

Review

Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands

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Abstract

Increasing connectivity is frequently proposed as an effective strategy to address biodiversity decline within fragmented habitats. Woodland habitats in Great Britain have been significantly reduced in area and are described as having ‘fragmented’ distribution. Many researchers have associated declines in woodland species with fragmentation. Currently, there is a concerted effort to increase connectivity (through increasing the number of physical links) between woodlands, often through the development of habitat networks, with the aim of increasing biodiversity. This aim is driven through rising interest in the role of landscape scale processes in biodiversity conservation and increasing concern of the fate of populations facing a predicted increase in habitat isolation through climate change.

In this paper, the evidence behind the assumption that increasing connectivity will increase biodiversity is reviewed, together with the assumptions made during development of models that identify potential networks within which connectivity is to be increased. Gaps identified within the evidence base lead to the suggestion of new research areas that will provide a firm basis from which more informed evaluation of increasing connectivity for biodiversity gain can be developed. Alternative approaches to enhancing woodland biodiversity in fragmented landscapes are proposed.

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Keywords: Increasing connectivity; Habitat networks; Forests; Fragmentation

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1. Introduction

It is frequently suggested that the loss and fragmentation of the wooded landscape has and will continue to result in a loss of biodiversity both in terms of the numbers of species and the genetic variation present within those species (Thomas, 1995; Peterken, 2002). Increasing physical linkage, through the creation of new woodland and semi-natural habitats in suitable locations is thought to reduce the detrimental effects of fragmentation on the biodiversity of woods by providing links and stepping stones between isolated populations of woodland species (Kirby, 1995; Peterken, 1995, 2002; Spellerberg, 1995). This assumes that increased fragmentation has led to a reduction in the biodiversity of current woods or placed biodiversity in an increasingly perilous state. Moreover, the addition of new habitats that expand and link habitats will reverse the effects of fragmentation (Watts et al., 2005).

Further interest in increasing connectivity has been stimulated by the prediction that climate change will shift the geographic range of habitats, forcing associated species to either track this shift through dispersal or face local extinction (Berry et al., 2002). If habitats are highly fragmented then species will not be able to reach their new ‘climate space’ and thus face extirpation as they become stranded in increasingly unsuitable habitat (Holt and Keitt, 2000; Hannah et al., 2002; Pearson and Dawson, 2003; Opdam and Wascher, 2004).

The biodiversity strategies recently produced for England and Scotland (Defra, 2002; Scottish Executive, 2004), emphasize the need for a landscape-scale approach. Stated aims for woodlands include “to ensure that forestry, woodland management and creation . . . contribute(s) to the conservation of biodiversity at a wider landscape scale” (Defra, 2002). The UK Biodiversity Action Plan also states: “A key conservation aim for many species is . . . to create conditions that allow particularly fragmented habitats to expand or, in the case of animal species, to retain or create wildlife corridors allowing natural migration, escape from danger and inter-breeding” (UK Biodiversity Steering Group, 1995). Reconnecting fragmented woodlands through the development of networks has been widely discussed and advocated (Peterken et al., 1995; Forestry Commission, 1998, 2000, 2001; Hampson and Peterken, 1998; SNH and FCS, 2003). Internationally, the European Union’s Habitat and Species Directive, adopted in 1992, proposes measuring connectivity (corridors and stepping stones) as a means of assuring favourable status for special areas of conservation (SACs) (EEC, 1992). The Pan-European Biological and Landscape Diversity Strategy (Council of Europe, 1996) proposes ecological networks to reduce the effects of isolation and increase viability in small areas (Nowicki et al.,

1996). This Pan-European Ecological Network (PEEN) is intended to be a coherent assemblage of natural and semi-natural landscape elements that when managed or conserved will ensure favourable conservation status of the ecosystems, habitats and species of European importance (Bennett, 1998). The proposal has been endorsed by 54 countries of the United Nations Economic Commission for Europe (UNECE).

