

The evidence base for ecological networks: lessons from studies of woodland fragmentation and creation

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Woodland Creation &
Ecological Networks

WrEN is an ongoing collaborative project between the University of Stirling and Forest Research

Working in partnership with the Forestry Commission, Natural England, Scottish Natural Heritage and Natural Resources Wales

Forest Research is the Research Agency of the Forestry Commission and is the leading UK organisation engaged in forestry and tree related research. The Agency aims to support and enhance forestry and its role in sustainable development by providing innovative, high quality scientific research, technical support and consultancy services.

Research at the Biological & Environmental Sciences Department of the University of Stirling seeks to understand the fundamental processes driving the evolution and maintenance of biodiversity from the genetic to the ecosystem level, how environments and ecosystems have changed over annual to millennial timescales and to predict and mitigate the future impacts of anthropogenic change and natural hazards.

Natural England is an Executive Non-departmental Public Body responsible to the Secretary of State for Environment, Food and Rural Affairs. Our purpose is to protect and improve England's natural environment and encourage people to enjoy and get involved in their surroundings.

Scottish Natural Heritage is funded by the Scottish Government. Our purpose is to: promote care for and improvement of the natural heritage; help people enjoy it responsibly; enable greater understanding and awareness of it; promote its sustainable use, now and for future generations.

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Summary

1. Landscape-scale conservation and ecological networks form a major component of policy responses to biodiversity loss in fragmented landscapes in the UK and other countries.
2. Ecological networks are typically conceptualised as a suite of core areas of habitat connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules.
3. Many conservation actions are now being targeted towards the establishment of ecological networks. Site or local level actions are aimed at restoring, improving and expanding existing habitats, while landscape level actions focus more heavily on creating new habitats, establishing corridors/stepping stones and improving the matrix between habitat patches.
4. There is on-going debate about the relative merit of, and balance between, these alternative conservation actions. The evidence needed to inform the targeting of actions towards particular network components, or combinations of components, is lacking. This uncertainty appears to be hindering the implementation of effective ecological networks on the ground.
5. A large number of test projects to implement landscape-scale ecological networks have been established, but it will be many years or decades until they can provide the necessary evidence base.
6. However, lessons can be learnt from ecosystems with a long history of habitat loss and fragmentation followed by many decades of habitat creation and restoration, such as woodlands in temperate agricultural landscapes.
7. This review forms part of a wider project (WrEN) aimed at extending the evidence base underpinning the implementation of ecological networks. Particular emphasis is given to reviewing studies of the impact on biodiversity of past woodland creation and secondary¹ woodland development.
8. The review adopts the framework proposed by Lawton *et al.* (2010), (see Figure 1) which depicts ecological networks as comprising both local (*Bigger/Better*) and landscape level attributes (*More/Joined*). Three specific questions were addressed:
 - What is the relative impact of different local (e.g. patch size, quality, age) and landscape (e.g. matrix permeability, corridors, surrounding habitat) components of an ecological network on the biodiversity of new and secondary woodlands in agricultural landscapes?
 - Do different taxa show contrasting responses to network components? and,
 - Is there sufficient evidence to justify targeting of resources and conservation action towards particular network components, or combinations of components?
9. An EndNote® library containing 827 references was constructed through interrogating a variety of literature databases and search engines and locating recent (1990-2013) empirical and experimental studies focusing on woodlands, ecological networks and biodiversity.
10. The 827 references were further sifted to yield 318 studies of specific relevance to temperate and boreal forest and agricultural/forest mixed landscapes. Each of these studies was appraised in detail and findings included in the review.
11. The findings of this review confirm that there is considerable variability in species responses to local and landscape variables. Nevertheless there are some guiding principles applicable to mixed woodland/agricultural landscapes in the UK and the different species assemblages they support.

¹ Woodland which has come into existence on land that at some time was completely cleared of trees thus breaking the continuity with original primeval woodland cover (Peterken, 1993)

12. Specialist woodland species (i.e. species restricted to woodland habitat) appear to respond differently to landscape and local factors than generalists (species found in a broad range of habitats), and in particular exhibit contrasting responses to different components of ecological networks. Further, these responses are cross-taxon and calibrated by whether woodland specialists have low, as opposed to intermediate, dispersal ability.
13. Specialist woodland species with poor dispersal abilities respond positively to increases in size and quality of new woodlands and negatively to degree of isolation. Benefits from increasing matrix permeability are equivocal for these species, particularly when overall habitat extent in the landscape is low.
14. Specialist woodland species with intermediate dispersal abilities benefit from measures to increase connectivity² such as the presence of linear and non-linear matrix features with structural affinity to the home habitat, especially where overall habitat extent in the landscape is low.
15. Generalist woodland species appear to benefit more from a large number of small patches in the landscape rather than a few larger ones and respond positively to the amount of edge habitat.
16. Where new woodlands are adjacent, or in close proximity, to ancient woodlands, community development can be relatively rapid (e.g. 50-80 years), but is affected by habitat quality (stand structure and tree species composition) and by past land use (woodland communities appear to develop more rapidly on former pasture than on former arable land).
17. Isolated woods (e.g. more than 2 km from existing woodland) have difficulty in acquiring specialist woodland flora and fauna even if large and of good quality.
18. Ecological continuity may be of less importance than forest structure in determining habitat quality. The occurrence of old-growth structure (large trees, deadwood) is particularly important for late successional species associated with decaying wood habitats.
19. These findings highlight the need for conservation managers to understand which types of species they are interested in conserving and to plan site/landscape management accordingly.
20. Given the limitations of the approach adopted in this review (i.e. broad and inclusive) there would be value in carrying out further review work with a more focused synthesis, selecting those studies which looked at both stand and landscape variables in tandem and were carried out specifically in temperate agricultural landscapes.
21. In addition to this further review work, there is also a need to obtain empirical evidence on the influence of local and landscape factors on the biodiversity of new and secondary woodlands in the UK.
22. Despite a long history of woodland loss and fragmentation, woodland cover in the UK has increased markedly over past 50 years helped in part by the creation of new woods on agricultural land funded by Woodland Grant and Agri-environment Schemes. These woods, together with secondary woodland established in the 19th and early 20th century provide us with a datable chronology of sites occupying historical test landscapes and contributing to *ad hoc* ecological networks. Within these sites, the responses to local and landscape factors of species with different ecological traits and dispersal abilities can be assessed, providing the evidence needed to underpin the further development of ecological networks

² A functional attribute of the landscape related to ecological processes such as the movement of particular species between habitat patches (Harrisson *et al.*, 2012; Watts *et al.*, 2005). Functional connectivity is distinct from connectedness or structural connectivity, which is based simply on physical distance or proximity. Unless otherwise stated the use of the term connectivity in this review refers to functional connectivity.

1. Background

Action to conserve biodiversity has centred traditionally on the protection and management of individual sites (Roberts *et al.*, 1992; Spencer and Kirby, 1992), with limited, and often *ad hoc* measures within the surrounding landscape (Watts *et al.*, 2010). More recently there has been an increased emphasis on landscape ecology with habitat creation and restoration targeted towards addressing habitat loss, fragmentation and connectivity at the landscape scale through the development of ecological networks (Watts *et al.*, 2010; Opdam *et al.*, 2009; Hopkins *et al.*, 2007). Ecological networks are typically conceptualised as a suite of core areas of habitat connected by buffer zones, corridors and smaller stepping stone patches that allow movement of species or their propagules (Watts *et al.*, 2005a).

In the UK and other countries, the development of ecological networks is being addressed through a number of policy initiatives (Newton *et al.*, 2012; Lawton *et al.*, 2010; Jongman and Pungetti, 2004) and individual large-scale projects e.g. Futurescapes (RSPB, 2010), Living Landscapes (The Wildlife Trusts, 2013) the Dutch National Ecological Network (Reijnen *et al.*, 2007) the Carpathians Ecological Network (Zingstra *et al.*, 2009) etc. In England, the recommendations in the *Making Space for Nature* report (Lawton *et al.*, 2010) are strongly reflected in the Natural Environment White Paper (HM Government, 2011), which contains a number of commitments that specifically address large-scale conservation and ecological networks. This includes the establishment of twelve large Nature Improvement Areas. Linked to this, a recent consultation on forestry and woodland policy in England recommended the further expansion of woodland cover and creation of “a coherent and resilient ecological network at a landscape scale” (Independent Panel on Forestry, 2012).

In Scotland, The Spatial Planning and Land Use Sector framework will guide the spatial development of Scotland until 2030 and endorses the creation of national ecological networks as a general principle and practice underlying all forms of land management and land use planning (Gimona *et al.*, 2012; Forestry Commission Scotland, 2009; Scottish Natural Heritage, 2009; The Scottish Government, 2009; Moseley and Smith, 2008). In Wales, The Welsh Assembly Government includes the development of ecological networks as part of its strategy for sustaining and enhancing woodland biodiversity (Welsh Assembly Government, 2009). A number of approaches to modelling and implementing woodland networks have been developed (Watts *et al.*, 2005b; Gkaraveli *et al.*, 2004), including spatial modelling of woodland expansion (Griffiths *et al.*, 2011) and connectivity mapping (Latham and Gillespie, 2009).

While the theoretical basis for the development of ecological networks is well developed (Humphrey *et al.*, 2009; Watts *et al.*, 2008; Humphrey *et al.*, 2005), practical implementation, presents a range of options, the relative importance of which is not always clear. For example, site or local level activities principally target the restoration, improvement and expansion of existing habitats, while landscape level actions focus more explicitly on improving connectivity by creating new habitats, establishing corridors/stepping stones and enhancing the matrix between habitat patches (Lawton *et al.*, 2010; Figure 1). However, the empirical evidence in support of a central focus on improving connectivity is equivocal (Eycott *et al.*, 2012; Hodgson *et al.*, 2009; Bailey, 2007; Davies and Pullin, 2007).

In a review of the impacts of fragmentation on woodland biodiversity, Bailey (2007) argues that there is a lack of firm evidence that species occurrence and abundance increases following attempts to improve connectivity between fragmented woods. Although fragmentation impacts the extent of habitat in the landscape, the size and quality of individual habitat patches, and the distance between patches (Dolman *et al.*, 2007; Lindenmayer and Fischer, 2007; Kupfer *et al.*, 2006), the definition of fragmentation in the strictest sense is the sub-division of habitat patches (Fahrig, 2003). In this sense, the importance of habitat fragmentation as a threat to biodiversity may have been over-

emphasised and that biodiversity losses could more likely be a result of regional loss of habitat area rather than fragmentation *per se* unless the amount of habitat in the landscape is particularly low, e.g. <30% cover (Bailey, 2007; Andr n, 1997; Andr n, 1994).

Further, in a review of climate change adaptation strategies for biodiversity, Mawdsley *et al.* (2009) emphasise the importance of increasing the extent, representation and replication of protected area networks and managing and restoring protected areas to facilitate resilience. The focus is firstly on restoring ecosystem function, with species-related components such as creating movement corridors and improving the permeability of the matrix being of secondary concern and targeted towards species facing extinction. Hodgson *et al.* (2009) endorse this view and suggest that "connectivity" is being over-emphasised in current climate change adaptation strategies. They argue that more robust and cost-effective strategies should be adopted which include maintaining and increasing the area of high quality habitats, prioritizing areas that have high environmental heterogeneity (see also Schippers *et al.*, 2009) and controlling other anthropogenically threatening processes.

