the maximum probability of dispersal between patches i and j (i.e. whichever value is higher, the probability of direct dispersal or the probability of dispersal via intermediate patches) (Saura & Pascual-Hortal 2007; Saura et al. 2011). Hence, this measure of connectivity takes into account within patch movement, between patch movement and the contribution of patches as stepping stones between other patches, therefore providing a robust and realistic estimate of landscape connectivity (Saura & Pascual-Hortal 2007; Saura et al. 2011).

$$ECA(PC) = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}$$

Equation 1

In order to calculate this metric, Conefor also requires the probability of dispersing a specified distance as an input variable, from which the probability of dispersal between habitat patches can then be derived (Saura & Torné 2009). For this purpose, maximum dispersal distances (MDD) for species within the observed forest species pool were calculated using dispeRsal software in R (Tamme et al. 2014). This package contains a number of models for predicting MDD using combinations of plant trait

data. Where measured MDD was available for species in dispeRsal, these values were used. For species where this was not available, MDDs were calculated using the dispeRsal model with the highest R-squared for which trait data were available (see Tamme *et al.* 2014 for full details of models). Models used and the number of species for which each was used to calculate MDD are shown in Table 6.1. Trait data were obtained from the LEDA traitbase and the Electronic Comparative Plant Ecology (Hodgson *et al.* 1995; Kleyer *et al.* 2008). Due to data limitations, it was only possible to obtain MDD data for 256 species of the 503 species which occurred in sampling plots. Since this still represents a large number of species across a gradient of dispersal abilities however, the estimates of landscape connectivity derived should represent an accurate estimate of forest connectivity for the existing species pool.

Table 6.1 Models used in dispeRsal software (Tamme *et al.* 2014) to predict species maximum dispersal distances.

Model explanatory variables	R squared (reproduced from Tamme <i>et al.</i> 2014)	Number of species
Measured MDD	NA	45
Dispersal syndrome, growth form, seed terminal velocity	0.60	162
Dispersal syndrome, growth form, seed mass	0.53	31
Dispersal syndrome, growth form	0.50	18

MDD values obtained through this process were then used as the maximum dispersal distance control parameter in the connectivity modelling. From Conefor, the ECA for

each individual species in each survey square was obtained, providing an estimate of functional connectivity for each of the 256 species for which trait data were available. Mean ECA values for each sampling landscape were then obtained by averaging these functional connectivity values. This provided a way of comparing different landscapes in terms of their average connectivity for the forest species pool.

Conefor was also used to calculate the proportion of ECA contributed simply by intra-patch connectivity (i.e. the area of habitat present) (Saura & Rubio 2010). This value, here termed “IntraFraction”, will be highest where species are incapable of moving between patches, and lowest where forest patches are closely linked (but not contiguous). As such it provides a measure of the way in which forest configuration is affecting landscape connectivity for different species. IntraFraction was treated in the same way as ECA, with values calculated for individual species and then averaged across the species pool to obtain a measure of the mean contribution of intra-patch connectivity to overall connectivity within each landscape.

6.2.3. Species niche modelling

In order to account for local environmental conditions within vegetation sampling plots, a series of species niche models contained in the R package MultiMOVE was used to generate probability of occurrence data for the same 256 species for which connectivity data were calculated. These models use climate (annual rainfall, minimum January temperature, maximum temperature in July), canopy (cover weighted canopy height) and soil data (Ellenberg values for pH, fertility and wetness) to calculate the probability of occurrence of species (Smart et al. 2010). Climate data

were obtained from Met Office long term average data

(<http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/>), while canopy height and mean Ellenberg values were calculated based on woody species occurring within plots.

For each species, probability of occurrence data within individual plots was combined to give an overall likelihood of that species occurring within one of the plots in each landscape. A predicted species richness within each survey landscape was obtained by summing the probability of occurrence across the 256 species. This output from MultiMOVE models the ability of forest conditions to support biodiversity and was therefore included as a continuous explanatory variable, MMrichness, in models of overall understorey species richness.

6.2.4. Matrix composition

The matrix composition was measured as the land use type which, not including broadleaved forest habitat, possessed the greatest percentage cover within each sampling landscape. This was determined using land cover data obtained from Countryside Survey 2007 (Norton et al. 2012). Each landscape was therefore assigned to a category; coniferous woodland, improved land (consisting of arable land or improved grassland), urban land, non-improved grassland (neutral, acid or calcareous grassland habitat) or other semi-natural habitat (bracken, bog, dwarf shrub heath). This was then used as a categorical explanatory variable in models of species richness.

6.2.5. Modelling approach

The model outputs described above; ECA, IntraFraction and MMrichness, along with matrix composition, were included in a Poisson generalised linear model of observed species richness values within sampling landscapes. This model was fit with a log link function, due to the count nature of the observed species richness response variable. Since squares varied in the number of forest plots contained, the total area sampled was used as an offset in all models to account for differing survey effort. ECA, MMrichness and plot area were log transformed prior to modelling to reduce the skew in their distribution. Interaction terms between MMrichness and ECA and between ECA and IntraFraction were also included, to investigate potential variation in the effects of connectivity dependent on the effects of local environment and landscape connectivity.

In order to compare the effects of different predictors, explanatory variables were standardised and centred using the R package “arm”. 95 percent confidence intervals around modelled parameter estimates were generated using the R package “MASS”. These parameter estimates and confidence intervals were then used to compare the effects of different explanatory variables on species richness data (Figure 6.2).

In order to investigate the impact on species richness of differences between the various factor levels of the matrix composition variable, a post-hoc Tukey GLHT test was applied to the model using the R package “multcomp”. This performs a pairwise comparison of the differences in response variable between all levels of a treatment factor (in this case matrix composition). In this case testing for significant differences

in forest community species richness in landscapes of varying composition to be (Table 6.2) (Bretz et al. 2011).

6.3. Results

6.3.1. Niche models and connectivity estimates

A strong positive effect of MMrichness on the observed species richness within landscapes was found (Figure 6.2). This suggests that the modelled species richness values generated by MultiMOVE, based upon local environmental conditions, are effective in predicting biodiversity in forest habitat. Both aspects of connectivity, ECA and IntraFraction also had significant effects on the number of forest understorey species present within sampling plots, indicating that landscape connectivity is also a significant and additionally important driver of forest diversity. Plots within landscapes which on average contained greater amounts of reachable forest habitat were less species rich, as were landscapes where most of the overall connectivity came solely from within patch connectivity. Hence, greater numbers of species were found where higher levels of between patch connectivity were observed, implying that species richness is highest where forest habitat is broken up into a number of

small, well connected patches rather than concentrated within an equivalent area of large, poorly connected patches. The interaction between MMrichness and ECA was also found to have a significant negative effect. This suggests that where MMrichness is highest, increasing landscape connectivity has a more negative effect on forest biodiversity. No effect was found for the interaction between overall connectivity and proportion of within patch connectivity.

6.3.2. Matrix composition

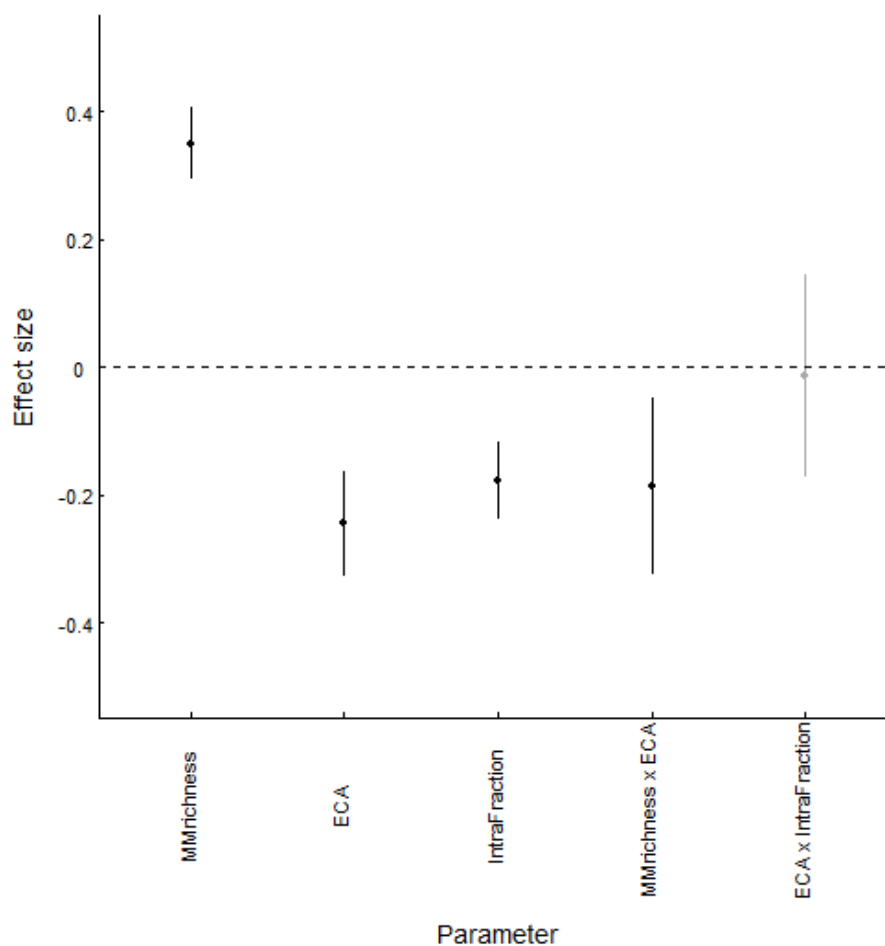


Figure 6.2 Effect sizes for parameters in modelling forest understorey species richness in 1 km landscapes. Error bars show 95% confidence intervals. Where confidence intervals do not overlap zero (shown here as a dashed line) this is indicative of a significant effect of this variable.