1.1. From science to policy

A recent study of the policy implemented to protect biodiversity in European agricultural landscapes, suggests that it has been unsuccessful for the target species (Kleijn et al., 2001, 2004). Without the scientifically sound evaluation of such policies that Kleijn et al. suggest, resources may continue to be misdirected into unsuccessful schemes. General landscape ecological theory can rarely be used to make exact predictions on how to conserve species in real landscapes (Harrison and Bruna, 1999). Landscapes are unique in terms of fragmentation pattern, nature of the surrounding matrix, composition of biota and the relative importance of the various effects of fragmentation (Villard, 2002). It is unlikely that all woodland species will respond equally as positively to attempts to restore functional connectivity through increasing physical linkage between woodlands. To seek a firm evidence base for this approach I review evidence that:

- processes associated with fragmentation, especially processes that reduce physical linkage, reduce or place biodiversity in an increasingly parlous state,
- that these processes can be arrested when fragmentation is halted and reversed when functional connectivity is increased through restoring physical linkage.

I then examine methodologies and models developed to inform decisions on increasing connectivity. Finally, I suggest where more information is needed to address gaps present in the evidence base and suggest alternative strategies for enhancing woodland biodiversity.

2. Methods

I searched for evidence on reduced biodiversity through processes associated with fragmentation and for increases in biodiversity following an increase in physical links using the Web of Knowledge and Ingenta search engines. I used keywords ‘fragment, woodland, forest, isolation, species’ for the first area and for the second part I also included ‘habitat, network, reverse, connect, link’. The search was conducted for

publications between the years 1980 and 2006. In addition, citations were also followed. Searches were generally limited to examples from Temperate European regions.

3. Biodiversity decline in fragmented habitats

Habitat loss and fragmentation are frequently identified as major causes of biodiversity loss. These losses are said to result from a number of inter-related processes; a reduction in total habitat area, reduction in patch size, both physically and through edge effects (Spellerberg, 1995), increasing number of patches and distance between patches. Often these processes are collectively referred to as ‘fragmentation’ (Fahrig, 2003). Biotic changes may also accompany the physical changes; new edge habitat can increase colonisation by generalist and invasive species, loss of keystone species may alter community structure and control (Crooks and Soulé, 1999) and populations may shrink and become isolated (Wilcox, 1980; Tilman et al., 1994; Andren, 1994). Genetic diversity may also decline in isolated populations (Spellerberg, 1995). Fragmentation can selectively affect different species (Krüss and Tschardtke, 1994; Zabel and Tschardtke, 1998), modifying community structure (Jacquemyn et al., 2001) and potentially altering ecological processes such as pollination, decomposition, nutrient cycling, seed dispersal and predation (Harrison and Bruna, 1999).

Reducing the physical links between woods, and increasing the physical distance between patches through the removal of woodland will reduce the *connectedness* of the wooded landscape. Reducing connectedness will decrease the rate at which species can move between woodlands (Peterken, 2002). However, more insidious effects are observed with the intensification of land uses around woodland patches. Biodiversity decline in habitat fragments is noted particularly in intensively used agricultural landscapes (Opdam et al., 1993) when the intensification of land uses surrounding fragments effectively isolates fragments further (Gascon et al., 1999). Simplification of the matrix from structurally diverse semi-natural habitats to far less diverse agricultural crops, will further inhibit the movement of some woodland species (Bellamy et al., 1996; Bright and Morris, 1996; Bennett et al., 2003). These isolation effects very much depend upon the specific dispersal modes used by different species. The *connectivity* of the landscape, that is ‘the degree to which landscape facilitates or impedes movement among resource patches’ (Taylor et al., 1993) will therefore vary according to the dispersal power of the species in question.

In reviewing fragmentation studies, Harrison and Bruna (1999), Fahrig (2003) and Bailey and Pryor (2004) identify gaps in the literature between general principles describing biodiversity loss through fragmentation and consistent empirical evidence. I have reviewed the literature for such evidence in European temperate woodlands primarily focussing on British woodland habitats (Bailey et al., 2002). A summary of evidence that species presence/numbers in four taxonomic groups will decline with fragmentation in European broadleaved woodland habitats is presented in Appendix A and is reviewed below.