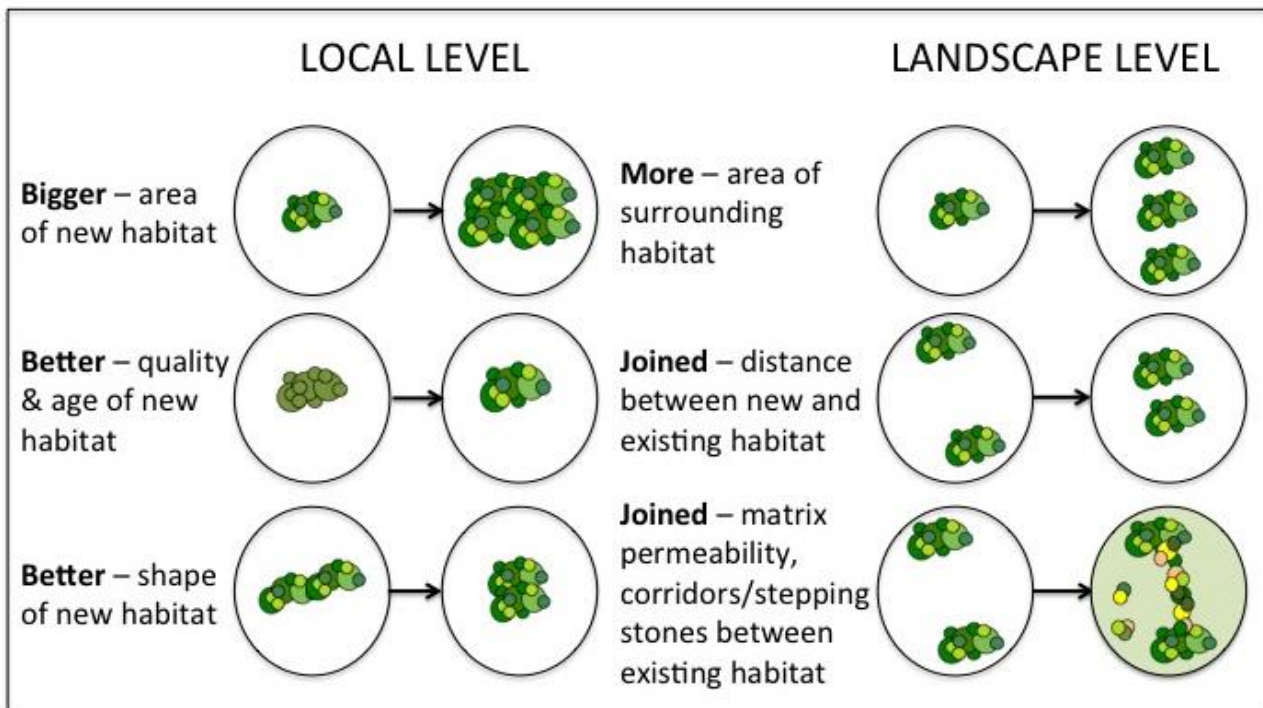


Figure 1 Schematic of approaches to targeting conservation action at local and landscape scales adapted from concepts set out in Lawton *et al.* (2010). The arrows depict positive changes, left to right, over time for each factor.

Hopkins *et al.* (2007) and others maintain that the impact of habitat fragmentation may be one of the most important factors affecting species dispersal. Many species of conservation concern are often separated from potential new habitat by large distances across increasingly hostile landscapes, which exceed their normal dispersal capabilities. Nevertheless, this report recommends the development of ecological networks to improve connectivity between patches as just one principle for helping species adapt to climate change, alongside the conservation of protected areas and other high quality habitats, reducing harmful anthropogenic impacts, and developing ecologically resilient and varied landscapes (Hopkins *et al.*, 2007). Concurring with this, Selman (2009) in a review of the status of the UK protected areas, concluded that they needed to be embedded in land use strategies such as habitat

networks based on gap-filling and anticipatory extension in response to climate change (Catchpole, 2008).

This debate and the uncertainty on the relative merit of, and balance between, alternative conservation actions (e.g. Lentini *et al.*, 2013; Doerr *et al.*, 2011; Hodgson *et al.*, 2011a), may be inhibiting the translation of the ecological network concept into action on the ground (Oliver *et al.*, 2012). In a time of budget cuts and limited resources, it is important to ensure that such conservation actions are underpinned by the best available evidence and implemented in the most effective way to secure biodiversity benefits. Unfortunately, the current brace of new policy initiatives and projects is unlikely to provide the necessary evidence base in support of ecological networks for many years or decades. However, lessons can be learnt from ecosystems with a long history of habitat loss and fragmentation followed by many decades of habitat creation and restoration; for example woodlands in temperate agricultural landscapes where many of the components of ecological networks have been inadvertently created (Mason, 2007).

This review forms part of a wider project (WrEN) aimed at extending the evidence base underpinning the implementation of ecological networks by using woodlands in agricultural landscapes as model systems to draw out guiding principles. Particular emphasis is given to studies of the impact of past woodland creation and secondary woodland development on biodiversity in temperate regions in the UK, Europe, North America and the southern hemisphere.

2. Aims & Scope

In this review we adopted a schematic approach to ecological networks based on the concepts in Lawton *et al.* (2010), which encapsulates the theoretical impacts of local (site) and landscape factors on biodiversity (Figure 1). Through evaluating published research we sought to address the following questions:

1. What is the relative impact of different local (e.g. patch size, quality, age) and landscape (matrix permeability, corridors, surrounding habitat) components of an ecological network on the biodiversity of new and secondary woodlands in agricultural landscapes?
2. Do different taxa show contrasting responses to network components? and,
3. Is there sufficient evidence to justify targeting of resources and conservation action towards particular network components, or combinations of components?

The aim was to build on recent reviews covering specific species groups (Brouwers and Newton, 2009a; Dolman *et al.*, 2007) or particular landscape components (Eycott *et al.*, 2012; Prevedello and Vieira, 2010). As we had a broad set of questions to address and wished to include a wide range of empirical evidence we conducted a traditional narrative review (cf. Fischer and Lindenmayer, 2007) rather than a systematic literature review which necessarily has a narrower focus and more restricted research question (Stewart *et al.*, 2005). The review considered the evidence relating to temperate woodland species for each of the overall categories of Lawton *et al.* (2010) for improving England's ecological networks: 'More, bigger, better and joined' (Figure 1).

Firstly, we assessed the impact of local level factors on biodiversity development in new and secondary woodlands, looking at issues associated with *Bigger* (Figure 1) such as patch size/area. Next we addressed site quality (*Better*), breaking it into constituent components covering stand age, structure and composition, edge effects/patch shape, ecological continuity/legacies/seed banks and land use history. We then looked at influences of the surrounding landscape, focusing particularly on the

extent/area (*More*) of habitat, landscape composition and habitat configuration. Finally, we reviewed evidence of the impacts of isolation on a range of different species groups (*Joined*), and the influence of matrix permeability including linear and non-linear features (*Joined*).

3. Methods

An EndNote® library was constructed from literature searches using the resources described in Table 1. For the Web of Knowledge™ literature searches, broad search terms were used in order to capture a wide range of potentially relevant studies. Wild cards (*) were used with some terms, e.g. "Dispers*" to include different variations of the same word (i.e. Disperse, Dispersal). Boolean operators (e.g. AND, NOT etc.) were used to allow combinations of search terms and restriction of scope.

Table 1 Details of literature search method

Category	Resource	Time envelope	Search terms/method
Digital databases	Web of Knowledge SM comprising BIOSIS Citation index SM , Web of Science®, Current Contents Connect®	2002-2013	Forest AND (separately) History NOT fire, Continuity NOT Fire, Connectivity, "Patch Size", Extent, Dispers*
			Woodland AND (separately) History NOT Fire, Continuity NOT Fire, Connectivity, "Patch Size", Extent, Availability, Size
			Woodland AND Size OR Extent OR Availability
			Biodiversity AND (separately) "Woodland Creation", "New woodland", "Farm woodland", "agri-environment"
Organisation websites and databases	Natural England, Scottish Natural Heritage, Natural Resources Wales, Joint Nature and Conservation Committee; Forest Research, Forestry Commission	1990-2013	All publication titles sifted for general relevance to topic of woodland creation, ecological networks and fragmentation
Literature reviews	Eycott <i>et al.</i> (2012), Prevedello and Vieira (2010), Brouwers and Newton (2009a), Bailey (2007), Dolman <i>et al.</i> (2007)	1990-2013	Cited studies sifted for general relevance to topic of woodland creation, ecological networks and fragmentation

Searches were refined by time (Table 1) and by discipline to include terms such as ecology, environmental science, entomology, zoology, etc. and filtered by locality/country to retain a focus on temperate and boreal forest and agricultural/forest mixed landscapes. Studies focusing on non-woodland species and habitats were excluded excepting hedgerows and shrub/scrub; urban studies were also excluded. In order to limit the number of studies to below 1000 for each search term combination, the time envelope for the search was reduced to 2008-2013 for some combinations (e.g. for Forest AND History). For each search term combination, a first sift was done on the basis of keywords, topic and titles. The focus was on selecting empirical and experimental studies; studies on modelling were not reviewed directly unless linked to species data.

Additional studies were identified through searches of organisation websites and Forest Research internal literature databases and from the reference lists of relevant review papers (Table 1). Duplicates were removed and a working database of 827 references constructed to include journal papers, conference papers/proceedings and published and unpublished reports. A second sift was

carried out on the basis of reading the abstract and if necessary part, or the full text of the published work, after which 318 studies were included directly in the review. Some of the full texts were obtained through the internet search engine Google Scholar® and from the journal repository JSTOR®.

4. *Bigger* – Area of new woodland

4.1 Theoretical aspects of species area relationships

Woodland size is thought to be of importance for biodiversity maintenance and development from two theoretical perspectives: Species Area Relationships (SAR)(Arrhenius, 1921)/island biogeography (Diamond, 1975; MacArthur and Wilson, 1967) and Nestedness (Berglund and Jonsson, 2003). Essentially SAR theory states that as the area of a habitat patch or woodland increases, so does the number of species. Nestedness theory is an allied concept where it is postulated that species-poor sites are a subset of species rich sites (Berglund and Jonsson, 2003). In other words in a highly nested population structure, poor sites do not contain additional species over and above those that are found in rich sites. For example, Berglund and Jonsson (2003), in a study of fungal and plant communities of old growth spruce forest found that sites had a highly nested structure, i.e. rare species were over-represented in the largest patches compared to the small patches.

Nestedness is an important consideration in the Single Large or Several Small reserve debate (Tjørve, 2012; Diamond 1975). Where species assemblages exhibit a highly nested structure, then conservation action is best focused towards conserving a few large sites.

4.2 Vascular plants

The context of the region and habitat/forest type is of key importance in determining which factors influence the species richness of woodland plants. In a study of 33 woods 0.1 to 30.6 ha in size established in first part of 20th century in the Vale of York, Usher *et al.* (1992) found that area was a good predictor of plant species richness but, contrary to some expectations of island biogeography theory, neither isolation nor woodland shape explained species richness. Rodriguez-Loinaz *et al.* (2012) showed that in Iberian mixed oak forests, the presence and/or cover of woodland herbaceous species and ferns was negatively affected by decreasing patch size, possibly due to a reduction in habitat quality. Data from forests and grasslands in north-central Europe suggest that further decreases in habitat area will lead to a change in plant species community composition towards relatively fewer clonal and long-lived plants with large seeds in small forest patches (Lindborg *et al.*, 2012). It is possible that community composition has already shifted in reaction to fragmentation (Baeten *et al.*, 2010) although see Keith *et al.* (2009) on other reasons for community homogenization in the UK.

Other studies have found that vascular plant species-richness and occurrence in forests in agricultural landscapes is influenced by combinations of factors influence such as habitat diversity, connectivity, forest age and forest area (Jacquemyn *et al.*, 2003b; Dumortier *et al.*, 2002). There is evidence for area thresholds; for example in suburban woods in northern Italy, the species richness of forest herbs increased rapidly above patch sizes of 1-1.5 ha and then levelled off after 35-40 ha (Digiovinazzo *et al.*, 2010). These thresholds may be influenced by the extent of edge; working in southwest France, Gonzalez *et al.* (2010) found that the species-area curve was much steeper within edge habitats compared to core habitats. The abundance of seed source habitats and the ecological quality of the target habitat can also determine the success rate of colonization above minimum area thresholds

(Liira *et al.*, 2012). In contrast, some studies have found that for herbaceous core forest species, patch area is a redundant variable in explaining species richness relative to habitat quality and patch age (Buffa and Villani, 2012; Honnay *et al.*, 1999a).