Comparisons between forest habitats in landscapes dominated by different non-forest matrix types identified a number of significant differences (Table 6.2). Plots located in forest surrounded mainly by improved land contained fewer species than those in landscapes which mostly consisted of non-improved grassland or coniferous forest. Landscapes with large amounts of urban land contained significantly fewer species than those mostly consisting of any other land use type tested. This suggests that the context of the landscape around forest patches is also an important determinant of understorey biodiversity.

Table 6.2 Table of contrasts for different levels of matrix composition in species richness models, according to a post-hoc Tukey test. Parameter estimates shown are a comparison of species richness at the first factor level shown relative to the second. Bold text indicates significant differences at the 95% confidence level.

Factor level contrasts	Estimate	Std. Error	z value	P value
Improved land – Coniferous forest	-0.11829	0.04274	-2.767	0.0401
Non-improved grassland – Coniferous forest	0.01971	0.04746	0.415	0.9930
Other semi-natural habitat – Coniferous forest	-0.05873	0.06677	-0.880	0.8949
Urban land – Coniferous forest	-0.51561	0.06512	-7.918	<0.001
Non-improved grassland – Improved land	0.13800	0.02906	4.749	<0.001
Other semi-natural habitat – Improved land	0.05956	0.05534	1.076	0.8031
Urban – Improved	-0.39732	0.05347	-7.431	<0.001
Other semi-natural habitat – Non-improved grassland	-0.07844	0.05931	-1.323	0.6547
Urban land – Non-improved grassland	-0.53531	0.05692	-9.405	<0.001
Urban land – Other semi-natural habitat	-0.45687	0.07515	-6.080	<0.001

6.4. Discussion

Species niche models constitute a potentially valuable way of predicting the response of plant communities to a number of global change drivers (Franklin 2013; Guisan et al. 2013). Here, estimates of biodiversity generated using such models were found to be strongly related to observed species richness data in forest communities. This suggests that local environmental conditions can be used to generate useful predictions of the spatial distribution of forest understorey biodiversity in agricultural landscapes (Elith & Leathwick 2009; Franklin 2013; Guillera-Arroita et al. 2015). In addition to the strong effect of local environmental conditions however, variables related to forest connectivity and wider landscape composition were also found to have a significant additional effect on forest species richness values. Thus including these factors when modelling the effects of environmental change is essential to fully understand and predict the occurrence of different plant species (Guisan & Thuiller 2005). Supplementing niche based models with information on landscape connectivity and matrix hostility is likely to be of greatest importance when designing large habitat reserves or wooded networks, which aim to control land use composition and forest configuration at large scales (Pascual-Hortal & Saura 2008; Gurrutxaga et al. 2011; Lentini et al. 2013; Humphrey et al. 2015).

Accounting for landscape connectivity is likely to be particularly necessary where the protection of rare and specialised forest plant species is a primary goal, since the occurrence of such species is often highly dispersal limited (Hermy et al. 1999; Verheyen et al. 2003; Kimberley et al. 2013). It is therefore not sufficient just to correctly predict patch suitability without considering constraints on patch occupancy. For example, forest specialist plants can take over 150 years to fully

colonise newly created forest habitat, leading to their frequent absence from younger forest areas, even where environmental conditions appear well suited (Ehrlén & Eriksson 2000; Brunet 2007; Ozinga et al. 2009; Baur 2014; Kimberley et al. 2015; Naaf & Kolk 2015). Failure to account for these immigration credits is likely to lead to an overestimation of forest diversity in newly created patches which are isolated from source populations (Jackson & Sax 2010; Kimberley et al. 2015; Naaf & Kolk 2015). The extent to which the connectivity of forest habitat and the composition of the wider landscape are likely to facilitate the occurrence of dispersal limited species is therefore an important consideration when developing management strategies to conserve forest specialist plants (Kimberley et al. 2014).

Although connectivity was found to influence forest species richness, our results suggest that this is unlikely to be as simple as finding greater biodiversity in landscapes with an increasing amount of forest connectivity. Both total landscape connectivity and the extent to which this is provided by within or between patch connectivity had significant effects on the number of forest species present. Since different amounts and spatial configurations of forest are likely to result in different understorey communities, targeted forest conservation and creation through the use of spatially explicit connectivity models is likely to provide the most effective means of designing land management strategies to counter habitat fragmentation (Lee & Thompson 2005; Quine & Watts 2009).

Here, biodiversity was found to be lowest where forest habitat was distributed into a small number of unconnected patches. This may be due to the dominance either of a small number of forest specialist species adapted for low light conditions where

these patches are large in area, due to the suppressive effect of shade on more competitive species, or of species typical of more fertile, better lit conditions capable of colonising isolated patches or surviving at forest edges where these patches are small in area (Willi et al. 2005; Chabrierie et al. 2013; Kopecky et al. 2013). Higher levels of between patch movement may also increase the ability of less capable dispersers to colonise smaller forest patches and persist as viable meta-populations alongside better dispersing species, thus increasing the biodiversity within the landscape (Johst et al. 2002; Honnay et al. 2005). As such, attempting to create links between forest habitat areas is likely to have a positive effect on many species; particularly those of intermediate dispersal ability (Bailey 2007; Laita et al. 2010; Saura & Rubio 2010). For such species, patches of lower quality may still be important contributors to connectivity, acting as stepping stones between more suitable areas (Saura & Rubio 2010; Saura et al. 2014). Understanding the extent to which patches contribute in this way is therefore likely to be important when determining areas of high conservation value forest habitat (Saura & Pascual-Hortal 2007; Baranyi et al. 2011).

Landscape configurations in which between patch connectivity is more important relative to within patch connectivity appear to be beneficial for overall forest biodiversity, yet the same positive effect may not be seen for forest specialist plants. Such species are usually found in large, long-established forest patches, and are therefore unlikely to be favoured in highly fragmented landscapes (Petit et al. 2004; Brunet 2007; Brunet et al. 2012; Kimberley et al. 2013; Kimberley et al. 2014). Presumably because such shaded and forest-dominated landscapes filter for a smaller number of specialist taxa, species richness is relatively low despite exhibiting

high connectivity. Alternatively, in newly wooded landscapes, unpaid immigration credit coupled with suppression of pre-existing shade-intolerant species would also result in low species richness. The very low dispersal ability of some forest specialist species mean that they are unable to travel even short distances between patches, meaning they are highly reliant on within patch connectivity (Saura & Rubio 2010). A combination of large habitat reserves and well-connected smaller patches is therefore likely to best balance the conservation of the range of forest species and high overall species richness (Grau et al. 2013).

The variation in species richness observed in forest patches surrounded by different land use types found here highlights the important effect of landscape context on species occurrence. Forest edges are often less shaded and subject to higher soil fertility and levels of disturbance (Murcia 1995). This is also linked to variation in species composition, which has been shown to differ considerably from forest edge habitat to patch interiors (Vallet et al. 2010; Pellissier et al. 2013). Recent evidence suggests these effects are dependent on the intensity of adjacent land use, with the use of fertilisers leading to an increase in nitrogen and phosphorous concentrations within forest habitat (Didham et al. 2015). These conditions favour faster-growing generalist species. Where these include tall perennial herbs their competitive effect can suppress more typical forest species leading to low biodiversity, particularly in forests adjacent to intensive farmland areas where edge effects are strongest (Willi et al. 2005; Chabrierie et al. 2013). This suggests that there is likely to be some benefit to land-sharing management scenarios, which aim to surround habitat reserves with less intensive agricultural land (Fischer et al. 2008). Our results suggest that buffering existing forest areas with semi-natural habitats such as rough

grassland may be an effective way of increasing species richness with forest patches. Further investigation into whether this is dependent upon the width of buffering habitat is needed to fully understand the potential buffer effect on forest communities however, since higher forest diversity may only be found in landscapes which have a large amount of semi-natural land, which is unlikely to be practically achievable in highly agricultural regions. Furthermore, connectivity was measured based upon a binary classification of forest habitat and non-habitat matrix. This is overly simplistic for forest plant species, for which a gradient of suitability across different land uses is more realistic (Kupfer et al. 2006). Hence, the softening of the matrix may have an additional positive effect on landscape connectivity by creating links between forest areas for species which are capable of existing within semi-natural habitat types (Donald & Evans 2006). Considering matrix hostility in connectivity models is therefore likely to improve their ability to predict and explain patterns in biodiversity and species occurrence (Kupfer et al. 2006; Watts et al. 2010).

6.5. Conclusions

Attempts to predict the effects of various global change drivers or management strategies on species assemblages rely on the accurate modelling of species occurrence under different conditions. Hence, proper understanding is needed of the way in which different factors, both at the local and landscape scales, influence the species which are likely to colonise forest habitat following environmental change, either due to alterations in habitat suitability through processes such as coppicing or pollutant deposition or as a result of changes in forest extent. While local conditions are likely to have a strong effect on which species become established (Dupré &

Ehrlén 2002; Kimberley et al. 2014), in some cases the inability of species to reach suitable habitat is likely to be the limiting factor on their occurrence (Bekker et al. 2005; Ozinga et al. 2009). Incorporating landscape scale connectivity and matrix suitability into models of forest understorey biodiversity added significantly to the predictive power of models based solely on abiotic conditions within the forest patch. Thus inclusion of dispersal distances and detailed land cover composition and configuration in models of change in forest communities is necessary to produce realistic projections of the future diversity and composition of forest plant species.

7. Conclusions

7.1. Local environment and forest community composition

Forest understorey community composition was found to be affected by a variety of different spatial and environmental variables, acting at both local and landscape scales. This highlights the fact that forest communities are the product of a complex set of filters acting on the occurrence of individual species through their combinations of life history traits and the way this affects both dispersal and establishment over time. Ensuring that the composition and configuration of habitats within landscapes are maintained in a way which supports important forest plant diversity is therefore essential to avoid the homogenisation of forest plant communities within agricultural landscapes and the loss of functional biodiversity.