3.1. Evidence of biodiversity loss in British Woodland

Evidence of biodiversity loss in British woodland following fragmentation can be sought from two main sources. Historic evidence of species presence, for example, from paleoecological sources that contain species in abundance that are now extinct or far more limited in their distribution, and studies of contemporary woodland. Historic evidence is of limited use unless fragmentation can be attributed as a major reason for species decline. Fossil beetle records in North Yorkshire (Buckland and Kenward, 1973; Hammond, 1974) indicate a decline that can be directly linked to habitat loss and fragmentation. Yet, the bulk of the evidence for biodiversity decline as a result of fragmentation has come from empirical studies of contemporary woodland habitats and associated species.

Decreases in bird species richness have often been associated with fragmentation (van Dorp and Opdam, 1987; Opdam, 1991; McCollin, 1993), with most woodland interior birds being restricted to sizeable mature woods (Opdam et al., 1985). Hinsley and co-workers (Hinsley et al., 1992, 1995a,b, 1996; Bellamy et al., 1996, 1998, 2000) have conducted one of the few extensive, empirical studies on bird communities in fragmented landscapes. They identified species that avoid the smallest woods (i.e., those with woodland interior requirements). Two species, nuthatch (*Sitta europaea*) and marsh tit (*Parus palustris*) were found to be particularly sensitive to area of patch (Hinsley et al., 1995a,b). Isolation was also found to have profound effects on woodland species. For example, the density of woodland within 0.5 km of a wood was found to be an important influence on the extinction and colonisation rates, particularly for dispersal of long-tailed tits (*Aegithalos caudatus*) (Hinsley et al., 1994). The amount of woodland within 1 km of wood edge was important for the dispersal of chaffinches and great spotted woodpeckers (*Dendrocopos major*) (Hinsley et al., 1995a,b). Hedgerow density in the surrounding landscape increased the probability of some species breeding in woods. Isolation of woods has also been found to be a significant factor in the distribution of bird species and woodland community composition (McCollin, 1993; Hinsley et al., 1994). Further work in North Western Europe also found a sensitivity of nuthatch to fragmentation, with density of woodland surrounding natal territories determining distance travelled during dispersal (Matthysen and Schmidt, 1987; Enoksson, 1987; Matthysen et al., 1995; van Langevelde, 2000).

Empirical work into the effects of habitat fragmentation only exists for a handful of mammals found in British woodland. With effects on dormice (*Muscardinus avellanarius*) and yellow-necked mouse (*Apodemus flavicollis*) found to be most profound (Bright et al., 1992; Bright and Morris, 1990, 1991, 1992; Bright, 1996; Marsh and Harris, 2000). The effects on red squirrel have been considered, but to a lesser extent (Bright, 1993). This species is more frequently considered in continental Europe, where grey squirrels are not a confounding factor in red squirrel distribution (e.g., Delin and Andren, 1999; Rodríguez and Andren, 1999). Effects of habitat fragmentation

on the wood mouse (*Apodemus sylvaticus*) and bank vole (*Clethionomys glareolus*) have been considered but not found to have severe limitations to population levels (Usher et al., 1995; Fitzgibbon, 1997).

The effect of habitat fragmentation on invertebrates is unevenly covered in the literature. Knowledge of the dispersal and colonisation powers of invertebrate groups is limited with the exception of widely studied groups such as the beetles and butterflies (Welch, 1990). A marked reduction in the ranges of butterflies has occurred in the last 50 years and has been attributed to habitat loss, compounded by fragmentation (Shreeve, 1995). Shreeve (1995) observed that dispersal power is related to the seral stage of vegetation to which the species is associated. Many species associated with long-lived trees have been shown to have very limited powers of dispersal, to such an extent that some have become isolated to one or two trees in one location (Welch, 1990; Alexander, 2004). Saproxyllic species limited to the later stages of decay are not tree species specific (other than to broadleaved or coniferous) but are confined by a lack of ability to reach decaying trees with suitable niches (Warren and Key, 1991). Thus, saproxyllic species will be among the invertebrate species most profoundly affected by reduced connectivity (Harding and Rose, 1986).