4.3 Lower plants

Lower plants also appear to be sensitive to forest area. Löbel *et al.* (2006), and Baldwin and Bradfield (2007) found that for bryophytes some dispersal-limited groups (perennial stayers) and microclimate-sensitive groups (closed canopy species, epixylic species, and liverworts) showed significant declines in either richness or frequency as patch size decreased. In contrast, colonists and open canopy species showed little association with patch size. Many, but not all, of the significant patch size relationships disappeared when the three smallest patches (0.6–1.8 ha) were eliminated from the analysis. These results suggest that patch sizes of 3.5 ha or larger may provide habitat capable of sustaining a diverse array of bryophyte functional groups in temperate rainforest landscapes (Baldwin and Bradfield, 2007).

4.4 Birds and mammals

There is evidence for both patch area and composition effects for bird populations, with larger woodlands supporting more woodland bird species (Dolman *et al.*, 2007). For forest specialist birds it may be better to buffer or create a few large woodlands rather than create a large number of smaller fragments of the same cumulative area (Dolman *et al.*, 2007). However, woodland structure and quality may be more important in determining species richness than size (Dolman *et al.*, 2007). Similarly, Alderman *et al.* (2005) found that the existence of a large core habitat area of mature deciduous woodland (minimum 2 ha) was critical in producing a self-sustaining population of nuthatches (*Sitta europaea*), but habitat management was also necessary to increase breeding habitat quality. The equivalent area in dispersed small mature woods failed to sustain populations. In a study of 50 birds species occupying farm woodlands in southern England species richness was positively associated with woodland area (Vanhinsbergh *et al.*, 2002). In contrast, smaller woodlands tended to support a greater overall abundance (but not species-richness) of birds (both woodland specialist and generalist species) than larger woodlands.

In six species of European bat, whilst roosts were more likely to be found in landscapes with greater woodland cover, the size of the nearest woodland patch did not appear to be important in determining roost location (Boughey *et al.*, 2011). Brown long-eared bats (*Plecotus auritus*) in south-east England have a mean foraging patch size of 4.4 ha (core area 2.1 ha) although patch quality, in terms of understory structure and composition is also important (Murphy *et al.*, 2012). Fuentes-Montemayor *et al.* (2013) found higher bat activity levels in small and isolated woodland patches (for the soprano pipistrelle *Pipistrellus pygmaeus* and *Myotis* spp.). Recent work on other mammals suggests that some species (for example dormice *Muscardinus avellanarius*) can use small (2.9 ha +/-1.4 ha) woodland fragments as home and breeding habitat (Buechner, 2008).

4.5 Invertebrates

Patterns observed for birds and mammals are not necessarily always the same for other animal groups (Hansson, 1997). A range of studies have confirmed the importance of patch size and shape for forest specialist invertebrates (Debinski and Holt, 2000) including gastropods (Kappes *et al.*, 2009a), wood crickets (Brouwers and Newton, 2009b), spiders and beetles (Usher and Keiller, 1998) and moths (Fuentes-Montemayor *et al.*, 2012; Usher *et al.*, 1993) although other impacts such as patch isolation

(Brouwers and Newton, 2009b; Usher *et al.*, 1993) and habitat quality (Soga and Koike, 2012) may work in tandem with forest area.

Saproxylic beetles with low mobility appear to need large areas to sustain populations (e.g. 100 ha; Irmeler *et al.*, 2010). Species with higher mobility can still show a positive relationship between occurrence/density and habitat patch area, even if connectivity is of lesser importance (Sahlin and Schroeder, 2010). The best predictor of moth species richness in a study of moth communities of farm woods in NE England was the herbaceous plant species richness within the woodlands although woodland area was positively related to species richness of Geometrid moths (Usher and Keiller, 1998). However, characteristic woodland species were influenced by isolation with less isolated woods being richer in species. In this study, woods of less than 1 ha did not have characteristic woodland moth communities and those larger than 5 ha were judged to be more valuable for the long-term conservation of woodland moth diversity (Usher and Keiller, 1998). In a similar study in central Scotland, moth abundance and richness were higher in large woodland patches located close to other woodlands (Fuentes-Montemayor *et al.*, 2012). However, Fuentes-Montemayor *et al.* (2012) also conclude that small woodland patches can potentially maintain relatively high moth abundance and richness, depending on their shape and proximity to other woodlands.

5. Better - Habitat/Patch quality

5.1 Relevant aspects of habitat quality

Habitat quality emerges frequently as a key determiner of species occurrence and abundance (Dolman *et al.*, 2007), whether that be birds and mammals in Italy (Mortelliti, 2013; Mortelliti *et al.*, 2010), woodland birds in the UK (Dolman *et al.*, 2007), small mammals in farm woodlands (Fitzgibbon, 1997), plants in fragmented Mediterranean woodland (Gonzalez-Varo *et al.*, 2012), upland Britain (Petit *et al.*, 2004) and Italy (Buffa and Villani, 2012), lower plants in boreal forests (Berglund and Jonsson, 2003) or carabid beetles and butterflies in woodlands (Berg *et al.*, 2011).

In some instances, patch area and quality are important (Berglund and Jonsson, 2003; lower plants; Honnay *et al.*, 1999b; vascular plants) whereas, in others, occurrence is explained solely by habitat quality (including age) (Buffa and Villani, 2012; vascular plants). In woodlands the main components of habitat quality affecting species abundance, community composition and diversity are broadly: 1) Stand age, structure and composition including edge effects (which are linked to patch shape); 2) Ecological continuity, legacies and land use history.

5.2 Stand age, structure and composition

Attributes of stand age, structure and composition all have significant impacts on the biodiversity of new woodlands (Blasi *et al.*, 2010; Dolman *et al.*, 2007; Humphrey *et al.*, 2003a), but it is only relatively recently that attempts have been made to consider stand structure impacts together with landscape level impacts (e.g. Fuentes-Montemayor *et al.*, 2012; Humphrey *et al.*, 2004).

Table 2 includes summary information from 30 studies covering stand growth stage, tree species composition, canopy cover, vertical stand structure, deadwood and edge effects. Stand age (as a surrogate for time for colonisation), growth stage and vertical structure share a close relationship, with older stands generally supporting larger trees. However, differences in tree composition can affect

structure/age relationships. For example, fast growing conifers can develop a diverse stand structure more rapidly than slower growing broadleaves. This results in there being less time for species ostensibly capable of inhabiting mature conifer stands to colonise, such as the foliose lichen *Lobaria scorbiculata* (Humphrey, 2005).

Secondary stands with larger trees and greater structural diversity support a wider range and abundance of woodland species such as spiders and carabid beetles (Oxbrough *et al.*, 2010), epiphytic lichens and bryophytes (Ellis and Coppins, 2010) and vascular plants (French *et al.*, 2008; Brunet, 2004). In secondary woodland adjacent to existing ancient woodland, forest specialist herbaceous species can become established after 60-80 years (Brunet *et al.*, 2011; Brunet, 2004), although the diversity of other species groups such as lichens and molluscs may take upwards of 160 years (Moning and Muller, 2009, Table 2).

Table 2 Influence of habitat quality (forest stand age, structure and composition) on species occurrence and diversity

Habitat quality feature	Response	Reference
Stand growth stage	Spider and beetle diversity influenced by stand structural development in second rotation plantations with numbers of forest-associated species increasing over the forest cycle	Oxbrough <i>et al.</i> (2010)
	In the first 5 years of the forest cycle there was a change in the spider fauna, with rare or specialist species of open ground being replaced by habitat generalists or species associated with forested habitats	Oxbrough <i>et al.</i> (2006)
	Stand structure manipulations have a potentially bigger impact on ground flora communities in plantation forests than edaphic and geographic (proximity to old woodland) or historic (previous land use) factors	French <i>et al.</i> (2008)
	Lichens affected more by stand structure (larger trees) and ecological continuity than by climate	Moning <i>et al.</i> (2009)
	Bird assemblages varied with growth stage in plantations	Wilson <i>et al.</i> (2006)
	In a multiple drivers study of epiphytes, occurrence of old-growth woodland exerted the most important control over species richness	Ellis and Coppins (2010)
Tree species composition	High tree species diversity and a high proportion of native tree species related to higher moth abundance and species richness in agriculture/forest mosaic landscapes	Fuentes-Montemayor <i>et al.</i> (2012)
	Dominant tree species and attributes related to forest structure and management were the most important factors determining plant diversity in forest patches 0.3 to 3 ha in size in Portuguese pine and eucalypt forests	Lomba <i>et al.</i> (2011)
	Germination of ancient forest species in post-agricultural forest sites affected through the litter characteristics of the dominant tree species	Thomaes <i>et al.</i> (2011)
	Lichens of conifer plantations had low species-richness compared to native Scots pinewood, or broadleaved woodland	Wolseley <i>et al.</i> (2006)
	Conifer stands (55 year old <i>Picea</i> spp.) not suitable secondary habitats for spiders and ground beetles of autochthonous deciduous woodland (ancient oak/beech)	Finch (2005)
Tree Species /canopy cover	Fast growing hybrid poplar plantations provide more rapid canopy closure than natural afforested fields and increased cover of native shade tolerant species; tree species type therefore impacts on habitat quality and rapidity of development of woodland functioning	Boothroyd-Roberts <i>et al.</i> (2013)
Canopy cover	Increased shading and nitrogen deposition is causing homogenisation of plant communities in the UK	Keith <i>et al.</i> (2009)
	Ground flora diversity decreased with increased shading in second rotation plantations	Cooper <i>et al.</i> (2008)
	Habitat quality in terms of shifts in woodland species composition (from herbs to grasses) may be declining in ancient woodland due to changing canopy dynamics, nitrogen deposition, and deer population increases	Corney <i>et al.</i> (2008)
	Bryophytes and lichens can colonise spruce trees even in the interior of stands if enough light can get in	Coote <i>et al.</i> (2008)
Vertical stand structure	Foraging bats need structurally diverse woodland with native tree and shrub species in the understorey and hedgerows to provide connectivity between woodlands	Murphy <i>et al.</i> (2012)

Table 2 cont:

Habitat quality feature	Response	Reference
Vertical stand structure/canopy cover/stand age	Forest specialist herbaceous species in post-agricultural oak forests approach the richness of adjacent continuously forested sites after 60-80 years, where a canopy cover of 70-80% is maintained by regular light thinnings and shrub layer is promoted	Brunet <i>et al.</i> (2011)
	Optimal stand characteristics for promoting forest herbs in secondary woodland in Estonia were: canopy closure 0.7-0.8, basal area of trees 10-20 m ² ha ⁻¹ and the presence of moderate understory management	Liira <i>et al.</i> (2012)
Stand age	Plant species richness increased linearly with stand age in plantations adjacent to ancient woodland, with the oldest adjacent plantations (70-80 years) approached species richness similar to that of the ancient woodlands	Brunet (2004)
	Carabid community composition differs between beech stands of different age	Jelaska <i>et al.</i> (2011)
	Threshold stand ages for lichen, mollusc and bird diversity ranged from 100 to 170 years in sub-montane beech forests and from 160 to 220 years in mixed montane forests	Moning and Muller (2009)
Spatial stand structure/canopy cover	Bat abundance and activity influenced by both local and landscape-level attributes. High activity levels of aerial hawkers (e.g. <i>Pipistrellus</i> spp.) related to low tree densities and an open understory, while gleaning species (e.g. <i>Myotis</i> bats) showed the opposite trend	Fuentes-Montemayor <i>et al.</i> (2013)
Deadwood	Diversity of substrata important for lichen and bryophyte species richness	Lõhmus <i>et al.</i> (2007)
	The availability of specific substrata (deadwood) and not ecological continuity at the stand or landscape scale is the main limiting factor for calicoid fungi in forests	Lõhmus and Lõhmus (2011)
	Lichen and bryophyte diversity similar in new natural afforestation and old managed forests provided there is time for substrate development and cryptogam dispersal (> 40 years old), few cuttings in the new forests (only about 20% of stands thinned), and short distances to long-term forests (67% of substrates within 250 m)	Lõhmus and Lõhmus (2008)
	Threshold amounts of coarse woody debris (20 m ² ha ⁻¹) are important for sustaining populations of specialised species such as shelled gastropods	Kappes <i>et al.</i> (2009b)
Edge effects	Significant periphery-to-core patterns of distribution detected over large ranges for common understory plant species in 1801 forest patches in France. Plant traits differentiated forest core from forest periphery species. Large gradient due to edges being forced outwards by afforestation on agricultural ground	Pellissier <i>et al.</i> (2013)
	Edge effects at the woodland/arable interface caused by elevated nitrogen levels in ancient woodlands to a distance of at least 100 m from arable farmland, resulting in an increase in nitrophilous plants and a reduction in Ancient Woodland Indicator Species	Willi <i>et al.</i> (2005)
	Forest specialist gastropods affected by edge effects 250 m into the stand	Kappes <i>et al.</i> (2009a)
	Higher abundance and species-richness of woodland macromoth specialists in woodland interior compared to edge; micromoth species composition also differed between edge and interior in relation to woodland shape	Fuentes-Montemayor <i>et al.</i> (2012)
	Species richness of Geometrid moths positively related to woodland shape with compact shapes being preferable to elongated	Usher and Keiller (1998)

The speed of colonisation of woodland species can be influenced by substrate availability and development. Such is the case for the diversity of epixylic lichens and bryophytes on deadwood in new forests, which may approach that of old forests within 40 years (Löhmus and Löhmus, 2008), (Table 2). Woodland species diversity is also affected by the occurrence of particular tree species or assemblages. For example, stands of non-native conifer species can have lower diversity for some species groups such as lichens (Wolseley *et al.*, 2006) or moths (Fuentes-Montemayor *et al.*, 2012). In contrast, late-successional deciduous forest can support a high abundance and species-richness of moth, including scarce and specialist species of conservation concern (Merckx *et al.*, 2012).

Edge effects on woodland species diversity are evident for a range of species in agricultural landscapes (Table 2), to the extent that depending on shape, new secondary woodland on former agricultural ground can appear to function as edge habitat (Pellissier *et al.*, 2013) with edge effects extending up to 100-250 m in forest stands depending on context (Kappes *et al.*, 2009a; Willi *et al.*, 2005).

Perhaps the most dominant impact on woodland species is canopy cover and shade (Table 2). Dense conifer stands can impede the colonisation of light demanding species such as epiphytic lichens (Cooper *et al.*, 2008; Humphrey *et al.*, 2004), and even in broadleaved woodland, increased shading due to lack of thinning/felling has been implicated in the shift of plant community composition and loss of woodland herbs (Keith *et al.*, 2009; Corney *et al.*, 2008). However, rapid canopy closure can also help reduce the vigour of weeds, encourage colonisation of shade tolerant species (Boothroyd-Roberts *et al.*, 2013) and can benefit some species groups such as mycorrhizal fungi (Humphrey *et al.*, 2000). Tree species composition has a key impact on this process in terms of degree of shade cast and litter properties (Thomaes *et al.*, 2011).

5.3 Ecological continuity, legacies and land use history

Ecological continuity at the stand scale has long been recognised as a significant factor in the maintenance of biodiversity (Brunet, 1993; Nordén and Appelqvist, 2001) and in the UK conservation effort has been targeted at protecting and restoring ancient woodland as the key repository of woodland species diversity (Goldberg *et al.*, 2007; Peterken, 1993). Ecological continuity is a different concept to that of stand age (Ellis and Hope, 2012). A site may have been wooded for many millennia, have long continuity as woodland, but currently have a young stand due to succession or management (Peterken, 1993). Conversely many old stands may be first generation woodland on the site, have an appropriate structure to provide old growth habitat (Humphrey, 2005), but the site may not have been wooded long enough to allow colonisation by specialist woodland species.

When woodland is cleared from a landscape, woodland species such as wood anemone (*Anemone nemorosa*) can survive in small fragments of sub-optimal habitat such as under dense heather (*Calluna vulgaris*) or in damp grassland (Peterken, 1993). These remnant patches or legacies can function as foci for the colonisation of re-established woodlands. Similarly, plantations established on ancient woodland sites frequently contain flora and fauna associated with vestiges of semi-natural habitat (Humphrey *et al.*, 2003a). The intensity of historic land use can also have an impact on habitat quality through alteration of soil conditions (Honnay *et al.*, 1999b), removal of legacies (Peterken, 1993) and creation of physical barriers to the colonisation of woodland species such as weedy vegetation and litter composition (Thomaes *et al.*, 2011).

In recent decades, research has shown that the importance of stand level continuity is context/species-specific and the recognition that, even in ancient woodlands, community composition and diversity changes over time, due to anthropogenic and environmental impacts (Jamrichova *et al.*,

2013). The importance of stand level continuity is related to species traits. For example, Humphrey and Bailey (2012) maintain that some deadwood-dependent insects are reasonably mobile and adapted to utilise transient resources at the landscape scale, whereas other species have very poor dispersal ability and are restricted to habitats with long continuity at the site scale such as ancient trees and associated decaying wood features (Lemperiere and Marage, 2010; Alexander, 2004). Similarly, in NW Germany, flightless weevils are considered to be relict species of ancient woodland, because they are all dependent on dead or dying wood for larval development, and appear unable to colonise isolated woods established after 1800 (Buse, 2012). In southern Germany, the proportion of forest plants and Hemiptera (bugs) was significantly higher in young oak stands (20-30 years) established on former ancient woodland compared to agricultural sites (Gossner *et al.*, 2008). Generalist bugs were significantly better represented in afforestation on agricultural sites whereas forest specialist bugs were commoner in reforestation of ancient sites. Saproxyllic beetles, especially those of old dead wood, were species-poor in all afforestations (Gossner *et al.*, 2008).

A number of studies have looked at the importance of ecological continuity for woodland vascular plants building on past work identifying lists of ancient woodland indicator plant species (Peterken, 2000; Peterken, 1974). In a study of plant communities in Irish plantations, Coote *et al.* (2012) found that although soil and other habitat quality factors were involved, historic woodland cover (i.e. plantation on, or adjacent to, semi-natural woodland) was the most important determiner of the development of the woodland ground flora community. However, in a study of 56 plantation and native woodland stands in the UK, site history was of less importance in determining species richness in planted forests than was distance to nearest ancient semi-natural woodland (Humphrey *et al.*, 2004).

In a study of 36-132 year old forest stands in Belgium, Bossuyt *et al.* (1999) found that the total cover, number and diversity of field layer species did not differ significantly between these stands and ancient stands. The diversity of ancient forest plant species correlated positively with the age of the recent forest and negatively with both the duration of its former agricultural land use and the distance to the ancient forest (Bossuyt *et al.*, 1999). In a similar study in NE Germany Wulf (2003) recorded clear differences in plant species complements between ancient (>200 years), old (150-100 years) or recent woodland. Besides the importance of habitat continuity, site factors and various life history traits of the plants explained the preferences for the different woodland types. Ancient woodland indicator species had significantly lower mean values for light, moisture, soil reaction and nitrogen, were more stress-tolerant and adapted to low-level anthropogenic disturbance.

There were also differences in the flora between the recent woodlands established on former arable land compared to those established on pasture (Wulf, 2004). Woodland species were more frequent on ex-pastures possibly because they could survive the relatively low intensity of disturbance in this habitat and also persist at low population density. Development of the woodland flora was more rapid in woodlands established on grasslands with higher numbers of endangered or relatively rare species (Wulf, 2004). In Danish forests, Svenning *et al.* (2009) found that many typical forest interior species, with poor dispersal and a record in the literature as ancient-forest species, were still concentrated in areas that were forested in 1805. Similarly, in the US, landscape and current management effects may also be of lesser important than historical continuity in maintaining a typical woodland flora (Brudvig and Damschen, 2011; Brown and Boutin, 2009). In contrast, Vojta and Drhovska (2012) found that old wood pastures in the Czech republic were no better for forest species than more recently overgrown pastures. The importance of habitat isolation, soil pH and light conditions for forest species community composition and richness was confirmed. Soil conditions were also a key determiner of the continued differences in the herb flora of secondary woodlands in Estonia (Paal *et al.*, 2011).

There is a debate on the importance of site continuity for lower plants as the effects of tree age and forest continuity are difficult to disentangle unless survey work is carefully designed (Ellis and Hope, 2012). For example Fritz *et al.* (2008) showed that in beech stands in southern Sweden, sites with over 350 years of continuity had significantly more lichen species compared to those with less than 160 years of continuity. These findings did not apply to bryophytes. Late succession stage lichens were missing in the younger sites primarily because of lack of substrates e.g. old beech. Similarly, Marmor *et al.* (2011) found that epiphytic lichens on Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) were more species-rich and formed distinct assemblages in old growth compared to recent first generation forests (<100 years). In both these studies, ecological continuity may have impacted diversity, but the effects of stand structure and age were also important.

In contrast, Ellis and Hope (2012) found no evidence for an effect of historical continuity on epiphyte composition or richness in Atlantic oakwoods in the UK. Both ancient and recent woods had a similar structure due to management. As stands age the oceanic epiphyte communities become saturated, restricting the accumulation of species richness on older and larger trees (Ellis, 2012).

5.4 Seed banks

The soil seed bank is also a source of potential colonising plant species in secondary stands. In a paper reviewing a range of seed bank studies Bossuyt and Honnay (2008) found that the similarity between seed bank and vegetation composition was low in forest. They concluded that the restoration of plant communities composed of late successional woody or herbaceous species must rely mainly on seed dispersal and not on *in situ* germination. Seed banks may also contain generalist competitive species that could swamp the regeneration of woodland specialists (Erenler *et al.*, 2010). Tree species diversity can have a much stronger influence on the size and composition of the seed bank than herb-layer diversity or composition, the latter revealing only a low similarity to the corresponding seed bank (Schmidt *et al.*, 2009).

There is a note of caution to apply to the results of these studies, however. In a review of seed bank studies, Plue *et al.* (2012) suggested that sampling of ancient forest species is inadequate in many studies, and the reality is that ancient forest species are not particularly rare in the seed bank compared to other species. More work is needed to substantiate whether this is the case in UK woodland using the sampling methods recommended by Plue *et al.* (2012).

6. More - Area, composition and configuration of surrounding habitat

6.1 Influence of surrounding habitat

One of the key factors affecting the development of biodiversity within new woodlands and the population viability of woodland species is the structure and composition of the surrounding landscape mosaic (Hodgson *et al.*, 2011; Fischer and Lindenmayer, 2007; Hinsley *et al.*, 1995; Andr n, 1994). Obviously there are a range of different criteria that can be used to define what might constitute a distinct landscape mosaic unit, for example using physiographic factors such as topography (Schaub *et al.*, 2011; Bennett *et al.*, 2006), socio political boundaries (Moseley and Smith, 2008), human perceived landscape character (Forestry Commission, 2011; HM Government, 2011; Fischer and

Lindenmayer, 2007; Hill *et al.*, 1993) or by using species-specific demographic and landscape use information (Bergman *et al.*, 2012; Humphrey *et al.*, 2009; Humphrey, 2005).