Local environmental variables were consistently found to have a significant effect on both trait composition and species richness within forest understorey communities throughout the analyses conducted in this thesis. This confirms previous studies which have concluded that the suitability of forest habitat is the primary constraint on the occurrence of most plant species (Dupré & Ehrlén 2002; Hérault & Honnay 2005). Shade and soil carbon content were the strongest predictors of mean trait values, highlighting the filtering effects of light availability and soil fertility on the species pool, and the importance of traits in determining species ability to survive in highly shaded or fertile conditions (Reich et al. 1998; Augspurger et al. 2005; Hodgson et al. 2011). This is most likely due to the trade-off in resource allocation towards dispersal versus persistence traits, with species only able to invest in either rapid growth and seed production to enable effective dispersal and colonisation of

available habitat, including woodland gaps, or shade tolerance and long term persistence to survive in highly shaded, undisturbed forest patches (Westoby 1998; Wright et al. 2004; Shipley et al. 2006). Differences in specific leaf area, seed terminal velocity and height between ancient woodland indicator plants and non-indicator species suggest that this trade-off strongly influences the habitats available to forest plant species. Hence, any conservation plan must take into account local patch conditions in combination with the degree of connectivity of habitat when attempting to manage understorey composition.

Almost all forest habitat across Britain has undergone some form of management throughout its history, with extensive timber extraction during the 20th century leading to relatively open, species-rich areas of forest (Goldberg et al. 2007; Smart et al. 2014). The abandonment of coppicing practices in recent years has led to the closing of canopies and the creation of more shaded conditions. This has led in turn to a reduction in both alpha and beta diversity as shade-tolerant plants dominate local species pools in increasingly undisturbed forest habitat (Smart et al. 2006; Verheyen et al. 2012; Smart et al. 2014). The loss of light demanding species in such situations is likely to explain why the amount of shade was found to have such a strong effect on forest community composition. Results here suggest that species with heavy, fast falling seeds are found more often in shaded plots, while intermediate levels of shading supported communities with a greater number of rare species. Controlling light availability through management processes such as coppicing or the felling of trees for timber is therefore likely to be important to ensure beta-diversity in forest habitats remains high, and prevent the local extinction of plant species that are most abundant in better lit gaps (Kopecky et al. 2013).

In addition to anthropogenic disturbances through woodland management, large scale disturbance events such as storms or disease can cause the loss of large numbers of adult trees. This can create gaps in forest habitat, allowing light demanding species to move into the changed conditions and thus deflecting community composition from its trajectory towards low biodiversity and high shade tolerance (Smart et al. 2014). Such disturbance may also interact with other drivers such as soil fertility. Results here suggest that where soil nitrogen levels are higher, ruderal plants, with lighter seeds and higher specific leaf area are more prevalent. In undisturbed forest habitat, growth of these shade-intolerant species is likely to be suppressed by the lack of light available. Following the creation of canopy gaps however, these species may be able to utilise increased macronutrient availability spilling over from surrounding intensive agricultural land, leading to their dominance within the forest understorey, in place of shade tolerant forest specialists and plants typical of lower productivity conditions (Chabrierie et al. 2013; Didham et al. 2015).

Since no disturbance history data were available for the forest habitat analysed here however, it was not possible to investigate the extent of these effects or the timescales over which they are likely to occur. A key area for future research therefore, is to investigate the extent to which future disturbance interacting with ongoing pollutant deposition is likely to cause biotic homogenisation, with forest communities becoming more similar in composition to the surrounding countryside; containing a high proportion of nutrient demanding generalist plants. Given the strong influence of local environment on trait composition and species richness within forest habitat found throughout this thesis, this process could offset any positive effects of increased forest habitat following afforestation, thus leading to a

loss of forest diversity even where connectivity and forest area has been maintained or increased. This may lead to a reduced role for forest habitat as a provider of ecosystem functions in agricultural landscapes, since lower forest biodiversity is likely to lead to a decrease in important taxa such as butterfly larval food plants, crop wild relatives and nectar plants for pollinating invertebrates (Donkersley et al. 2014; Mitchell et al. 2014). Furthermore, analysis of ancient woodland indicator plants found that a large number of species which are more typical of low or intermediate productivity semi-natural habitats are restricted to ancient forest in agricultural landscapes. Better lit, more fertile conditions due to disturbance and pollutant deposition are likely to reduce the ability of forest habitat to act as a refuge for these species.

7.2. Forest age and spatial configuration

Previously, conflicting evidence has been found for the importance of stochastic extinctions through reduced population sizes and movement between habitat patches in determining species occurrence, when compared to niche differentiation dependent on habitat quality (Honnay et al. 1999; Herault & Honnay 2005; Honnay et al. 2005; Liira et al. 2014). The lack of a significant effect of patch area when local patch characteristics have been included has led some authors to conclude that the area of forest habitat patches is simply a surrogate for habitat quality for vascular plants and landscape connectivity, while meta-population dynamics have been considered less relevant within forest communities due to the high persistence and low dispersal ability of most plant species (Honnay et al. 2005; Liira et al. 2014; Humphrey et al. 2015). Results here show that both patch size and landscape connectivity have a significant effect on a number of aspects of community

composition, after accounting for the effects of abiotic conditions, and in some cases these effects are similar in magnitude to those of local environmental variables. This indicates that the spatial configuration of forest habitat and the composition of the wider landscape does have an important effect on populations of many forest plants. Rare species with fast falling seeds and no persistent seedbank are mostly restricted to large forest patches, while forest patches with many links to other areas of forest habitat possess the greatest understorey biodiversity. The importance of different life history characteristics in determining the response of species to both environmental conditions and landscape configuration means that the loss and fragmentation of forest habitat is likely to lead to the homogenisation of forest communities in remaining habitat (McKinney & Lockwood 1999; Smart et al. 2006; Vellend et al. 2007). As such, conservation efforts should focus on the maintenance of large networks of forest habitat in order to preserve vulnerable forest species and avoid the loss of important functional diversity.

Efforts were made to maximise the amount of directly observed data used in analyses, however in order to include the greatest sample of British forest patches it was often necessary to estimate some variables indirectly. For example measured soil conditions were not available for all vegetation sampling plots. In such cases, these variables were assessed using mean Ellenberg values of woody species present. While the resulting predictors are likely to provide a useful surrogate for edaphic conditions, their ability to explain plant composition data is likely to be reduced by the imperfect relationship between the observed Ellenberg values and the real conditions they represent. Similarly, trait data for a number of species were imputed based upon species within taxonomic groups. This allowed the maximum

possible amount of data to be used, but is likely to have limited the explanatory power of statistical models. Performing analyses over such a range of forest conditions leads to a high degree of noise within data sets, reducing the ability to identify weaker relationships (Smart et al. 2012). A more complete coverage of directly measured trait and environmental data and of rare species occurrence may therefore have resulted in the identification of further significant trends where expected relationships were not found (such as the lack of effect of spatial variables on mean seed weight values). Furthermore, many plant species may occur at relatively low frequencies within forest patches. Since the vegetation sampling plots used in this thesis are relatively small (at most covering 200 square metres), a number of less common species present, especially in large patches, may be missed. These species are in many cases likely to be those most strongly influenced by landscape composition, further weakening detectable trends. Investigation into species-area relationships within forest patches and the way in which these are affected by variation in environmental conditions and forest spatial configuration is therefore needed to fully understand the mechanisms driving the occurrence of rare forest plant species.

A number of schemes are now in place to promote the conservation and restoration of forest habitat and to increase the connectivity of forest networks (Quine & Watts 2009; Quine et al. 2011; Welsh Government 2012). In addition, road verges and stream-sides are becoming more shaded and dominated by woody vegetation, while a degree of successional growth of secondary woodland has occurred on many areas of semi-natural habitat (Carey et al. 2007; Carey et al. 2008). These new areas of forest habitat in intensive agricultural landscapes are likely to benefit forest species

by increasing the area of habitat patches and reconnecting existing areas of ancient forest, thereby contributing to a range of ecosystem services including flood control, nutrient interception and the provision of niche space for pollinating invertebrates and pollinator plants (Humphrey et al. 2009; Quine et al. 2011; Donkersley et al. 2014).

Although this thesis suggests that large forest patches and well-connected landscapes will be of benefit to many vulnerable forest species, forest community composition is also highly dependent on both forest age and local environmental conditions (Jacquemyn et al. 2003). Secondary forest, has been shown to differ greatly in terms of species composition and environmental conditions even in large, well connected patches, as forest specialist plants are slow to colonise new areas of habitat. The slow response of many species to changes in forest habitat extent is likely to mean that many of the benefits of newly created forest habitat are slow to materialise. Furthermore, in dynamic landscapes, where overall forest habitat is remaining steady but individual patches are being lost and created, communities are likely to fail to maintain the levels of forest diversity seen in more stable forest areas due to the inability of slow colonising forest specialists to keep up with the rate of landscape change (Johst et al. 2002; Verheyen et al. 2004). As such, the use of spatial patterns to project changes in forest biodiversity without considering existing extinction debts or immigration credits may be unrealistic due to the non-equilibrium relationship between species and environment (Thuiller et al. 2008). Understanding the strength of lag effects and the extent to which they affect species with different traits is therefore necessary to understand dispersal limitation and the way in which

this is likely to slow the accumulation of functional diversity within newly planted forest habitat or following successional growth.

In this thesis, historical forest extent data was used to separate older forest habitat from that which was more recently established, however only a coarse measure of forest age was available. This meant that only a relatively broad comparison between the effects of spatial variables in old versus young forest habitat was possible.

Furthermore, it is possible that some patches identified as old due to their presence on historical maps underwent a non-linear change in area between data points, for example losing habitat area which was then subsequently regained. Such changes may well have led to the loss of some forest specialists entirely, due to their inability to recolonize the restored patch after their local extinction following the initial loss of habitat area, despite the apparent lack of change in area indicated. Further analysis using more detailed data on forest age and land use history would allow a gradient of longevity to be established which would lead to more accurate assessment of the way in which forest community composition changes over time in response to changes in environmental conditions and habitat extent. Such understanding is important because it is likely to enable the likely effects of key global change drivers such as climate change, habitat loss and nutrient deposition on forest plant assemblages to be better predicted. Furthermore, no data were available on the previous land use at secondary forest sites. Variation in the starting conditions of forest habitat may have important implications for resulting forest diversity (Flinn & Vellend 2005; Baeten et al. 2011) and affect the length of time taken for new habitat areas to gain forest species (Baeten et al. 2009). Greater knowledge of these processes is therefore still required in order to understand the way in which newly

created broadleaved forest habitat and wooded networks are likely to develop in response to projected scenarios of global change.