Area effects have been found to influence the distribution of a number of vascular plant species associated with ancient woodland. For species in farm woods there was a strong species-area relationship for some woodland plants (Usher et al., 1992; Usher, 1995). Isolation effects however are often blurred by the complexity of influences that determine woodland ground flora distribution. Vascular plants can be segregated according to their affinity for ancient woods. This affinity inversely reflects their ability to disperse and colonise other woods (Peterken, 1974, 2000; Peterken and Game, 1984; Verkaar, 1988; Hodgson and Grime, 1990; Rose, 1999). Ancient woodland species are slow to colonise recent forest patches (e.g., Peterken and Game, 1984; Brunet and von Oheimb, 1998; Bossuyt et al., 1999; Dzwonko, 2001; Verheyen et al., 2003). Peterken and Game (1984) found the exacting habitat requirements of specialists make colonisation extremely difficult even if the species is successful in reaching a suitable habitat. In woods above 3 ha in size, there were far more species present in ancient woodlands than recent woods. From this work, Peterken and Game suggest that woodland flora develops within a few decades and then increases very slowly, if at all, with one third of ancient woodland species failing to colonise recent woods. Jacquemyn et al. (2003) conducted one of the handful of studies examining vascular species dispersal to recently created woodlands. They found seed dispersal events rarely occurred over 100 m. Barriers to colonisation can include modified soil structure or chemistry. For example, colonisation rates of plants in abandoned agricultural land in Belgium were profoundly affected by modified soil chemistry (Honnay et al., 1999).

This review indicates that in the UK, species occurrence can be limited in fragments of woodland and that fragmentation is having a negative impact on woodland species distributions. In a few studies in which measures of the intensification of

surrounding land uses were included, i.e., loss of semi-natural habitats, they were found to be a contributing factor to species decline (Bellamy et al., 1996; Bright and Morris, 1996; Honnay et al., 2002a,b; Bennett et al., 2003). This review has also indicated that it is difficult to attribute species loss to either reduced connectivity or reduction of patch area. Controlling for effects of net reduction of habitat area and, therefore, reduced heterogeneity in studies of fragmented landscapes is difficult (Harrison and Bruna, 1999; Fahrig, 2003), and seldom attempted in most studies considering real landscapes (but see Beier and Noss, 1998). Thus, attributing declines to either habitat loss or reduced connectivity is infrequently achieved (McGarigal and Cushman, 2002; Fahrig, 2003). When reviewing studies that have controlled for habitat loss (e.g., McGarigal and McComb, 1995; Trzcinski et al., 1999), Fahrig (2003) found fragmentation per se has a very small effect when compared with that of habitat loss. This effect was equally as likely to be positive as negative (e.g., Tschardt et al., 2002). Furthermore, Fahrig (2003) notes that in many studies the sample size is often only two, as fragmentation is a landscape scale process (McGarigal and Cushman, 2002), and comparisons are made with a fragmented and unfragmented landscape. This small sample size weakens inferences that can be made on the effects of fragmentation, given other differences between landscapes that cannot be controlled (Fahrig, 2003). Substituting space for time in fragmentation studies is also problematic. Differences in species composition within fragments are put down to processes associated with fragmentation. The conclusions of such studies, therefore, have as their basis indirect correlative analyses (Wiens, 1992). Although some studies have used controls (e.g., Dzwonko, 1993; Bright et al., 1994), flaws can still exist. Variability and auto-correlation among landscapes can further weaken conclusions that might be drawn (Wiens, 1992).

Fragmentation is more and more frequently portrayed as a spatial problem by theoretical studies that focus on dispersal between fragments. However, the empirical studies reviewed here generally suggest that fragmentation also involves additional processes including habitat degradation, modification and edge effects. Assumptions have to be made about patches, sometimes ignoring inconsistencies in patch management history and natural variability in patch quality, and essentially, there is no pre-treatment control (Wiens, 1992; McGarigal and Cushman, 2002).

3.2. Cryptic fragmentation effects

The more subtle consequences of habitat loss and fragmentation (for example, loss of genetic diversity, and modification of community structure) are still infrequently examined in the literature. Although genetic changes are often cited as detrimental to population viability (through loss of and changes to differentiated populations, loss of variation between individuals of the same population and changes to the levels of inbreeding (Sherwin and Moritz, 2000)), real examples are rare (Richards, 1997; Saccheri et al., 1998; Segelbacher et al., 2003). This leads some commentators to conclude that although

changes are likely to be detrimental, they are often not cause for immediate conservation concern (Lande, 1988) as they are considered to be a symptom of population decline rather than a cause (Holsinger and Vitt, 1997). Yet preventing the erosion of genetic variation, to protect genetic diversity at a local scale appears prudent particularly in light of environmental change. Currently, little is known about gene flow events across heterogeneous landscapes (Sork et al., 1999) or the demographic consequences of gene flow (McCauley et al., 2001). The concurrent development of genetic marker systems to quantify genetic diversity and gene flow (e.g., microsatellites) and statistical techniques that acknowledge the specific requirements and assumptions of this data are making such investigations more accessible (Lowe, 2004) and should enable researchers to uncover the real implications of different levels of fragmentation for detrimental genetic modification of populations.