The spatial scale at which landscape units are recognised is determined in part by the objective of the study, practicalities of data capture and analysis, as well as species requirements. For example, Humphrey *et al.* (2003b) used a 1 km² as a threshold for defining a wooded landscape unit, Jamoneau *et al.* (2012) a 25 km² for dynamic agricultural landscapes, and Økland *et al.* (1996) a 100 km² sampling unit. Other studies have used buffers at a range of scales, e.g. a 1-5 km radius for plants and fungi in a temperate broadleaved ecosystem (Paltto *et al.*, 2006), 250-3000 m for different moth assemblages in mixed woodland/agricultural landscapes (Fuentes-Montemayor *et al.*, 2012).

6.2 Species responses

Fischer and Lindenmayer (2007) argue that human perceived landscape patterns in many cases correlate with species assemblages, supporting the approach of Bennett *et al.* (2006) who identified three categories of emergent properties of mosaic structure that influence biota: 1) the extent of habitat; 2) the composition of the habitat mosaic and; 3) the spatial configuration of mosaic elements. These properties are also closely related to the “Joined” concept (section 8) in terms of matrix permeability and habitat connectivity.

In general, the extent (Fuentes-Montemayor *et al.*, 2012), proportion (Fuentes-Montemayor *et al.*, 2011a; Paltto *et al.*, 2006; Andrén, 1997; Andrén, 1994) or overall amount (Brunet and Isacson, 2009a; Franc *et al.*, 2006) of a particular habitat within the landscape unit is directly related to individual species or species assemblages dependent upon that habitat (Bennett *et al.*, 2006). For birds and mammals in a continuous landscape, there is evidence that habitat loss is the dominant factor affecting species assemblages down to 30% habitat cover in the landscape, after which the impacts of isolation and patch size compliment habitat loss, and the nature of the surrounding matrix also has an impact (Andrén, 1997; Andrén, 1994).

A number of studies tend to support the importance of threshold amounts of habitat cover for determining species occurrence. For example, Boughey *et al.* (2011) found that bat roosts were more likely to be found in landscapes with greater amounts of broadleaved woodland, with the highest impact being change in cover from 0-20% (Table 3). Mortelliti *et al.* (2011) suggest that management to enhance connectivity in the landscape for small mammals is likely to be effective only when habitat cover is more than 5-10% supporting contentions that measures to increase species frequency and abundance should be targeted at well-wooded landscapes (Mortelliti, 2013; Hodgson *et al.*, 2011).

Over the past decade, positive relationships have been recorded between woodland extent and the diversity and abundance of a wide range of different species groups including, for example woodland birds (Dolman *et al.*, 2007), woodpeckers (Charman *et al.*, 2010); bats (Boughey *et al.*, 2011), mammals (Mortelliti *et al.*, 2011), invertebrates (Fuentes-Montemayor *et al.*, 2012), fungi (Edman *et al.*, 2004), vascular plants and cryptogams (Pena *et al.*, 2011; Paltto *et al.*, 2006; Humphrey *et al.*, 2004; Table 3). The scale of influence varies by species group depending on mobility and habitat specificity (and may be affected by study restrictions).

Relatively few studies have looked at the impact of overall landscape composition and spatial configuration on species assemblages (Bennett *et al.*, 2006). The proportions of different elements present in the landscape may affect the species composition of faunal assemblages (Table 3; Oliver *et al.*, 2010). In general, increased heterogeneity sustains higher species-richness (Bennett *et al.*, 2006), benefiting relatively mobile animal species with those with broad habitat preferences (Oliver *et al.*



al., 2010; Schippers *et al.*, 2009). There may also be impacts of different spatial patterns of habitat, e.g. clumped versus dispersed distributions (Table 3; Fuentes-Montemayor, *et al.*, 2011a; Fuentes-Montemayor *et al.*, 2011b; Heikkinen *et al.*, 2004). Fuentes-Montemayor (2011a) found that the most important factors associated with bat activity on farmland related to woodland configuration in the surrounding landscape. In practice, however, it is difficult to separate out the large-scale impacts of spatial configuration from the nested impacts of isolation and changes in connectivity between patches. These latter issues are dealt with more fully in sections 7 and 8.

Table 3 Effects of overall extent of surrounding woodland habitat, and composition and configuration of the habitat mosaic on woodland taxa

Taxon	Response	Reference
Vascular Plants	Recovery of short-lived forest herbs increased with the availability of forest habitat in the landscape although small perennial forest herbs generally unsuccessful in colonizing post-agricultural forest even in relatively densely forested landscapes	De Frenne <i>et al.</i> (2011)
	Plant species composition and diversity in Iberian woods responded primarily to suitable habitat proportions in the surrounding landscape and secondarily to soil pH. Responses differed among life forms; tree and shrub diversity increased with increases in the proportion of ecologically similar habitat in the surrounding landscape	Pena <i>et al.</i> (2011)
	Amount of ancient woodland patches in the landscape more important than patch size <i>per se</i> for Ancient woodland Indicator plants at the 10 km scale in broadleaved woodlands	Mouflis and Buckley (2004)
	Local density of Red Data Book vascular plants increased with increasing proportion of suitable broadleaved woodland habitat up to 1-5 km from the study sites	Paltto <i>et al.</i> (2006)
Lower plants	Local density of Red Data Book lichens, bryophytes and wood-inhabiting fungi species increased with increasing proportion of suitable broadleaved woodland habitat up to 1-5 km from the study sites	Paltto <i>et al.</i> (2006)
	Variation in spore deposition of the fungi <i>Fomitopsis rosea</i> and <i>Phlebia centrifuga</i> significantly related to the proportion of old spruce (<i>Picea</i> spp.) forest (140 years+) within a 3 km radius	Edman <i>et al.</i> (2004)
	Counts of bryophytes in conifer plantations positively correlated with the amount of semi-natural woodland within 1 km	Humphrey <i>et al.</i> (2004)
Birds & Mammals	The spatial structure of bird patterns in agricultural-forest mosaics in Finland (25 ha scale) is caused in large part by the clumping of habitats either preferred or avoided by birds; the abundance of bird pairs is not necessarily related to landscape heterogeneity as such, but depends more on the distribution of the most important habitats for birds	Heikkinen <i>et al.</i> (2004)
	Habitat quantity and landscape variables much more important than habitat quality in explaining the occurrence of hazel grouse (<i>Bonasa bonasia</i>)	Kajtoch <i>et al.</i> (2012)
	Meta-populations of woodland birds perform equally or better in heterogeneous landscape types that are a mix of linear, large and small habitat elements, creating a "synergy" not present in more homogeneous landscapes	Schippers <i>et al.</i> (2009)
	Woodland bird specialists likely to benefit more from buffering existing woods or creating large woodlands rather than achieving a greater total area of woodland through establishing small fragments	Dolman <i>et al.</i> (2007)
	Strong relationship between the probability of woodland use by lesser spotted woodpecker (<i>Picoides minor</i>) and the extent of woodland within a 3 km radius, suggesting selection for more heavily wooded landscapes	Charman <i>et al.</i> (2010)
	Woods located within sparsely wooded landscapes less valuable to specialist woodland birds species	Dolman <i>et al.</i> (2007)
	Highly mobile bat species (e.g. <i>P. pipistrellus</i> and <i>Myotis</i> bats) are likely to benefit from woodland creation and management at large (up to 3 km) spatial scales in agricultural landscapes	Fuentes-Montemayor <i>et al.</i> (2013)
	Higher bat activity levels were observed in small and isolated woodland fragments, and in scarcely wooded landscapes with increased habitat heterogeneity	Fuentes-Montemayor <i>et al.</i> (2013)

Table 3 cont:

Taxon	Response	Reference
Birds & Mammals	Roost location for 6 native bat species was positively associated with either the extent or proximity of broadleaved woodland, with the greatest effect of increasing woodland extent seen between 0% and 20% woodland cover	Boughey <i>et al.</i> (2011)
	Most important factors associated with bat activity on farmland were metrics related to woodland configuration in the surrounding landscape. Patterns of higher bat abundance and activity at small and isolated woodland patches suggest that bats utilize this habitat more intensively in landscapes where woodland is scarce. <i>P. pipistrellus</i> being strongly influenced by the landscape at large scales (e.g. within 2 km of the monitoring site) and common pipistrelle <i>P. pygmaeus</i> by the landscape at smaller scales (within 500 m of the monitoring site)	Fuentes-Montemayor (2011b); Fuentes-Montemayor <i>et al.</i> (2013)
	Habitat loss, rather than habitat fragmentation <i>per se</i> a major driver of distribution patterns for red squirrel (<i>Scuiris vulgaris</i>) and dormouse in Italy. Structural connectivity (hedgerow networks) played an important role in determining the distribution of dormouse when forest cover more than 5-10% in the landscape	Mortelliti <i>et al.</i> (2011)
Invertebrates	Area of oak dominated woodland key habitats within 1 km of sites and regional amount of dead oak wood, were the main predictors of variation in local species richness of oak beetles	Franc <i>et al.</i> (2006)
	Orb weaving spiders recorded in groups of cherry trees showed species-specific responses in body weight and population density in relation to amount of forest in the landscape mediated through prey abundance	Bucher and Entling (2011)
	Total amount of habitat in an unfragmented forest area more important for the diversity of saproxylic beetles than the spatial distribution of this habitat	Brunet and Isacsson (2009a)
	Forest carabid species assemblages in agricultural landscape less frequent in contexts with low amounts of woodland and hedgerows	Aviron <i>et al.</i> (2005)
	Heterogeneous landscapes that contain a variety of suitable habitat types were associated with more stable population dynamics for 35 British butterfly species from 166 sites; topographic heterogeneity may also promote stability; results were robust to different measures of population variability, differences in mean abundance among sites, and to the spatial scale (radius 1-5 km around the centres of sites) at which landscapes were analysed	Oliver <i>et al.</i> (2010)
	Percentage cover of rough grassland and scrub within 250 m of the trapping site was the most important landscape predictor for both micro- and macromoth abundance and macro- moth species richness in agricultural/forest landscape	Fuentes-Montemayor <i>et al.</i> (2011a)
	Woodland extent was the most important landscape parameter influencing moths, mostly at relatively small spatial scales (500 m); macromoth 'woodland species' were influenced by woodland extent at larger spatial scales (1500 m)	Fuentes-Montemayor <i>et al.</i> (2012)

7. *Joined* – Impacts of isolation between new and existing habitat

7.1 Isolation and dispersal limitation

Recent studies have emphasised the lack of information on species dispersal and responses to landscape structure and fragmentation (Baguette *et al.*, 2013; Brouwers and Newton, 2010b; Bailey, 2007). A review of species in the UK found that only 28 out of 1245 species of conservation concern had published information on dispersal distances (Catchpole, 2007). Nevertheless, over recent years there has been an accumulation of empirical studies covering a range of taxa where dispersal abilities are implied from observations of species distributions (e.g. Eycott *et al.*, 2006). In this section we ask whether dispersal restriction is a key factor in the distribution, movement and development of species populations in new or secondary woodlands.

7.2 Vascular plants

In a review of the restoration potential of secondary woodlands, Honnay *et al.* (2002) concluded that it takes at least a century to restore the understory layer of recent forests, even when the target stand is adjacent to a well-developed ancient forest; recruitment restriction and dispersal limitation of the target species were judged to be the limiting factors. Similarly, Verheyen and Hermy (2001) and Hérault and Honnay (2005) maintain that the low colonizing capacity of ancient forest plants cannot be attributed to a single cause; both dispersal and recruitment are limiting but the relative importance varies depending on species.