7.3. Summary

Here, the characteristics of species which are likely to be vulnerable to habitat loss and fragmentation were identified and the importance of different factors quantified using a detailed, national scale dataset on forest species occurrence. Important local conditions were accounted for in all analyses of understorey community composition, allowing the partial effects of spatial variables such as landscape connectivity and forest patch size to be quantified. Hence, a unique assessment of the relative effects of both local and landscape scale variables in the same analyses was possible. This resulted in the detection of a number of significant relationships between aspects of landscape spatial configuration and understorey community composition. The novel understanding will help inform future decision making on the best way to manage wooded networks in agricultural landscapes and to predict the likely effects of habitat loss and fragmentation on forest plant assemblages (Humphrey et al. 2015). Evidence suggests that, in general, forest biodiversity will benefit from the creation and conservation of large, well connected forest patches within a landscape of semi-natural habitats, although this is likely to depend heavily both on the suitability of the forest environment and upon sufficient time being allowed for slow colonising species to establish populations in any newly created forest patches.

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Appendices

Appendix 1: Supplementary data for Chapter 3

Table A1. List of the 561 plant species used in the CART analysis, their designated AWI status and the node into which they were classified by the decision tree. Species nomenclature is that of Stace (1997).

Species	AWI status	Terminal node in CART analysis (Figure 3.1)
Acer campestre	Non-AWI	17
Acer platanoides	Non-AWI	17
Acer pseudoplatanus	Non-AWI	17
Achillea millefolium	Non-AWI	15
Achillea ptarmica	Non-AWI	15
Aconitum napellus	AWI	10
Adoxa moschatellina	AWI	9
Aegopodium podagraria	Non-AWI	12
Aesculus hippocastanum	Non-AWI	17
Agrimonia eupatoria	Non-AWI	12
Agrostis canina sens.lat.	Non-AWI	11
Agrostis canina sens.str.	Non-AWI	11
Agrostis capillaris	Non-AWI	15
Agrostis stolonifera	Non-AWI	15
Agrostis vinealis	Non-AWI	15
Aira praecox	Non-AWI	16
Ajuga reptans	Non-AWI	11
Alchemilla alpina	Non-AWI	15
Alchemilla filicaulis	AWI	11
Alchemilla glabra	Non-AWI	15
Alchemilla vulgaris agg.	Non-AWI	11
Alchemilla xanthochlora	Non-AWI	15
Alliaria petiolata	Non-AWI	16
Allium ursinum	AWI	3
Alnus glutinosa	Non-AWI	17
Alopecurus geniculatus	Non-AWI	15
Alopecurus pratensis	Non-AWI	15
Anagallis arvensis	Non-AWI	16
Anagallis tenella	Non-AWI	15
Anchusa arvensis	Non-AWI	16
Anemone nemorosa	AWI	9
Angelica sylvestris	Non-AWI	15
Anisantha sterilis	Non-AWI	16
Anthoxanthum odoratum	Non-AWI	15

<i>Anthriscus sylvestris</i>	Non-AWI	10
<i>Apium nodiflorum</i>	Non-AWI	12
<i>Aquilegia vulgaris</i>	AWI	12
<i>Arenaria serpyllifolia</i>	Non-AWI	16
<i>Armoracia rusticana</i>	Non-AWI	11
<i>Arrhenatherum elatius</i>	Non-AWI	15
<i>Artemisia vulgaris</i>	Non-AWI	15
<i>Arum maculatum</i>	Non-AWI	3
<i>Asperula cynanchica</i>	Non-AWI	15
<i>Aster tripolium</i>	Non-AWI	15
<i>Athyrium filix-femina</i>	AWI	4
<i>Atriplex littoralis</i>	Non-AWI	16
<i>Atriplex patula</i>	Non-AWI	16
<i>Atriplex portulacoides</i>	Non-AWI	10
<i>Atropa belladonna</i>	Non-AWI	11
<i>Avena fatua</i>	Non-AWI	16
<i>Avena sativa</i>	Non-AWI	16
<i>Ballota nigra</i>	Non-AWI	12
<i>Bellis perennis</i>	Non-AWI	15
<i>Betula pendula</i>	Non-AWI	17
<i>Betula pubescens</i>	Non-AWI	17
<i>Blackstonia perfoliata</i>	Non-AWI	16
<i>Blechnum spicant</i>	AWI	3
<i>Brachypodium pinnatum</i>	Non-AWI	15
<i>Brachypodium sylvaticum</i>	AWI	10
<i>Brassica napus</i>	Non-AWI	16
<i>Briza media</i>	Non-AWI	15
<i>Briza minor</i>	Non-AWI	16
<i>Bromopsis erecta</i>	Non-AWI	11
<i>Bromopsis ramosa</i>	AWI	11
<i>Bromus hordeaceus</i>	Non-AWI	16
<i>Bromus racemosus</i>	Non-AWI	16
<i>Bryonia dioica</i>	Non-AWI	17
<i>Buxus sempervirens</i>	Non-AWI	17
<i>Calamagrostis canescens</i>	AWI	13
<i>Calamagrostis epigejos</i>	AWI	15
<i>Calluna vulgaris</i>	Non-AWI	15
<i>Caltha palustris</i>	Non-AWI	15
<i>Calystegia sepium</i>	Non-AWI	10
<i>Campanula latifolia</i>	AWI	14
<i>Campanula rotundifolia</i>	Non-AWI	15
<i>Campanula trachelium</i>	AWI	13
<i>Capsella bursa-pastoris</i>	Non-AWI	16
<i>Cardamine amara</i>	AWI	11
<i>Cardamine flexuosa</i>	Non-AWI	11
<i>Cardamine hirsuta</i>	Non-AWI	16

<i>Cardamine hirsuta/flexuosa</i>	Non-AWI	11
<i>Cardamine hirsuta/flexuosa</i>	Non-AWI	16
<i>Cardamine impatiens</i>	AWI	16
<i>Cardamine pratensis</i>	Non-AWI	15
<i>Carex acutiformis</i>	AWI	15
<i>Carex binervis</i>	Non-AWI	11
<i>Carex caryophyllea</i>	Non-AWI	15
<i>Carex digitata</i>	AWI	12
<i>Carex dioica</i>	Non-AWI	15
<i>Carex disticha</i>	Non-AWI	15
<i>Carex echinata</i>	Non-AWI	15
<i>Carex flacca</i>	Non-AWI	15
<i>Carex hirta</i>	Non-AWI	15
<i>Carex laevigata</i>	AWI	11
<i>Carex nigra</i>	Non-AWI	15
<i>Carex otrubae</i>	Non-AWI	15
<i>Carex ovalis</i>	Non-AWI	15
<i>Carex pallescens</i>	AWI	12
<i>Carex panicea</i>	Non-AWI	15
<i>Carex paniculata</i>	Non-AWI	15
<i>Carex pendula</i>	AWI	11
<i>Carex pilulifera</i>	Non-AWI	12
<i>Carex pulicaris</i>	Non-AWI	11
<i>Carex remota</i>	AWI	15
<i>Carex rostrata</i>	Non-AWI	15
<i>Carex strigosa</i>	AWI	11
<i>Carex sylvatica</i>	AWI	12
<i>Carex viridula subsp.oedocarp</i>	Non-AWI	11
<i>Carlina vulgaris</i>	Non-AWI	16
<i>Carpinus betulus</i>	Non-AWI	17
<i>Carum verticillatum</i>	Non-AWI	11
<i>Castanea sativa</i>	Non-AWI	17
<i>Centaurea nigra</i>	Non-AWI	12
<i>Centaurea scabiosa</i>	Non-AWI	10
<i>Centaurium erythraea</i>	Non-AWI	16
<i>Cephalanthera longifolia</i>	AWI	3
<i>Cerastium fontanum</i>	Non-AWI	15
<i>Cerastium semidecandrum</i>	Non-AWI	16
<i>Ceratocarpus claviculata</i>	AWI	16
<i>Chaerophyllum temulum</i>	Non-AWI	16
<i>Chamaecyparis lawsoniana</i>	Non-AWI	17
<i>Chamerion angustifolium</i>	Non-AWI	11
<i>Chenopodium album agg.</i>	Non-AWI	16
<i>Chrysosplenium alternifolium</i>	AWI	11
<i>Chrysosplenium oppositifolium</i>	AWI	11