Consequences for community structure are not fully understood. Change is evident, but implications for stability from this change are not apparent. Most work to date has focussed on bird community composition. For example, bird community composition has been found to vary with wood area (Fuller, 1982; Blake and Karr, 1984; Opdam et al., 1985; Nilsson, 1986; van Dorp and Opdam, 1987; Opdam, 1991; McCollin, 1993). Small wood fragments may support many edge species and rarely contain forest interior species (Diamond and May, 1976; Opdam et al., 1985; van Dorp and Opdam, 1987; Opdam, 1991; McCollin, 1993). Plant community composition has also been found to be influenced by species dispersal rates (Jacquemyn et al., 2001; Butaye et al., 2001) and insect communities associated with old growth forest fungus have been shown to become simplified over time following isolation (Komonen et al., 2000).

3.3. Legacy of past landscape change

It is difficult to anticipate over what period previous modification to landscape structure will alter the present woodland community. Can we be confident in attributing recent change in community composition to recent fragmentation events? Wu et al. (2002) suggest that for some species at least, their occurrence will track landscape change with a noticeable time-lag. Indeed population and meta-population studies have illustrated that this time-lag can vary according to species and resulting landscape structure (Tilman et al., 1994; Hanski, 1998, 1999; Nagelkerke et al., 2002; Ovaskainen and Hanski, 2002). Whatever attempts are made to reverse fragmentation, a temporal buffer for lag effects, firstly from continued effects from past fragmentation and secondly, for the time it takes for new links to modify species distributions must be included in project evaluation.

Many authors of fragmentation studies conclude by emphasising the need to reconnect fragments as their results indicate greater species richness in more connected landscapes. This assumes not only that fragmentation per se has had a significant impact on biodiversity, but also that by replacing the once removed habitat in fragmented landscapes dispersal and

colonisation will occur as before (Dolman and Fuller, 2003) and species loss and detrimental community effects will be effectively reversed. I shall now explore evidence available to corroborate these latter assumptions.

4. Increasing connectivity leads to increases in woodland biodiversity

There is little systematic research available on the effects of restoration programmes intended to increase connectivity (by increasing physical links between woodlands) in fragmented landscapes (Henle et al., 2004). This dearth of information has been attributed to the lack of a suitable experimental framework and scientific evaluation in such programmes (Saunders et al., 1996), but will also reflect the anticipated timescales for such actions to have a measurable impact. Brotons et al. (2003) found the development of a forest reserve network had an important role in the distribution of old growth forest birds. Data are also available from the large tropical field project in the Brazilian Amazon (Beirregard et al., 1992). The regeneration of a once removed corridor resulted in the recolonisation of a rainforest fragment by an ant species (after 1 year) (Simberloff and Cox, 1987) and some more common understory birds, within 6–9 years (Stouffer and Bierregard, 1995). Some species of wood ant have been observed to colonise previously isolated habitat if connectivity is improved (Hughes, personal communication, 2004). Evidence of the utility of increasing the permeability of the landscape to species movement, by increasing the proportion of semi-natural land uses in the matrix between woodlands, is not available. Drawing conclusions from indirect sources, i.e., from correlative studies that compare fragmented with less fragmented landscapes, are unsatisfactory for the reasons noted in Section 3.1.