Empirical studies suggest that for forest herbs, community assembly can be considered a two-stage process in which restricted seed availability followed by low recruitment limits colonization (Baeten *et al.*, 2009). The need for disturbed micro-sites can be crucial, but depends on species-specific life histories and the prevailing site conditions (Baeten *et al.*, 2009). Similarly, Vojta and Drhovska (2012), comparing old wood pastures with ancient forests with a long continuity in woody cover, found that the former contained the same forest species as more recently overgrown pastures. However, Verheyen *et al.* (2003a) found persistent differences between ancient and recent forests in terms of life-form spectra, and specifically in terms of the number and abundance of geophytes. In wet woods community recovery took place after 70 years, but was much longer in oak woods due to establishment restrictions.

In other studies, the restriction of plant species to ancient woodlands seems to be mainly caused by their inability to colonize recent woodlands, especially isolated stands (Jacquemyn *et al.*, 2003b; Wulf, 1997). At the spatial and temporal scales of human land use, slow-migrating plant species, and those unable to cross gaps may be in danger of regional extinction (Matlack, 2005). However, Oliver *et al.* (2009) conclude that geographic variation in realized niche breadth is common and relatively large, especially near range boundaries, and that species may be able to adapt to climate change by occupying different habitat niches.

Hermy and Verheyen (2007) contend that dispersal limitation is more important than recruitment limitation in the distribution of Ancient Forest Species (AFS) as recent forests are generally suitable for the establishment of AFS. In support of this Van der Veken *et al.* (2012) found that many AFS survived transplantation outside their (current) natural range. Inter-specific differences in colonization rates of forest herbs within contiguous forest landscapes may be largely determined by the size of local

source population and inherent characteristics of propagules (Brunet, 2004; Verheyen and Hermy, 2004). Verheyen *et al.*, (2003c) found that herb species characterized by low dispersability (i.e. large seeds, low fecundity, unassisted dispersal) are relatively slow colonizers and conclude that this (and not recruitment) is a key factor limiting the colonization of some forest plant species. Similarly, Sorrells and Warren (2011) in a study of new woods in the US concluded that ant-dispersed plants exhibit difficulty in moving to suitable habitat in the landscape and suggests that deforestation and fragmentation limit their occurrence in understory herbaceous communities.

Orczewska (2009) recorded putative colonization rate of woodland plants in different woodland types on ex-agricultural ground of between 0.79-1.63 m/year for poor dispersers and 2-3 m/year for more mobile species. Ancient woodland indicator plants had much slower colonisation rates at e.g. 0.68 m/year, but secondary woods next to ancient wood seemed capable of acquiring species especially if they were wetter woodland types (Orczewska, 2010). Migration in pinewoods on less fertile sites was slower; ancient and recent pinewoods differed in herb layer species composition despite the secondary succession having lasted for over 50-60 years (Orczewska and Fernes, 2011).

Brunet *et al.* (2012) found that the rate of colonisation of 14-18 year old broadleaved forests was related to the height of the colonising plants, indicating the potential for relatively fast colonization by some forest plants, e.g. those dispersed by wind or animals (Wulf and Heinken, 2008; Humphrey *et al.*, 2003a). Brunet *et al.* (2012) conclude that planted post-agricultural forests can start to contribute to restoration of forest plant diversity shortly after canopy closure when located adjacent to older forests. The richness of forest specialists may approach the richness of continuously forested sites after 60-80 years in non-fragmented plantations (Brunet *et al.*, 2011), and even some forest herbs with no observable dispersal vectors seem able to spread into secondary woodland given time (Davie *et al.*, 1998).

Humphrey *et al.* (2003a) contend that there is a high potential for conifer stands to develop deciduous woodland flora if adjacent to ancient deciduous forests and Humphrey (2005) recommended retaining stands over 80 years of age adjacent to existing ancient woodland to allow time for colonisation. In a study of ancient forest plant species and ant-dispersed species, both the number and cover of species correlated positively with the age of the recent forest (range of 36-132 years) and negatively with both the duration of its former agricultural land use and the distance to ancient forest stands (Bossuyt *et al.*, 1999).

The degree of isolation of new or secondary woodland from ancient woodland appears to be a key factor in restricting colonisation by woodland species (Mouflis and Buckley, 2004; Graae *et al.*, 2003; Jacquemyn *et al.*, 2003a; Verheyen *et al.*, 2003b; Dzwonko, 2001; Jacquemyn *et al.*, 2001). Brunet (2004) recorded no increase in species-richness in isolated stands between the ages of 40 and 80 years and richness decreased with increasing distance from ancient woodlands, suggesting that new woodland should be built out from cores of ancient woodland to optimise ground flora development (Brunet, 2007). Brunet *et al.* (2000) in an earlier study of ancient woods paired with secondary woods found that after 70 years, colonization of ca. 50 % of the woodland species had taken place in the secondary site within 50 m from the ancient woodland border.

Species more negatively affected by patch isolation tend to be habitat specialists and clonal perennials that produce fewer seeds (Dupre and Ehrlen, 2002). Rodriguez-Loinaz *et al.* (2012) found that patch isolation in Iberian oakwoods had a negative effect on the presence of forest specialist herbs and ferns. Similarly, only 50% of ancient woodland species lacking adaptation to long-range dispersal had successfully colonised Dutch polders 60 years after woodland establishment (Pierik *et al.*, 2010). Evaluating the colonisation of 44-year-old pine patches on sand dunes up to 17.4 km distance from mature forest, Takahashi and Kamitani (2004) showed that ant-dispersed and other species with low

dispersal only migrated to the closest woods. Although long-distance dispersal is considered to be a possible mechanism for colonisation/migration given sufficient time frames (Pearson and Dawson, 2005; Dawson *et al.*, 2004; Jacquemyn *et al.*, 2003a) there is contrasting evidence. For example, some studies have suggested an involvement of large mammals in the dispersal of epizoochorous³ species (Boulanger *et al.*, 2011) others have not (Panter and Dolman, 2012; Schmidt *et al.*, 2004).

7.3 Lower plants

The development of lower plant communities comprises a key component of the diversity of new woodlands. In a review of lichen epiphyte diversity, Ellis (2012) suggests that diversity may depend on constraints imposed by the ability of species to disperse into suitable habitat: (i) the dispersal distances of propagules may be limited in space (isolation); and (ii) the likelihood of dispersal (and establishment) into a suitable habitat may increase with the temporal continuity of that habitat, i.e. the time available for colonisation may weaken the effect of isolation. Ellis (2012) concludes that there is strong evidence of dispersal limitation (at the scale of different stands of trees) in lichens, but that it is difficult to provide broad generalizations on the relative importance of habitat quality and landscape context due to the lack of species-specific information.

Over a 9-year study period the mean dispersal distance for lungwort (*Lobaria pulmonaria*) within stands was estimated at 35 m, with a recorded maximum of 75 m (Öckinger *et al.*, 2005). Similarly, Fedrowitz *et al.* (2012) found restricted rates of colonisation in seven cyanolichen species and predicted that some species would face extinction over the next 50 years in small isolated habitat patches. Juriado *et al.* (2011) evaluating the dispersal of *Lobaria* in different wood types in Estonia found that vegetative dispersal distance between host trees was only 15-30 m in managed stands. Löbel *et al.* (2006) conclude that the sensitivity of epiphytes to habitat fragmentation is mediated through decreasing forest sizes, habitat alteration at forest edges and increasing dispersal distances. However, there is evidence that improving connectivity benefits colonization rates in oak epiphytes; species with wider niches and small propagules had better dispersal, with some species showing frequent long-distance dispersal (Johansson *et al.*, 2012).

Bryophytes may be less restricted by dispersal (Pharo *et al.*, 2004), and diversity of lower plants may increase over time if enough time is given for colonisation. For example, cryptogam diversity of new natural afforestation in Estonia (<40 years old) was not significantly lower than in old managed forests provided that the distance between old and new forest was within 250 m (Löhmus and Löhmus, 2008).

7.4 Birds and mammals

Birds and mammals exhibit some sensitivity to habitat fragmentation and restriction in movement. Dolman *et al.* (2007) conclude that connectivity is most useful for generalist species for which patch size is not as important as it is for woodland specialists. In a study of gap crossing of birds in lowland Scottish woodland, Creegan and Osborne (2005) found that different birds perceive connectivity differently e.g. goldcrests (*Regulus regulus*) would move across gaps in woodland cover of up to 46 m whereas chaffinches (*Fringill acoelebs*) would cross gaps of 150 m. Broughton *et al.* (2010) showed that marsh tits (*Poecile palustris*) exhibited short dispersal distances (704-1065 m) in fragmented landscapes in lowland England. The results suggested that dispersal behaviour was sensitive to

³ Transportation of propagules on the outside of vertebrate animals

isolation resulting in poor settling success outside of the natal wood, and implying that habitat fragmentation may be a contributory factor in the decline of the marsh tit population in Britain.

Dormice in Saxony appear able to exist in very small isolated woods (e.g. <3.0ha) and can disperse 250-500 m over open fields (Buechner, 2008). Earlier work by Fitzgibbon (1997) found that proximity to nearest woodland, extent of adjoining hedgerows and types of crops in neighbouring fields were all factors influencing small mammals in farm woodlands.

In a study examining the effects of landscape scale configuration of woodland on bat roosting location, *P. pipistrellus*, *P. pygmaeus*, lesser horse-shoe bat (*Rhinolophus hipposideros*), serotine bat (*Eptesicus serotinus*) and Natterer's bat (*Myotis nattereri*) all selected roosts closer to broadleaved woodland than expected by chance, with 90% of roosts located within 440 m of broadleaved woodland (Bouhey *et al.*, 2011). Fuentes-Montemayor *et al.* (2013) found higher bat activity levels in small and isolated woodland fragments, which might reflect a more intensive use of woodland in areas where this habitat is scarce. Similar findings have been reported for other taxa such as birds (Vanhinsbergh *et al.*, 2002). Flight is energetically expensive (Thomas and Suthers, 1972) and intensively managed agricultural land is a hostile (low permeability) matrix which is avoided by many species (Walsh and Harris, 1996). Therefore, bats might 'choose' to use nearby resources more intensively rather than commute long distances to remote foraging areas. This suggests that woodland creation is more important (and should be prioritised) in sparsely wooded areas.

7.5 Invertebrates

In a review of studies evaluating invertebrate movements, Brouwers and Newton (2009a) documented rates for 30 insect species (17 carabid (ground) beetle, eight butterfly, two bark beetle, two ant, and one moth species) associated with woodland habitat. Woodland carabids were the most restricted in movement, covering on average only 2.1 m/day. Earlier studies recorded negative relationships between isolation and species richness in invertebrate groups such as spiders (Usher *et al.*, 1993), moths (Usher and Keiller, 1998) and phytophagous insects in general (Dennis *et al.*, 1995). Dispersal ability can be linked to physiognomy. For example, plant dwelling arthropods (e.g. Hemiptera) with permanently reduced wings have low dispersal abilities; winged taxa disperse more effectively (Moir *et al.*, 2005). In studies of wood crickets on the Isle of Wight, Brouwers and Newton (2009b) found that species presence was most accurately predicted by fragment isolation than by woodland area alone. Further, male crickets could traverse up to 55m away from woodland habitat through semi-natural and grazed grassland (Brouwers *et al.*, 2011), swim and orientate themselves towards woodland if less than 50 m away (Brouwers and Newton, 2010a).

Woodland butterflies are also impacted by fragmentation although recent studies have produced contrasting results depending on species. Bergerot *et al.* (2012) showed that for a widespread woodland butterfly, daily movement distances decreased with increasing distance to the nearest woodland. In contrast, Clarke *et al.* (2011) recorded considerable movements by the wood white butterfly *Leptidea sinapsis* between areas of adult concentration and egg-laying areas and across barriers.