<i>Circaea lutetiana</i>	Non-AWI	15
<i>Cirsium acaule</i>	Non-AWI	9
<i>Cirsium arvense</i>	Non-AWI	15
<i>Cirsium heterophyllum</i>	AWI	11
<i>Cirsium palustre</i>	Non-AWI	16
<i>Cirsium vulgare</i>	Non-AWI	16
<i>Claytonia perfoliata</i>	Non-AWI	16
<i>Claytonia sibirica</i>	Non-AWI	16
<i>Clematis vitalba</i>	Non-AWI	17
<i>Clinopodium vulgare</i>	Non-AWI	15
<i>Cochlearia danica</i>	Non-AWI	16
<i>Cochlearia officinalis sens.l</i>	Non-AWI	16
<i>Colchicum autumnale</i>	AWI	3
<i>Conium maculatum</i>	Non-AWI	17
<i>Conopodium majus</i>	AWI	12
<i>Convallaria majalis</i>	AWI	3
<i>Convolvulus arvensis</i>	Non-AWI	10
<i>Cornus sanguinea</i>	Non-AWI	17
<i>Corylus avellana</i>	Non-AWI	17
<i>Crataegus monogyna</i>	Non-AWI	17
<i>Crepis capillaris</i>	Non-AWI	16
<i>Crepis paludosa</i>	Non-AWI	15
<i>Crithmum maritimum</i>	Non-AWI	9
<i>Cruciata laevipes</i>	Non-AWI	9
<i>Cynosurus cristatus</i>	Non-AWI	15
<i>Cystopteris fragilis</i>	Non-AWI	3
<i>Cytisus scoparius</i>	Non-AWI	10
<i>Dactylis glomerata</i>	Non-AWI	15
<i>Dactylorhiza fuchsii</i>	Non-AWI	3
<i>Dactylorhiza maculata</i>	Non-AWI	4
<i>Danthonia decumbens</i>	Non-AWI	15
<i>Daphne laureola</i>	AWI	11
<i>Daphne mezereum</i>	AWI	10
<i>Daucus carota</i>	Non-AWI	16
<i>Deschampsia cespitosa</i>	Non-AWI	15
<i>Deschampsia flexuosa</i>	Non-AWI	15
<i>Digitalis purpurea</i>	Non-AWI	16
<i>Dipsacus fullonum</i>	Non-AWI	16
<i>Doronicum pardalianches</i>	Non-AWI	11
<i>Drosera intermedia</i>	Non-AWI	15
<i>Drosera longifolia</i>	Non-AWI	11
<i>Drosera longifolia</i>	Non-AWI	11
<i>Drosera rotundifolia</i>	Non-AWI	14
<i>Dryopteris aemula</i>	AWI	3
<i>Dryopteris affinis</i>	AWI	3
<i>Dryopteris carthusiana</i>	AWI	3

<i>Dryopteris dilatata</i>	Non-AWI	4
<i>Dryopteris filix-mas</i>	Non-AWI	4
<i>Dryopteris remota</i>	Non-AWI	3
<i>Eleocharis quinqueflora</i>	Non-AWI	4
<i>Elymus caninus</i>	AWI	12
<i>Elytrigia repens</i>	Non-AWI	11
<i>Empetrum nigrum</i>	Non-AWI	11
<i>Epilobium brunnescens</i>	Non-AWI	11
<i>Epilobium ciliatum</i>	Non-AWI	15
<i>Epilobium hirsutum</i>	Non-AWI	15
<i>Epilobium montanum</i>	Non-AWI	15
<i>Epilobium obscurum</i>	Non-AWI	11
<i>Epilobium palustre</i>	Non-AWI	15
<i>Epilobium parviflorum</i>	Non-AWI	15
<i>Epilobium tetragonum</i>	Non-AWI	15
<i>Epipactis helleborine</i>	AWI	4
<i>Epipactis leptochila</i>	AWI	3
<i>Epipactis purpurata</i>	AWI	3
<i>Equisetum arvense</i>	Non-AWI	4
<i>Equisetum fluviatile</i>	Non-AWI	4
<i>Equisetum palustre</i>	Non-AWI	3
<i>Equisetum sylvaticum</i>	AWI	4
<i>Equisetum telmateia</i>	AWI	4
<i>Erica cinerea</i>	Non-AWI	15
<i>Erica tetralix</i>	Non-AWI	15
<i>Erigeron acer</i>	Non-AWI	16
<i>Eriophorum angustifolium</i>	Non-AWI	4
<i>Eriophorum vaginatum</i>	Non-AWI	4
<i>Euonymus europaeus</i>	Non-AWI	17
<i>Eupatorium cannabinum</i>	Non-AWI	15
<i>Euphorbia amygdaloides</i>	AWI	9
<i>Euphrasia officinalis</i> agg.	Non-AWI	16
<i>Fagus sylvatica</i>	Non-AWI	17
<i>Fallopia japonica</i>	Non-AWI	11
<i>Festuca altissima</i>	AWI	11
<i>Festuca arundinacea</i>	Non-AWI	15
<i>Festuca gigantea</i>	AWI	10
<i>Festuca ovina</i> agg.	Non-AWI	11
<i>Festuca pratensis</i>	Non-AWI	15
<i>Festuca rubra</i> agg.	Non-AWI	11
<i>Festuca vivipara</i>	Non-AWI	11
<i>Filipendula ulmaria</i>	Non-AWI	15
<i>Filipendula vulgaris</i>	Non-AWI	15
<i>Fragaria vesca</i>	AWI	15
<i>Fraxinus excelsior</i>	Non-AWI	17
<i>Fuchsia magellanica</i>	Non-AWI	11

<i>Galega officinalis</i>	Non-AWI	10
<i>Galeopsis tetrahit</i> agg.	Non-AWI	16
<i>Galium aparine</i>	Non-AWI	16
<i>Galium mollugo</i>	Non-AWI	12
<i>Galium odoratum</i>	AWI	9
<i>Galium palustre</i>	Non-AWI	12
<i>Galium saxatile</i>	Non-AWI	12
<i>Galium uliginosum</i>	Non-AWI	15
<i>Galium verum</i>	Non-AWI	15
<i>Gaultheria shallon</i>	Non-AWI	11
<i>Geranium dissectum</i>	Non-AWI	16
<i>Geranium molle</i>	Non-AWI	16
<i>Geranium robertianum</i>	AWI	16
<i>Geranium sanguineum</i>	AWI	9
<i>Geranium sylvaticum</i>	AWI	9
<i>Geum rivale</i>	AWI	15
<i>Geum rivale</i> x <i>urbanum</i>	Non-AWI	11
<i>Geum urbanum</i>	Non-AWI	15
<i>Glechoma hederacea</i>	Non-AWI	11
<i>Glyceria declinata</i>	Non-AWI	11
<i>Glyceria fluitans</i>	Non-AWI	12
<i>Glyceria maxima</i>	Non-AWI	10
<i>Gnaphalium sylvaticum</i>	AWI	11
<i>Gnaphalium uliginosum</i>	Non-AWI	16
<i>Gymnocarpium dryopteris</i>	AWI	3
<i>Hedera helix</i>	Non-AWI	17
<i>Helianthemum nummularium</i>	Non-AWI	12
<i>Helictotrichon pratense</i>	Non-AWI	11
<i>Helictotrichon pubescens</i>	Non-AWI	11
<i>Heracleum sphondylium</i>	Non-AWI	16
<i>Hirschfeldia incana</i>	Non-AWI	16
<i>Holcus lanatus</i>	Non-AWI	15
<i>Holcus mollis</i>	AWI	14
<i>Hordelymus europaeus</i>	AWI	10
<i>Hordeum distichon</i> sens.lat.	Non-AWI	16
<i>Hordeum murinum</i>	Non-AWI	16
<i>Humulus lupulus</i>	Non-AWI	17
<i>Hyacinthoides non-scripta</i>	AWI	3
<i>Hydrocotyle vulgaris</i>	Non-AWI	11
<i>Hymenophyllum wilsonii</i>	AWI	3
<i>Hypericum androsaemum</i>	AWI	11
<i>Hypericum hirsutum</i>	AWI	15
<i>Hypericum humifusum</i>	Non-AWI	15
<i>Hypericum perforatum</i>	Non-AWI	15
<i>Hypericum pulchrum</i>	AWI	15
<i>Hypericum tetrapterum</i>	AWI	11

<i>Hypochaeris glabra</i>	Non-AWI	16
<i>Hypochaeris radicata</i>	Non-AWI	11
<i>Ilex aquifolium</i>	Non-AWI	17
<i>Impatiens capensis</i>	Non-AWI	16
<i>Impatiens glandulifera</i>	Non-AWI	16
<i>Iris foetidissima</i>	AWI	3
<i>Iris pseudacorus</i>	Non-AWI	3
<i>Jasione montana</i>	Non-AWI	16
<i>Juglans regia</i>	Non-AWI	17
<i>Juncus bufonius sens.lat.</i>	Non-AWI	4
<i>Juncus bulbosus</i>	Non-AWI	4
<i>Juncus conglomeratus</i>	Non-AWI	4
<i>Juncus effusus</i>	Non-AWI	4
<i>Juncus inflexus</i>	Non-AWI	4
<i>Juncus squarrosus</i>	Non-AWI	4
<i>Juniperus communis</i>	Non-AWI	17
<i>Koeleria macrantha</i>	Non-AWI	15
<i>Lactuca serriola</i>	Non-AWI	16
<i>Lamiastrum galeobdolon</i>	AWI	12
<i>Lamium album</i>	Non-AWI	12
<i>Lamium hybridum</i>	Non-AWI	16
<i>Lamium purpureum</i>	Non-AWI	16
<i>Lapsana communis</i>	Non-AWI	16
<i>Larix kaempferi</i>	Non-AWI	17
<i>Lathyrus linifolius</i>	AWI	9
<i>Lathyrus pratensis</i>	Non-AWI	10
<i>Lathyrus sylvestris</i>	AWI	10
<i>Lathyrus tuberosus</i>	Non-AWI	10
<i>Lavatera arborea</i>	Non-AWI	17
<i>Leontodon autumnalis</i>	Non-AWI	15
<i>Leontodon hispidus</i>	Non-AWI	15
<i>Leontodon saxatilis</i>	Non-AWI	11
<i>Lepidium campestre</i>	Non-AWI	16
<i>Leucanthemum vulgare</i>	Non-AWI	15
<i>Ligustrum vulgare</i>	Non-AWI	17
<i>Lilium martagon</i>	Non-AWI	4
<i>Limonium vulgare</i>	Non-AWI	15
<i>Linum catharticum</i>	Non-AWI	16
<i>Listera ovata</i>	AWI	3
<i>Lithospermum officinale</i>	AWI	10
<i>Lolium multiflorum</i>	Non-AWI	16
<i>Lolium perenne</i>	Non-AWI	15
<i>Lonicera periclymenum</i>	AWI	17
<i>Lotus corniculatus</i>	Non-AWI	12
<i>Lotus pedunculatus</i>	Non-AWI	12
<i>Luzula pilosa</i>	AWI	3