One area that has received much attention in reversing fragmentation effects is the utility of corridors in fragmented landscapes (e.g., Wiens, 2002; Catchpole, 2004). Simberloff et al. (1992) found that, at best, corridors extend the amount of available habitat for foraging and at worst Simberloff et al. viewed them as an expensive diversion, lacking a sound scientific basis. They suggested a stringent cost–benefit analysis including an evaluation of alternative strategies. Dawson (1994) reviewed the evidence for species use of corridors and found very little evidence that they were used. Certainly, evidence of corridor use by woodland species (invertebrates and plants) is scarce (Vermeulen, 1995; Speight, 2000; Smart et al., 2001). However, Beier and Noss (1998) and Bennett (2004) suggests care must be taken to avoid undue pessimism, arguing that evidence from a few well designed studies does support the utility of corridors as conservation tools, and that a shortage of testable results is inevitable given the long time scales likely for species movement especially along new linkages.

The high ecological value placed on hedgerows partly reflects the assumption that they play a vital role as corridors between woodlands in fragmented landscapes. Yet a recent review found little empirical evidence that movement of

woodland species increased with hedgerow presence (Davies and Pullin, 2006). However, this review and that by Davies and Pullin (2006) did find some anecdotal evidence of species using hedgerows as corridors. For example, Petit and Burel (1998) provide evidence that one species of beetle will use hedgerows as corridors, but this use was dependent on quality and could not be used to predict occupancy. Bright (1998) found that dormice would readily move along hedgerows and although constrained by the presence of gaps, would use hedgerows for dispersal.

Studies have highlighted differential selection of functional groups of woodland species that do use corridors (Roy and de Blois, 2006). Less tolerant and less common woodland species, often those species with the weakest dispersal ability, are rarely found in corridors. Both Dawson (1994) and Hill et al. (1994) are sceptical of potential for corridors to act as conduits for specialised species concluding that species most likely to utilise corridors would be those of moderate dispersal ability. Furthermore, some studies note a correlation between woodland species number, functional group and corridor 'quality' (Hinsley and Bellamy, 2000). Corridor quality can represent width, height, volume, and for more specialist species, maturity (Hinsley and Bellamy, 2000), all factors that correlate with presence of microhabitats required by specialist species (Roy and de Blois, 2006). Whilst these studies are recording foraging, or use of the corridor as habitat rather than for dispersal, the association between functional groups of species and corridor quality, can inform the properties of corridors most likely to be used by the widest range of taxa for dispersal. For vascular plants, it seems that the corridor must be able to serve as suitable habitat, sustaining populations in order that they are able to disperse incrementally (Pollard et al., 1974) (but see Bright, 1998). For many species a corridor would need to develop habitats associated with mature woodland before they may use it, which could be a matter of many decades if not centuries.

Given that mean annual temperature in the UK is expected to increase by between 3 and 6 °C by the 2080s (Hulme et al., 2002) fundamental changes in woodland community composition can be expected (Broadmeadow and Ray, 2005). For example, under 2050s high emissions scenario (Hulme et al., 2002) significant changes are expected to the vegetation

community composition of NVC Class W11 (Upland Oak-woods). As these woods already have a restricted range, are corridors developed now likely to be sufficiently mature to be beneficial in enabling associated species to avoid range contraction? Pearson and Dawson (2005) conclude that landscape scale modification such as increased connectivity are unlikely to enable plant species to disperse at such rates necessary to keep pace with climate change. It is difficult to reach a decision on the effectiveness of corridors on reversing fragmentation effects, due to conflicting evidence. Reaching a decision is particularly difficult when it is likely that climate change will exacerbate isolation in ways we cannot exactly predict.

5. Modelling new landscape linkages

5.1. Spatially explicit population models, generic species and the matrix

In response to the paucity of empirical evidence of species responses to changing landscape structure, models have been developed to anticipate effects of increased connectivity on species movement. Such models are intended to enable land managers to evaluate consequences of new habitat location (e.g., through the development of habitat networks) for species of conservation concern.

For specific species, spatially explicit population models (SEPMs) are used to design optimal landscapes and conservation strategies to enhance populations (e.g., Opdam et al., 2003). These models require detailed information on species dispersal rates and ability (across contrasting matrix in the case of the more complex models), demography and colonisation requirements (for example, Verboom and Pouwels, 2004) (see Table 1). The level of detail that can be incorporated into SEPMs has implications for accuracy of model outputs (Jepsen et al., 2004). SEPMs can vary greatly in the degree of complexity and approach which can have profound effects on predicted outcomes (Jepsen et al., 2004). They are also frequently found to be sensitive to unknown and unmeasurable parameters (Harrison et al., 1993; Ruckelshaus et al., 1997).