Some of the most extensive empirical studies of dispersal in woodland invertebrates have focused on saproxylic species. Brunet and Isacson (2009b) recorded a negative relationship between the distance to old-growth forest and the occurrence of red-listed saproxylic beetle species in secondary woodland in Swedish beech forests, although this was not the case for non red-listed species. Non red-listed species were able to find habitat within a few km radius and the total amount of habitat in

an unfragmented forest area was more important for species diversity than the spatial distribution of this habitat (Brunet and Isacsson, 2009a).

Irmeler *et al.* (2010) working in Northern Germany showed that species richness of saproxylic beetles in beech, oak and alder woods declined with distance from inner wood habitat. Species with low dispersal ability were not found in non-wooded habitat more than 30 m from the edge; those with higher mobility extended beyond 30 m. Irmeler *et al.* (2010) conclude that woods of >100 ha are necessary to maintain the highest richness of the least mobile saproxylic species. In contrast, Abrahamsson *et al.* (2009) found that saproxylic beetles dependent on birch stumps were not dispersal restricted. Similarly, the aspen hoverfly can move up to 1 km or more to exploit transient bark habitats on fresh fallen aspen (Rotheray *et al.*, 2009). Longhorn and stag beetles can disperse up to 1.6 km or 1 km respectively (Drag *et al.*, 2011; Thomaes, 2009), and insects inhabiting wood decay fungi may not be limited by dispersal (Jonsson and Nordlander, 2006).

These studies point to different dispersal strategies in saproxylic species suggesting that some species are adapted to dispersing considerable distances to exploit habitat that has high temporal and spatial variability in occurrence (Humphrey and Bailey, 2012). Therefore, secondary old growth, even in isolated small patches, could have greater potential for saproxylic species diversity than expected, and may provide important new strongholds for recovery and recolonisation of an important share of old-growth related species (Vandekerckhove *et al.*, 2011). In contrast, other saproxylics that are more dispersal restricted are confined to decaying wood and ancient trees with long continuity (Humphrey and Bailey, 2012; Alexander, 2004).

8. *Joined* - Improving the matrix

8.1 Approach to analysing connectivity

Harrison *et al.* (2012) define connectivity as including a range of movement dimensions such as species mobility (dispersal/migration), gene flow and demographic continuity. As outlined in the previous section, substantial evidence from recent studies suggests that fragmented wooded landscapes can hinder species movement and population viability. Increasing connectivity between fragmented habitat patches is proposed as a means of aiding species dispersal and facilitating large-scale population shifts in response to climate change and land-use impacts (Doerr *et al.*, 2011; Mawdsley *et al.*, 2009; Watts *et al.*, 2007).

Connectivity can be enhanced through a range of measures such as: increasing existing habitat patch size and quality, creating new habitat, improving the permeability of the matrix to species movement, and creating linkage features such as corridors and stepping stones between habitats (Watts and Handley, 2010; Mawdsley *et al.*, 2009). Connectivity is species-specific, because different species have different habitat requirements and dispersal and gap-crossing abilities; one species might have no trouble moving across a landscape that greatly inhibits the movement of another species (Kindlmann and Burel, 2008).

Hodgson *et al.* (2009) argue that the importance of connectivity is being overemphasized and that quantifying its benefits *per se* is plagued with uncertainty. Further, Hodgson *et al.* (2011) maintain that connectivity can be co-incidentally improved by targeting more concrete metrics such as habitat area and habitat quality that have bigger effects than variations in spatial arrangement of habitats or properties of the intervening land. Hodgson *et al.* (2011) also suggest that even if structural features in the matrix have a measurable effect on dispersal rates, this does not necessarily lead to significant increases in population viability. However, Doerr *et al.* (2011) believe that Hodgson *et al.* (2011) have

overlooked recent more detailed research on dispersal behaviour and structural connectivity, which has improved understanding of functional connectivity and revealed that it will not necessarily increase simply with habitat extent.

In the subsequent two sections, we review the evidence as to whether linear (e.g. corridors) or non-linear matrix features (e.g. stepping stones) enhance connectivity between woodland patches in agricultural landscapes.

8.2 Linear features and corridors

In this section a “corridor” is defined as a linear element of the same vegetation type as the habitat patch but *not capable of supporting a breeding population* (Eycott *et al.*, 2008). Over recent decades, a considerable number of reviews have presented empirical evidence in support of the benefit of corridors for maintaining and enhancing species populations (Tewksbury *et al.*, 2002; Vos *et al.*, 2002; Hobbs and Wilson, 1998, Dawson, 1994; Andrews, 1993; Niemelä, 2001) particularly animal populations (Bennett, 2003) although woodland plants also seem to benefit from hedgerow corridors in agricultural landscapes (Corbit *et al.*, 1999; Burel and Baudry, 1990). Nevertheless there is continued debate about the value of corridors in enhancing connectivity. For example, Davies and Pullin (2007) concluded that there is currently insufficient evidence to allow an evaluation of the effectiveness of hedgerow corridors in promoting the population viability of woodland fauna. However, Davies and Pullin (2007) did note that there was anecdotal evidence of positive local population effects and indications that some species use hedgerows as movement conduits.

In a review of measures to increase woodland connectivity, Bailey (2007) concluded that buffering existing woodlands and enhancing matrix quality by reducing land use intensity, and protecting and increasing the cover of semi-natural habitats and refugia, would likely take less time to yield conservation benefit than establishing corridors, as habitats in the former will mature more rapidly.

In contrast, Eycott *et al.* (2008) found quantitative evidence that corridors facilitate the movement of individual animals in some circumstances, although this evidence comes from a limited range of studies and it is not possible to generalise across taxa and landscapes. Landscape features between habitat patches, such as corridors and intervening matrix structure, may have a role in enhancing connectivity for relatively mobile groups like butterflies, birds and large herbivores. For these species, measures to create corridors and an intervening matrix with structural affinity to the “home” habitat may enhance population persistence and could promote longer distance movement.

Moreover, in a meta-analysis of relevant studies Eycott *et al.* (2012) found that, on average, corridors significantly increased inter-patch movement for a range of animal species. Corridors with high structural contrast to the matrix were more likely to increase movement in circumstances where inter-patch distance was high and where subjects in a patch were presented with a choice of matrix types.

There is evidence in support of the hypothesis that linear features enhance movements of a range of woodland species, including mammals, birds and invertebrates (Table 4). The value of hedgerows both as surrogate habitat and movement corridor for forest plants was confirmed in two studies (Wehling and Diekmann, 2009a; Wehling and Diekmann, 2009b). These findings support evidence from the Quebec province in Canada where hedgerows were able to provide connections for woodland herbs (Roy and de Blois, 2006). Herb diversity increased in hedgerows over time and with increased cover of nearby forests (Roy and de Blois, 2006), leading to the conclusion that there could be long-

term benefits in maintaining and even creating linear habitats such as hedgerows (Roy and de Blois, 2008).

Table 4 Linear features that enhance the movement of woodland species (studies since 2008)

Linear feature	Role	Reference
Wooded corridor	Connectivity crucial for the conservation and management of hazel grouse populations in fragmented landscapes; necessary to sustain wooded corridors between larger forest patches	Kajtoch <i>et al.</i> (2012)
Woodland edge corridor	Wood crickets able to live in, and move along, mature woodland edges directly bordering agricultural land	Brouwers <i>et al.</i> (2011)
Habitat corridors	Populations of the ringlet butterfly a woodland edge species show sensitivity to local dispersal behaviour, particularly the use of habitat corridors and other functional dispersal routes	Powney <i>et al.</i> (2012)
Hedgerows	Provide temporary habitat and movement "guides" for birds thus increasing connectivity	Schippers <i>et al.</i> (2009)
	Forest plant species are capable of growing in hedgerows and will survive equally well in forest and its "surrogate" habitat	Wehling and Diekmann (2009a)
	In hedgerow-forest transects, about 77% of all forest plant species (including some endangered taxa) occurring in the neighbouring forests were also found in the adjacent hedgerows	Wehling and Diekmann (2009b)
	<i>P. auritus</i> need hedgerows to provide connectivity between woodland foraging patches	Murphy <i>et al.</i> (2012)
	Play an important role in determining the distribution of the hazel dormouse, but not of the red squirrel	Mortelliti <i>et al.</i> (2011)
Tree-lined Hedgerows	Value as foraging habitat for barbastelle bats (<i>Barbastella barbastellus</i>) associated with broadleaved woods in southern England and for enhancing connectivity with roost sites	Zeale <i>et al.</i> (2012)

In order to mitigate climate change impacts on species, Hannah (2008) suggests that improving connectivity on the periphery of protected areas may be a more effective strategy than establishing corridors linking protected areas. However, corridors serving other purposes, such as large carnivore movement, may be useful for accommodating species range shifts as well. Taxa such as small mammals may be more capable of inter-patch movements without corridors than is frequently assumed (Mabry and Barrett, 2002). In support of this, Liira *et al.* (2012), examining the dispersal of plants into wooded parks in Estonia, found no evidence that woody linear corridors were required to facilitate movement; many of the species could cross ostensibly hostile agricultural landscape.

8.3 Non-linear features

Recent approaches to the assessment of landscape function recognise the importance of the landscape matrix in facilitating species movements and enhancing population viability (Watts *et al.*, 2010; Adriaensen *et al.*, 2003; Ricketts, 2001). In agricultural forest mosaic landscapes, non-linear features of the matrix may be as important as corridors for maintaining biodiversity (Prugh *et al.*, 2008; Fitzgibbon, 1997). For example, in a study of forest bird species in Catalonia, Spain Rubio and Saura (2012) showed that stepping stone patches played a prominent role as irreplaceable providers of habitat connectivity. However, this was only the case within a relatively narrow set of conditions characterised by limited habitat availability, high habitat fragmentation and for species with modest to intermediate dispersal abilities.

Matrix restoration through Agri-Environment Schemes may improve a number of ecosystem functions (Donald and Evans, 2006) as well as benefiting a range of species (Dennis and Hardy, 2007; Downs and Racey, 2006; Dennis, 2004), and may lead to higher conservation returns than focusing exclusively on manipulating the size and configuration of remnant habitat patches (Prugh *et al.*, 2008). Matrix types more structurally similar to home habitat tended to increase inter-patch movement in animal populations compared to more dissimilar matrix types (Eycott *et al.*, 2012; Prevedello and Vieira, 2010) although the effects are weaker than those of patch size or isolation (Prevedello and Vieira, 2010) and benefit relatively mobile groups like butterflies, birds and large herbivores (Eycott *et al.*, 2008).

Further evidence is emerging of differences in the resistance of different matrix types to movement. For example, Van Buskirk (2012) found that open fields and urban areas were more resistant to gene flow in two amphibian species than forested land; roads and highways also reduced matrix permeability. Gene flow through urban areas was reduced by only 24-42% relative to forest; a divided highway reduced gene flow by 11-40% and was 7-8 times more resistant than a secondary road. Similarly, Janin *et al.* (2009) undertaking least-cost modelling for toads as indicator of other species showed that the matrix had a strong influence on toad occurrences in habitat patches, and Villard and Hache (2012) suggested that conifer plantations were too dissimilar to the home habitat of a deciduous woodland bird to allow species movement.

In contrast, initial investigations of the movement of wood crickets between the forest populations across the Isle of Wight suggest that the non-forested matrix does not prevent some migration through the landscape (Vanhala *et al.*, 2009). In a study in the Scottish Highlands Caryl *et al.* (2012) found that pine martens used tussock grasses and shrubs in the matrix as complementary habitats to normal forest habitats, and these were of key importance in highly fragmented landscapes with low forest cover. The role of the matrix in enhancing movement of forest plants is equivocal; land uses such as fields and grasslands can act as barriers (Wehling and Diekmann, 2008). However, Jamoneau *et al.* (2012) found that in mixed landscapes of ancient woodland and agriculture in France, beta-diversity and variation in the presence/absence of herb species were also influenced by the intensity of landscape management, via the permeability of both forest edges and the matrix.