<i>Luzula sylvatica</i>	AWI	3
<i>Lychnis flos-cuculi</i>	Non-AWI	15
<i>Lycopus europaeus</i>	Non-AWI	14
<i>Lysimachia nemorum</i>	AWI	11
<i>Lysimachia nummularia</i>	Non-AWI	11
<i>Lysimachia vulgaris</i>	AWI	15
<i>Lythrum portula</i>	AWI	16
<i>Mahonia aquifolium</i>	Non-AWI	10
<i>Malus sylvestris</i>	Non-AWI	17
<i>Malva sylvestris</i>	Non-AWI	10
<i>Matricaria discoidea</i>	Non-AWI	16
<i>Medicago lupulina</i>	Non-AWI	16
<i>Melampyrum pratense</i>	AWI	16
<i>Melampyrum sylvaticum</i>	AWI	16
<i>Melica nutans</i>	AWI	13
<i>Melica uniflora</i>	AWI	9
<i>Melittis melissophyllum</i>	AWI	9
<i>Mentha aquatica</i>	Non-AWI	15
<i>Mercurialis perennis</i>	AWI	12
<i>Milium effusum</i>	AWI	12
<i>Mimulus guttatus</i>	Non-AWI	15
<i>Moehringia trinervia</i>	AWI	16
<i>Molinia caerulea</i>	Non-AWI	15
<i>Montia fontana</i>	Non-AWI	16
<i>Myosotis arvensis</i>	Non-AWI	16
<i>Myosotis scorpioides</i>	Non-AWI	15
<i>Myosotis secunda</i>	Non-AWI	11
<i>Myosotis sylvatica</i>	AWI	11
<i>Myosoton aquaticum</i>	Non-AWI	14
<i>Myrica gale</i>	Non-AWI	12
<i>Narcissus pseudonarcissus</i>	AWI	9
<i>Nardus stricta</i>	Non-AWI	15
<i>Narthecium ossifragum</i>	Non-AWI	4
<i>Odontites vernus</i>	Non-AWI	16
<i>Oenanthe crocata</i>	Non-AWI	10
<i>Ononis repens</i>	Non-AWI	12
<i>Ophioglossum vulgatum</i>	AWI	3
<i>Orchis mascula</i>	AWI	3
<i>Oreopteris limbosperma</i>	AWI	4
<i>Origanum vulgare</i>	Non-AWI	15
<i>Oxalis acetosella</i>	AWI	12
<i>Parietaria judaica</i>	Non-AWI	11
<i>Paris quadrifolia</i>	AWI	3
<i>Pastinaca sativa</i>	Non-AWI	16
<i>Pedicularis sylvatica</i>	Non-AWI	11
<i>Persicaria amphibia</i>	Non-AWI	11

<i>Persicaria bistorta</i>	Non-AWI	10
<i>Persicaria hydropiper</i>	Non-AWI	16
<i>Persicaria maculosa</i>	Non-AWI	16
<i>Petasites albus</i>	Non-AWI	11
<i>Petasites fragrans</i>	Non-AWI	11
<i>Petasites hybridus</i>	Non-AWI	15
<i>Phalaris arundinacea</i>	Non-AWI	15
<i>Phalaris canariensis</i>	Non-AWI	16
<i>Phegopteris connectilis</i>	AWI	3
<i>Phleum bertolonii</i>	Non-AWI	11
<i>Phleum pratense sens.lat.</i>	Non-AWI	11
<i>Phragmites australis</i>	Non-AWI	17
<i>Phyllitis scolopendrium</i>	AWI	3
<i>Picea abies</i>	Non-AWI	17
<i>Picea sitchensis</i>	Non-AWI	17
<i>Picris echioides</i>	Non-AWI	16
<i>Picris hieracioides</i>	Non-AWI	15
<i>Pilosella officinarum</i>	Non-AWI	11
<i>Pimpinella major</i>	AWI	12
<i>Pimpinella saxifraga</i>	Non-AWI	15
<i>Pinguicula vulgaris</i>	Non-AWI	15
<i>Pinus contorta</i>	Non-AWI	17
<i>Pinus nigra</i>	Non-AWI	17
<i>Pinus sylvestris</i>	Non-AWI	17
<i>Plantago coronopus</i>	Non-AWI	16
<i>Plantago lanceolata</i>	Non-AWI	12
<i>Plantago major</i>	Non-AWI	15
<i>Plantago maritima</i>	Non-AWI	12
<i>Plantago media</i>	Non-AWI	15
<i>Platanthera chlorantha</i>	AWI	3
<i>Poa annua</i>	Non-AWI	16
<i>Poa humilis</i>	Non-AWI	11
<i>Poa nemoralis</i>	AWI	14
<i>Poa pratensis sens.lat.</i>	Non-AWI	11
<i>Poa trivialis</i>	Non-AWI	15
<i>Polygonatum multiflorum</i>	AWI	3
<i>Polygonatum odoratum</i>	AWI	3
<i>Polygonum aviculare agg.</i>	Non-AWI	16
<i>Polypodium vulgare sens.lat.</i>	AWI	3
<i>Polystichum aculeatum</i>	AWI	3
<i>Polystichum setiferum</i>	AWI	4
<i>Populus canescens</i>	Non-AWI	17
<i>Populus tremula</i>	Non-AWI	17
<i>Potentilla anserina</i>	Non-AWI	15
<i>Potentilla erecta</i>	Non-AWI	15
<i>Potentilla reptans</i>	Non-AWI	15

<i>Potentilla sterilis</i>	AWI	11
<i>Primula elatior</i>	AWI	13
<i>Primula veris</i>	Non-AWI	15
<i>Primula vulgaris</i>	AWI	12
<i>Prunella vulgaris</i>	Non-AWI	12
<i>Prunus avium</i>	Non-AWI	17
<i>Prunus domestica</i>	Non-AWI	17
<i>Prunus laurocerasus</i>	Non-AWI	17
<i>Prunus padus</i>	Non-AWI	17
<i>Prunus spinosa</i>	Non-AWI	17
<i>Pseudotsuga menziesii</i>	Non-AWI	17
<i>Pteridium aquilinum</i>	Non-AWI	4
<i>Puccinellia distans</i>	Non-AWI	15
<i>Puccinellia maritima</i>	Non-AWI	11
<i>Pulicaria dysenterica</i>	Non-AWI	15
<i>Pulmonaria longifolia</i>	AWI	9
<i>Pyrola minor</i>	AWI	11
<i>Quercus cerris</i>	Non-AWI	17
<i>Quercus ilex</i>	Non-AWI	17
<i>Quercus petraea</i>	Non-AWI	17
<i>Quercus robur</i>	Non-AWI	17
<i>Radiola linoides</i>	AWI	16
<i>Ranunculus acris</i>	Non-AWI	15
<i>Ranunculus auricomus</i>	AWI	12
<i>Ranunculus bulbosus</i>	Non-AWI	15
<i>Ranunculus ficaria</i>	Non-AWI	9
<i>Ranunculus flammula</i>	Non-AWI	12
<i>Ranunculus repens</i>	Non-AWI	12
<i>Raphanus raphanistrum</i>	Non-AWI	16
<i>Rhinanthus minor</i>	Non-AWI	16
<i>Rhododendron ponticum</i>	Non-AWI	17
<i>Ribes nigrum</i>	AWI	10
<i>Ribes rubrum</i>	AWI	10
<i>Rorippa nasturtium-aquaticum</i>	Non-AWI	11
<i>Rosa arvensis</i>	AWI	10
<i>Rosa canina</i> agg.	Non-AWI	17
<i>Rubia peregrina</i>	Non-AWI	10
<i>Rubus caesius</i>	AWI	9
<i>Rubus fruticosus</i> agg.	Non-AWI	11
<i>Rubus idaeus</i>	Non-AWI	12
<i>Rubus saxatilis</i>	AWI	9
<i>Rubus spectabilis</i>	Non-AWI	10
<i>Rumex acetosa</i>	Non-AWI	15
<i>Rumex acetosella</i>	Non-AWI	15
<i>Rumex crispus</i>	Non-AWI	15
<i>Rumex hydrolapathum</i>	Non-AWI	10

Rumex obtusifolius	Non-AWI	15
Ruscus aculeatus	AWI	3
Sagina procumbens	Non-AWI	15
Salicornia agg.	Non-AWI	16
Salix alba	Non-AWI	17
Salix aurita	Non-AWI	17
Salix caprea	Non-AWI	17
Salix cinerea	Non-AWI	17
Salix fragilis	Non-AWI	17
Salix repens agg.	Non-AWI	11
Salix viminalis	Non-AWI	17
Sambucus nigra	Non-AWI	17
Sambucus racemosa	Non-AWI	17
Sanguisorba minor	Non-AWI	9
Sanicula europaea	AWI	9
Scabiosa columbaria	Non-AWI	15
Schoenus nigricans	Non-AWI	10
Scirpus sylvaticus	AWI	4
Scrophularia auriculata	Non-AWI	15
Scrophularia nodosa	AWI	15
Scutellaria galericulata	Non-AWI	11
Scutellaria minor	AWI	13
Sedum anglicum	Non-AWI	11
Sedum telephium	AWI	11
Selaginella selaginoides	Non-AWI	11
Senecio aquaticus	Non-AWI	16
Senecio erucifolius	Non-AWI	15
Senecio jacobaea	Non-AWI	15
Senecio sylvaticus	Non-AWI	16
Senecio vulgaris	Non-AWI	16
Serratula tinctoria	AWI	15
Sibthorpia europaea	AWI	11
Silene dioica	AWI	12
Silene latifolia	Non-AWI	12
Sison amomum	Non-AWI	16
Sisymbrium officinale	Non-AWI	16
Smyrniolum olusatrum	Non-AWI	16
Solanum dulcamara	Non-AWI	17
Solanum nigrum	Non-AWI	16
Solidago virgaurea	AWI	15
Sonchus arvensis	Non-AWI	15
Sonchus asper	Non-AWI	16
Sonchus oleraceus	Non-AWI	16
Sorbus aucuparia	Non-AWI	17
Sorbus torminalis	Non-AWI	17
Stachys officinalis	AWI	9