When autecological information is not available SEPMs and other models can be parameterised according to the anticipated

Table 1
Examples of models used to inform the restoration of connectivity in European fragmented landscapes

Methodology	Aim of model	Target species/habitat	Location	Reference
Landscape scale planning using forest growth models	Reverse fragmentation through forest operations	Old forest patches	Finland	Kurttila et al. (2002)
LARCH (network analysis, PVA)	Defines ecological networks	Selected species	The Netherlands	Verboom and Pouwels (2004)
Landscape ecological criteria	Define blocks of woodland for expansion	Beech woodlands	Chilterns, UK	Lee et al. (2002)
Multi-criteria	Define areas suitable for woodland	Native and ancient woodland	Snowdonia, UK	Gkaraveli et al. (2004)
BEETLE (cost–distance analysis of matrix)	Definition of forest habitat networks	Generic species	Scotland and Wales, UK	Latham et al. (2004), Ray et al. (2004)
Criteria defined by species	Definition of habitat clusters	Butterfly	UK	Holloway et al. (2003)

requirements of a ‘generic species’, for example, the Biological and Environmental Evaluation Tools for Landscape Ecology (BEETLE) model (Ray et al., 2004; Latham et al., 2004). Generic species are defined by the user to represent real species with varying dispersal and colonisation abilities and even contrasting habitat area and quality requirements. They have the advantage of possibly representing a group of species with similar habitat requirements, dispersal ability, etc., and so findings have a general applicability. In the absence of autecological data they enable varying scenarios of landscape pattern to be evaluated for species most likely to benefit from restoring connectivity. However model validation is not possible using the generic species approach.

Recent recognition of the role of matrix in the differential dispersal of species (Ricketts, 2001) has led to the inclusion of analogies of matrix penetrability within SEPMS. This is achieved through the application of percolation theory and least cost-path analysis (Chardon et al., 2003; Adriaensen et al., 2003; Sutcliffe et al., 2003). However, such models need further parameterising with species specific rates of crossing the myriad of matrix types, information that is simply not available for most species. Even if this information were available, what implications it would have for population and community responses in fragments would likely still remain elusive (Harrison and Bruna, 1999). Accounting for the behaviour and dispersal abilities of individuals of a particular species is rarely achieved forcing an underlying level of generalisation in most models (Burel and Baudry, 1995, 1999).

5.2. *The focal species approach*

One approach to the use of models in defining habitat networks is to identify ‘Focal Species’. Focal species models use threat based indicators, based on habitat requirements of species sensitive to fragmentation of a particular habitat. The requirements of the focal species are used to provide management guidelines for the reconstruction of fragmented landscapes (Lambeck, 1997).

A number of shortcomings have been noted with the focal species approach. Inherent is the assumption of nestedness, i.e., a landscape that is designed to meet the requirements of the most demanding species will encompass the requirements of all other species that are similarly threatened (e.g., Bani et al., 2002). Species that are differentially sensitive to a threat are assumed to form a nested hierarchy with respect to that threat (Freudenberger and Brooker, 2004). Thus, it is assumed that the most sensitive species requirements will therefore act as an umbrella encompassing less sensitive species needs (Simberloff, 1998). However, interactions between a range of threats may act to confound species response disrupting nested relationships. This assumption is rarely tested, particularly across taxa (Jeanneret et al., 2003). Full appraisal would require an assessment of all threats operating at the landscape scale and assessment of how a wide range of taxa would respond to these threats (Freudenberger and Brooker, 2004). The large data requirements needed for full cross-taxon assessment act as a barrier to further development (Lindenmayer et al., 2002).