9. Discussion

9.1 Limitations of the approach

This review sought to evaluate the relative importance of stand (*Bigger/Better*) versus landscape-scale (*More/Joined*) factors on the development of biodiversity in new and secondary woodlands. As expected, the relative influence of these factors varies depending on species and landscape context (Fuentes-Montemayor *et al.*, 2013; Jamoneau *et al.*, 2011; Smith *et al.*, 2008; Kolb and Diekmann, 2004) and it is challenging to provide a definitive overview of the findings. Only a few studies (e.g. Jamoneau *et al.*, 2011) have looked at the impacts of the full range of stand and landscape variables together and then only on selected species groups. Consequently the reporting of significant impacts of one variable or another on biodiversity needs to be accompanied by the caveat that other variables were not assessed and could have had an important influence. This is particularly the case for studies where stand quality (e.g. Oxbrough *et al.*, 2010 and others, see section 5.2) was the dominant factor and only a few additional variables were assessed, if at all. In addition, in such a wide ranging review, studies that covered forest landscapes as well as mixed agricultural/forest landscapes were included. In other words, some results were reported from landscapes where the matrix was forest rather than agriculture (e.g. Öckinger *et al.*, 2005), and although these were patch based studies (e.g. secondary stands at varying distances from ancient stands) the findings may not be directly applicable to landscapes where agriculture constitutes the matrix and the dominant land use.

9.2 Emerging findings

Despite there being considerable variability in species responses to the range of local and landscape variables assessed in this review, there are nevertheless some guiding principles applicable to mixed woodland/agricultural landscapes in the UK and the different species assemblages they support. Firstly, woodland specialists exhibit contrasting responses to different components of ecological networks at landscape and local levels compared to generalists. Further the responses are calibrated by whether woodland specialists have low or medium dispersal ability and these differences in responses appear to apply across taxa (Table 5).

Large woodland patches benefit rare species and woodland specialists with low dispersal ability to a greater degree than small patches (Table 5), with threshold size for species occurrence varying from 1.5-2.5 ha for woodland herbs, 1.5-3.5 ha for lichens, >2 ha for birds, > 4 ha for bats (foraging area), > 5 ha for moths etc. For vascular plants, there is a suggestion that the Species Area Relationship may begin to level off at 30-40 ha but this was only found in one study (Digiovinazzo *et al.*, 2010). Generalist woodland species appear to benefit more from a large number of small patches rather than a few larger ones, whereas specialists with medium dispersal ability, for example some saproxylic hoverflies (Rotheray *et al.*, 2009), are affected less by patch size, but more by the spatial and temporal availability of suitable habitat.

Aspects of habitat quality relating to stand structure (age and composition), edge effects, ecological continuity and land-use impacts all have significant impacts on the occurrence and diversity of woodland specialist species (Table 5). Stand (tree) age has a particular impact on herbaceous vascular plants, epiphytic and epixylic lichens, and molluscs with community development taking 40-80 years (>160 years for molluscs). Time to canopy closure is also a significant determiner of site quality having both positive impacts e.g. through reduction in vigour of weedy species, and negative impacts through excessive shade e.g. in dense conifer stands. Edge effects have important consequences for the balance between generalist and specialist species, with more generalists and

fewer specialists in woodlands with a greater proportion of edge (Table 5). The degree to which edge effects extend into the stand appears to vary with species group and land use history, but can be 100 m or more and is also related to woodland shape; longer thinner woods having a higher edge to area ratio.

Table 5 Summary of influence of local (site/patch/stand) and landscape factors on woodland species across all taxa

Scale	Factor (see Fig 1)	Potential Action	Generalists*	Specialists low dispersal**	Specialists medium dispersal***
Local	Bigger	Increasing patch size	-	+	NR
Local	Better	Increasing stand quality (age and composition)	NR	+	+
Local	Better	More compact shape less edge	-	+	+
Local	Better	Greater ecological continuity (patch age)	NR	NR?	NR
Landscape	More	More surrounding habitat	+	+	+
Landscape	Joined	Decreasing isolation	NR	+	NR
Landscape	Joined	Presence of corridors	+	NR	+
Landscape	Joined	Presence of other matrix features	+	NR	+

+ = positive response e.g. increase in species richness or species' occurrences

- = negative response e.g. decrease in species richness or species' occurrences

NR = no response, or limited information

* e.g. many small mammals such as the wood mouse *Apodemus sylvaticus*

** e.g. ancient woodland vascular plants including perennial herbs such as wood anemone *Anemone nemorosa*

*** e.g. relatively mobile invertebrates such as hoverflies associated with deadwood e.g. the aspen hoverfly *Hammerschmidtia ferruginea*

Ecological continuity (patch age rather than tree age) and past land use may also affect the species-richness of woodland specialists (Table 5), although few studies specifically separate tree age from patch age and there is a question mark over whether ecological continuity is as significant a factor for some species groups as previously assumed (Ellis and Hope, 2012). The occurrence of old-growth structure (large trees, deadwood) appears to be of particular importance for late successional species associated with decaying wood habitats.

Woods established on former pastures support a greater richness of woodland herbaceous species than those established on ex-arable sites. Soil alteration, in particular the high incidence of immobile phosphorous associated with arable land use, appears to restrict colonisation of woodland species. One caveat that needs to be attached to the importance of habitat structure and continuity is that most studies recorded benefits where new/secondary woodlands were adjacent or in close proximity to

existing ancient woodland. Habitat structure and continuity was of less importance in determining species occurrence and diversity in isolated stands.

Positive relationships have been recorded between the amount of woodland in the surrounding landscape and a wide range of different species groups, including woodland birds, bats, small mammals, invertebrates, fungi, vascular plants and cryptogams. Both specialist and generalist species appear to benefit from increased woodland cover in the landscape (Table 5). The scale of influence varies by species group (and may be affected by study restrictions), but is generally in the range of 1-5 km distance from the study patch. There is general support in the literature regarding the importance of threshold amounts of surrounding habitat for determining species occurrence or for enhancing species diversity and abundances. Suggested threshold values range from 5% up to 30% cover depending on the species under study (Andrén, 1994).

Woodland specialists with low dispersal abilities are affected negatively by degree of isolation (Table 5). New, isolated (e.g. more than 2-5 km from existing woodland) woods rarely acquire specialist woodland flora and fauna even if large and of good quality with suitable conditions for establishment. Where new woods are less isolated, i.e. adjacent or in close proximity to ancient woodland, community development can take place 50-80 years after establishment depending on habitat quality (stand structure and tree species composition) and by past land use (pasture v arable). Habitat utilisation appears to be the key to understanding dispersal capabilities across taxa. Species adapted to transient habitats with spatio-temporal continuity at the landscape scale have better dispersal ability; those adapted to habitats with long-term continuity at the site scale appear to be dispersal restricted.

Woodland specialists with poor dispersal do not appear to benefit from increasing matrix permeability (Table 5) especially when overall habitat extent in the landscape is low. Both linear (corridors) and non-linear features in the matrix are important for enhancing the movement of relatively mobile species groups such as butterflies, birds and large herbivores especially if the structure of the feature contrasts to that of the surrounding matrix and has affinity to the structure of the home habitat (e.g. hedgerows). In other words, matrix permeability influences species movements most where a clear choice is offered to an insect or animal to move through one type of structure as opposed to another. Certain species groups such as amphibians seem to be particularly sensitive to differences in matrix permeability. Species with intermediate dispersal abilities (e.g. pine martens) appear to benefit most from corridors where landscapes have low amounts of habitat and high degree of fragmentation. However, a few studies show that some plants and mammals can cross ostensibly hostile matrices and movement does not seem to be enhanced by the presence of corridors.

10. Conclusions

It is clear that no single landscape management strategy can meet the need of all species groups. Strategies need to be clearly linked to objectives, which might range from intentions to increase biodiversity generally in the landscape, facilitate species movements in relation to climate change, or focus specifically on maintaining and increasing the diversity of specialist woodland species with limited dispersal capability. As an example of the latter Jamoneau *et al.* (2011) propose a strategy for conserving woodland forest specialists in changing rural landscapes by preserving the largest, oldest habitat fragments and favouring species movements by enhancing the permeability of the surrounding matrix. The findings from this review concur with this approach, but also highlight the importance of creating new habitat both adjacent and in close proximity to existing high value woodland where woodland cover is significantly less than 30% in the landscape. More specifically, the findings of the review can be brought together in a set of guiding principles, which are set out in Box 1 below.

Box 1: Guiding principles based on review findings

- 1) Woodland specialist species respond differently to local and landscape factors than generalists, and to the different components of ecological networks. Further these responses are cross-taxon and calibrated by whether woodland specialists have low, as opposed to intermediate, dispersal ability
- 2) Woodland specialists with poor dispersal abilities are impacted positively by size and quality of new woodlands and negatively by degree of isolation. Further, benefits from increasing matrix permeability are equivocal, particularly when overall habitat extent in the landscape is low
- 3) Woodland specialists with intermediate dispersal abilities benefit from measures to increase connectivity such as the presence of linear and non-linear matrix features with structural affinity to the home habitat, especially where overall habitat extent in the landscape is low
- 4) Generalist woodland species appear to benefit more from a large number of small patches in the landscape rather than a few larger ones and respond positively to the amount of edge habitat
- 5) Where new woodlands are adjacent or in close proximity to ancient woodlands, community development can be relatively rapid (e.g. 50-80 years), but is also affected by habitat quality (stand structure and tree species composition) and by past land use (pasture v arable)
- 6) Isolated woods (e.g. more than 2-5 km from existing woodland) have difficulty in acquiring specialist woodland flora and fauna even if large and of good quality
- 7) Ecological continuity may be of less importance than forest structure in determining habitat quality with the occurrence of old-growth structure (large trees, deadwood) of particular importance for late successional species associated with decaying wood habitats

11. Further research

The principles set out in Box 1 are based on a wide range of studies covering different species groups across many countries and may not be wholly applicable in a UK setting. Given the limitations of the approach adopted in this review (i.e. broad and inclusive) there would be value in carrying out further review work with a more focused synthesis, selecting those studies which looked at both local and landscape variables in tandem and were carried out specifically in temperate agricultural landscapes.

In addition to this further review work, there is also a need to obtain empirical evidence on the influence of local and landscape factors on the biodiversity of new and secondary woodlands in the UK. This will enable us to learn lessons from past landscape change and provide the evidence needed to underpin the implementation of ecological networks.

The UK has a long history of loss and fragmentation of woodland (Mason, 2007; Peterken, 1996) leading to impoverishment of biodiversity (Watts, 2006; Humphrey *et al.*, 2004) and loss of ecosystem functioning (Quine *et al.*, 2011). However, over the last 50 years, programmes of woodland creation, including Woodland Grant Schemes and Agri-Environment Schemes have helped to increase woodland cover to approximately 12% (Watts, 2006; Vanhinsbergh *et al.*, 2002; Crabtree, 1996). These woods together with secondary woodland established in the 19th and early 20th century provide us (albeit inadvertently) with a series of historical test landscapes. Most importantly, many of these new woodlands were established at a known date on former agricultural land and can be identified through either grant scheme records or the Ordnance Survey digitised historical map series (Edina, 2013).

These woods are essentially a “blank canvas”, containing few, if any, woodland species before the date of woodland establishment. Therefore, the presence of woodland species within these sites must be due to a combination of local level characteristics (e.g. habitat area and quality), how long the site has been wooded, and its location in the landscape (Figure 1). By selecting a replicated chronology of woodland creation sites, and assessing species groups with a range of different traits (e.g. dispersal ability, habitat preferences, ecological function), it should be possible to obtain the necessary spatial and temporal evidence to inform the implementation of effective ecological networks. This is the basis for the development of the project Woodland Creation and Ecological Networks (WrEN) of which this review is a part.

12. References

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