<i>Stachys palustris</i>	Non-AWI	12
<i>Stachys sylvatica</i>	AWI	12
<i>Stellaria graminea</i>	Non-AWI	15
<i>Stellaria holostea</i>	AWI	12
<i>Stellaria media</i>	Non-AWI	16
<i>Stellaria neglecta</i>	AWI	16
<i>Stellaria nemorum</i>	AWI	14
<i>Stellaria palustris</i>	Non-AWI	12
<i>Stellaria uliginosa</i>	Non-AWI	15
<i>Suaeda maritima</i>	Non-AWI	16
<i>Succisa pratensis</i>	Non-AWI	15
<i>Symphoricarpos albus</i>	Non-AWI	10
<i>Symphytum tuberosum</i>	Non-AWI	9
<i>Tamus communis</i>	AWI	17
<i>Taraxacum agg.</i>	Non-AWI	11
<i>Taxus baccata</i>	Non-AWI	17
<i>Teucrium scorodonia</i>	Non-AWI	12
<i>Thymus polytrichus</i>	Non-AWI	11
<i>Tilia cordata</i>	Non-AWI	17
<i>Tilia platyphyllos</i>	Non-AWI	17
<i>Tilia x vulgaris</i>	Non-AWI	17
<i>Tofieldia pusilla</i>	Non-AWI	4
<i>Torilis japonica</i>	Non-AWI	16
<i>Trichophorum cespitosum</i>	Non-AWI	11
<i>Trientalis europaea</i>	Non-AWI	12
<i>Trifolium campestre</i>	Non-AWI	16
<i>Trifolium dubium</i>	Non-AWI	16
<i>Trifolium medium</i>	Non-AWI	12
<i>Trifolium pratense</i>	Non-AWI	12
<i>Trifolium repens</i>	Non-AWI	12
<i>Trisetum flavescens</i>	Non-AWI	15
<i>Triticum aestivum</i>	Non-AWI	16
<i>Trollius europaeus</i>	AWI	12
<i>Tsuga heterophylla</i>	Non-AWI	17
<i>Tussilago farfara</i>	Non-AWI	15
<i>Ulex europaeus</i>	Non-AWI	10
<i>Ulex gallii</i>	Non-AWI	10
<i>Ulmus glabra</i>	Non-AWI	17
<i>Ulmus procera</i>	Non-AWI	17
<i>Umbilicus rupestris</i>	Non-AWI	15
<i>Urtica dioica</i>	Non-AWI	15
<i>Vaccinium myrtillus</i>	AWI	15
<i>Valeriana officinalis</i>	AWI	15
<i>Veronica arvensis</i>	Non-AWI	16
<i>Veronica beccabunga</i>	Non-AWI	15
<i>Veronica chamaedrys</i>	Non-AWI	15

<i>Veronica filiformis</i>	Non-AWI	11
<i>Veronica hederifolia</i>	Non-AWI	16
<i>Veronica montana</i>	AWI	11
<i>Veronica officinalis</i>	Non-AWI	15
<i>Veronica persica</i>	Non-AWI	16
<i>Veronica serpyllifolia</i>	Non-AWI	11
<i>Viburnum lantana</i>	Non-AWI	17
<i>Viburnum opulus</i>	Non-AWI	17
<i>Vicia cracca</i>	Non-AWI	10
<i>Vicia lathyroides</i>	Non-AWI	16
<i>Vicia sativa</i>	Non-AWI	16
<i>Vicia sepium</i>	AWI	9
<i>Vicia sylvatica</i>	AWI	12
<i>Vicia tetrasperma</i>	Non-AWI	16
<i>Vinca minor</i>	Non-AWI	9
<i>Viola canina</i>	Non-AWI	12
<i>Viola hirta</i>	Non-AWI	9
<i>Viola odorata</i>	AWI	9
<i>Viola palustris</i>	AWI	11
<i>Viola reichenbachiana</i>	AWI	11
<i>Viola riviniana</i>	AWI	12
<i>Wahlenbergia hederacea</i>	AWI	11

Appendix 2: Supplementary data for Chapter 4

Table A2. Model averaged effect sizes and selection probability values for seed weight.

	Estimate	Std. Error	Lower CI	Upper CI	Relative Importance
(Intercept)	-0.201	0.069	-0.335	-0.066	
Distance to edge	0.066	0.050	-0.031	0.164	0.527
Patch area	0.030	0.055	-0.078	0.139	0.182
Buffer forest	0.045	0.062	-0.076	0.166	0.213
Age	-0.037	0.051	-0.138	0.063	0.349
Age x Distance to edge	-0.142	0.094	-0.325	0.042	0.114
Age x Patch area	-0.135	0.103	-0.337	0.067	0.013
Age x Buffer forest	0.000		0.000	0.000	0.000
Shade 1	0.112	0.073	-0.030	0.254	1.000
Shade 2	0.360	0.078	0.207	0.513	1.000
C:N ratio	-0.102	0.055	-0.209	0.005	0.746
Soil moisture	-0.079	0.049	-0.175	0.018	0.585
Soil pH	0.029	0.064	-0.097	0.155	0.203
Plot type	0.009	0.062	-0.113	0.132	0.161
Northing	-0.215	0.057	-0.326	-0.103	1.000

Table A3. Model averaged effect sizes and selection probability values for seed terminal velocity.

	Estimate	Std. Error	Lower CI	Upper CI	Relative Importance
(Intercept)	-0.230	0.067	-0.361	-0.098	
Distance to edge	-0.017	0.054	-0.123	0.088	0.775
Patch area	-0.056	0.060	-0.174	0.062	0.311
Buffer forest	0.159	0.058	0.045	0.272	1.000
Age	-0.010	0.051	-0.110	0.090	0.777
Age x Distance to edge	-0.257	0.093	-0.440	-0.075	0.745
Age x Patch area	-0.065	0.111	-0.283	0.153	0.043
Age x Buffer forest	0.017	0.102	-0.183	0.216	0.136
Shade 1	0.124	0.071	-0.016	0.264	1.000
Shade 2	0.431	0.076	0.282	0.580	1.000
C:N ratio	-0.010	0.066	-0.139	0.120	0.165
Soil moisture	-0.149	0.049	-0.245	-0.053	1.000
Soil pH	0.206	0.050	0.108	0.304	1.000
Plot type	0.151	0.060	0.034	0.267	1.000
Northing	0.031	0.052	-0.070	0.132	0.218

Table A4. Model averaged effect sizes and selection probability values for specific leaf area

	Estimate	Std. Error	Lower CI	Upper CI	Relative Importance
(Intercept)	-0.122	0.072	-0.263	0.020	
Distance to edge	-0.060	0.052	-0.161	0.042	0.401
Patch area	0.008	0.055	-0.100	0.116	0.192
Buffer forest	0.022	0.059	-0.094	0.137	0.188
Age	-0.080	0.050	-0.178	0.018	0.582
Age x Distance to edge	0.059	0.092	-0.121	0.239	0.052
Age x Patch area	0.047	0.101	-0.150	0.245	0.008
Age x Buffer forest	0.000	0.000	0.000	0.000	0.000
Shade 1	0.103	0.072	-0.037	0.244	0.940
Shade 2	0.197	0.077	0.045	0.348	0.940
C:N ratio	-0.305	0.068	-0.437	-0.172	1.000
Soil moisture	-0.123	0.051	-0.222	-0.024	1.000
Soil pH	0.094	0.063	-0.029	0.218	0.503
Plot type	0.241	0.059	0.125	0.357	1.000
Northing	0.093	0.054	-0.014	0.199	0.604

Table A5. Model averaged effect sizes and selection probability values for seed bank persistence

	Estimate	Std. Error	Lower CI	Upper CI	Relative importance
(Intercept)	0.210	0.070	0.073	0.346	
Distance to edge	-0.032	0.055	-0.139	0.075	0.335
Patch area	-0.129	0.059	-0.244	-0.014	0.910
Buffer forest	-0.093	0.069	-0.228	0.042	0.439
Age	-0.037	0.054	-0.144	0.069	0.654
Age x Distance to edge	0.172	0.102	-0.028	0.371	0.172
Age x Patch area	0.213	0.110	-0.002	0.429	0.470
Age x Buffer forest	0.130	0.119	-0.102	0.362	0.064
Shade 1	-0.108	0.074	-0.254	0.038	1.000
Shade 2	-0.370	0.079	-0.525	-0.215	1.000
C:N ratio	0.048	0.067	-0.084	0.179	0.167
Soil moisture	0.036	0.049	-0.059	0.131	0.187
Soil pH	0.143	0.054	0.037	0.249	1.000
Plot type	0.009	0.057	-0.103	0.120	0.096
Northing	0.108	0.055	-0.001	0.216	0.807

Table A6. Model averaged effect sizes and selection probability values for species rarity

	Estimate	Std. Error	Lower CI	Upper CI	Relative Importance
(Intercept)	-0.178	0.073	-0.320	-0.035	
Distance to edge	0.074	0.057	-0.038	0.187	0.523
Patch area	0.102	0.060	-0.015	0.219	0.820
Buffer forest	0.037	0.073	-0.106	0.179	0.281
Age	0.004	0.057	-0.107	0.115	0.586
Age x Distance to edge	-0.137	0.107	-0.346	0.072	0.130
Age x Patch area	-0.233	0.117	-0.463	-0.004	0.437
Age x Buffer forest	0.169	0.129	-0.085	0.422	0.048
Shade 1	0.105	0.078	-0.048	0.257	1.000
Shade 2	0.313	0.083	0.150	0.476	1.000
C:N ratio	0.212	0.076	0.063	0.362	1.000
Soil moisture	-0.074	0.052	-0.176	0.027	0.468
Soil pH	0.124	0.067	-0.008	0.255	0.726
Plot type	-0.045	0.062	-0.167	0.077	0.213
Northing	-0.176	0.058	-0.289	-0.062	1.000

Appendix 3: Supplementary data for Chapter 5

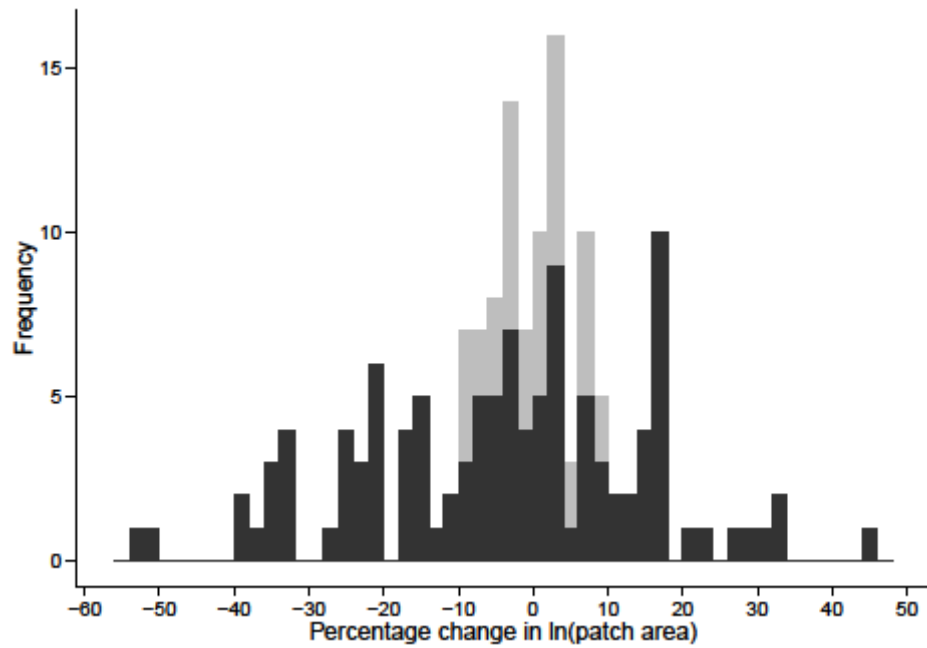


Figure A1. Histograms showing the amount of change observed for three aspects of forest spatial configuration between 1899 and 2007 in forest patches over 100 years in age across Great Britain, around 151 vegetation sampling plots. Grey area shows the data removed prior to modelling.

Table A7: Effect sizes and 95% confidence intervals for explanatory variables in the model for seed weight.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	0.114	-0.075	0.312
Change in patch area	0.146	-0.073	0.358
Mean x Change in patch area	0.387	-0.046	0.784
Plot type	-0.095	-0.289	0.109
Northing	-0.169	-0.355	0.018
C:N ratio	-0.241	-0.494	-0.005
Soil pH	-0.275	-0.528	-0.014
Shade 1	0.305	0.025	0.532
Shade 2	-0.005	-0.167	0.191

Table A8: Effect sizes and 95% confidence intervals for explanatory variables in the model for seed terminal velocity.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	0.239	0.007	0.470
Change in patch area	-0.032	-0.247	0.216
Mean x Change in patch area	0.057	-0.429	0.552
Plot type	0.148	-0.033	0.352
Northing	-0.056	-0.283	0.168
C:N ratio	-0.144	-0.381	0.079
Soil pH	-0.034	-0.300	0.224
Shade 1	0.315	0.098	0.573
Shade 2	0.153	-0.014	0.320

Table A9: Effect sizes and 95% confidence intervals for explanatory variables in the model for specific leaf area.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	0.007	-0.218	0.192
Change in patch area	-0.168	-0.378	0.035
Mean x Change in patch area	-0.446	-0.937	0.000
Plot type	0.367	0.201	0.521
Northing	0.043	-0.167	0.285
C:N ratio	-0.275	-0.487	-0.055
Soil pH	0.167	-0.086	0.408
Shade 1	0.205	-0.001	0.389
Shade 2	0.072	-0.087	0.218

Table A10: Effect sizes and 95% confidence intervals for explanatory variables in the model for seedbank persistence.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	-0.308	-0.472	-0.092
Change in patch area	-0.159	-0.358	0.032
Mean x Change in patch area	-0.451	-0.839	-0.057
Plot type	0.105	-0.075	0.291
Northing	0.114	-0.074	0.294
C:N ratio	0.173	-0.066	0.405
Soil pH	0.335	0.079	0.577
Shade 1	-0.242	-0.481	0.026
Shade 2	0.019	-0.140	0.175

Table A11: Effect sizes and 95% confidence intervals for explanatory variables in the model for rarity.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	0.310	0.086	0.518
Change in patch area	-0.018	-0.244	0.189
Mean x Change in patch area	-0.097	-0.594	0.376
Plot type	-0.100	-0.297	0.097
Northing	-0.192	-0.416	0.020
C:N ratio	0.003	-0.295	0.275
Soil pH	0.018	-0.270	0.304
Shade 1	0.209	-0.061	0.461
Shade 2	0.116	-0.048	0.298

Table A12: Effect sizes and 95% confidence intervals for explanatory variables in the model for species richness.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	-0.091	-0.313	0.124
Change in patch area	-0.006	-0.207	0.226
Mean x Change in patch area	-0.129	-0.596	0.316
Plot type	-0.055	-0.215	0.091
Northing	0.423	0.197	0.647
C:N ratio	0.040	-0.226	0.238
Soil pH	0.243	0.024	0.451
Shade 1	-0.063	-0.248	0.154
Shade 2	-0.187	-0.330	-0.038

Table A13: Effect sizes and 95% confidence intervals for explanatory variables in the model for ancient woodland indicator richness.

Explanatory variable	Parameter estimate	Lower CI	Upper CI
Mean patch area	0.544	0.151	0.995
Change in patch area	-0.112	-0.436	0.247
Mean x Change in patch area	-0.664	-1.555	0.215
Plot type	-0.206	-0.457	0.071
Northing	0.357	-0.089	0.753
C:N ratio	-0.128	-0.604	0.276
Soil pH	0.194	-0.209	0.590
Shade 1	0.768	0.297	1.424
Shade 2	-0.316	-0.747	0.033

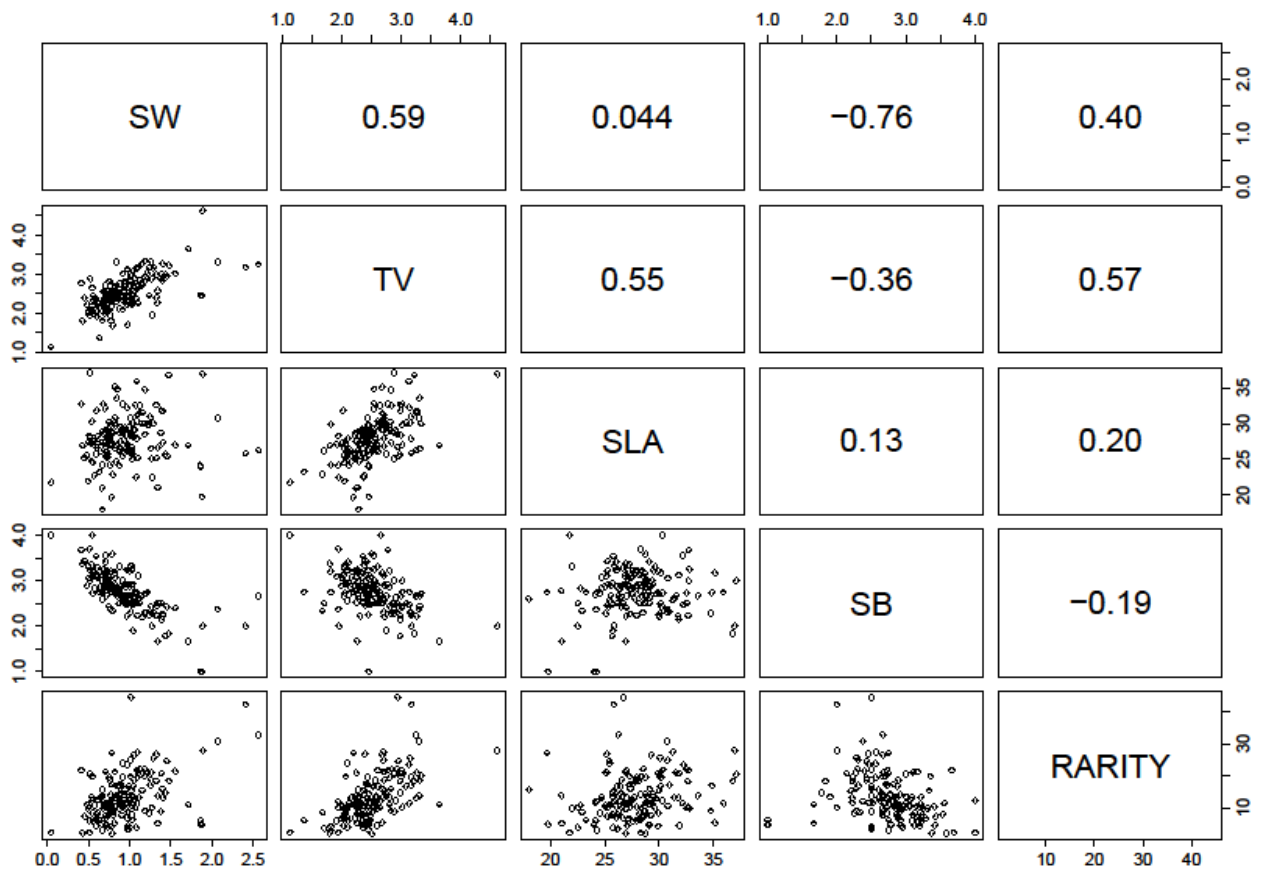


Figure A2. Pairs plot displaying correlations between mean trait values within vegetation sampling plots.