5.3. *Predicted species distributions and population viability assessment*

New landscape links can also be defined using predicted species distributions or population viability analysis (PVA) (see Table 1 for example). Predicted species distributions (e.g., Jennings, 2000) are used as an alternative to survey data with the aim of side-stepping the uncertainty associated where survey data are incomplete (Wilson et al., 2005). However, the various methods used to predict species presence can define very different reserve networks (Wilson et al., 2005). Population viability analysis can support decision making in the design of alternative land use scenarios (Frank, 2004) by allowing alternative landscape scenarios to be simulated, assessed, compared and ranked according to their effect on populations (e.g., Baguette and Schitckzelle, 2003). But, see Verboom et al. (1993), Ralls and Taylor (1997) and Baguette et al. (2000) for weaknesses with this approach. It appears that there is great potential for linking population dynamics models with spatially explicit models to inform network development. Yet, Donahue et al. (2003) note that population dynamics models rarely contain data on organismal movement, and highlight the need for more detailed investigations on inter-patch movement and influence on population dynamics.

All the approaches described in this section have great potential to inform land managers on where best to target resources to restore connectivity. However, all have the same characteristic of only being as good as the data on which they are based and that a lack of autecological data weakens their usefulness. Models have the ability to increase in complexity, based on detailed scenarios, land cover information and user defined generic species attributes. Yet, our inability to validate outcomes of even the most simplistic models can also undermine their credibility. The following section explores the development of methodologies, including some using techniques described here, for defining networks that increase connectivity.

6. **Methodologies used to inform the increase of connectivity in fragmented landscapes**

A number of methodologies have been developed to plan increased connectivity of forests in Europe, most of which employ some form of spatial modelling, but vary in the complexity of that modelling (Table 1). Multi-criteria approaches have been used frequently. For example, in Snowdonia, UK, Gkaraveli et al. (2004) classified a land cover map as either suitable or unsuitable for conversion to woodland, based on nature conservation objectives, landscapes, archaeological and agri-economic constraints. The potentially suitable areas were then evaluated using a multi-criteria model, with criteria including woodland conservation status, distance from biologically valuable woods, elevation, topography and conflict with other habitats. BEETLE is a modelling tool for measuring size, arrangement and function of wooded and open habitat networks using a generic focal species approach and evaluation of matrix permeability (Latham et al., 2004; Ray

et al., 2004). The Dutch model Landscape ecological analysis and rules for the configuration of habitat (LARCH) determines ecological networks for specific species in a patchy landscape and assesses the sustainability of these networks (Verboom and Pouwels, 2004).

When autecological information is available for a species, very detailed scenarios can be developed. Holloway et al. (2003) identified clusters of woodlands suitable for and within dispersal distance of the heath fritillary (*Meliticta athalia*), and suggest that this process could be repeated for each UKBAP species, should sufficient autecological and habitat data be available. In Finland, Kurttila et al. (2002) adopted a landscape scale planning approach to aggregate old forest patches to reverse fragmentation through forest operations.

7. Additional considerations

7.1. Species movement

Individuals move in different ways at different stages of their life thus using and being influenced by landscape patterns and changes to varying degrees. It is helpful to consider these different types of movement and the potential for landscape modification to influence these movements in fragmented landscapes.

Local movements are within the home range of an individual, they may be to avoid predation, or to optimise living conditions (Jongman, 2004). For example, foraging will cause an individual to move short distances often on a daily basis. There is evidence that some species (generally ubiquitous but sometimes quite dispersal limited (e.g., dormice, carabid beetles)) will use existing links for such movement and even for residence (Burel, 1996; Eden and Eden, 1999). Thus recent woodland, corridors and hedgerows are effectively increasing the home-range of these species. However, it is likely that these structures are perceived to be lower quality habitat for some species, but sufficient to help sustain local populations by providing additional resources.

Migration is regular movement on a seasonal basis, typically over long distances and en masse (Jongman, 2004). Habitat fragmentation can have major impacts on migrations, yet most examples are confined to North America. In the UK, there is anecdotal evidence of fences interrupting seasonal red deer movement between open hill and forest (Latham, personal communication, 2005). Such disruptions to movement during migration could have severe implications to species persistence in light of climate change.

Dispersal is movement away from place of birth and often from the family group to a new reproductive site. It is generally one-way (Jongman, 2004). Disruption of dispersal through fragmentation is considered to be the principle cause of biodiversity decline, which policy is determined to reverse. Increasing connectivity may also increase local movement that may be equally as important for species persistence.

To form a basis for current conservation planning one must speculate which functional groups of dispersing species increasing connectivity may benefit. The groups are best

identified by using responses to landscape structure (Wiens et al., 2002). Species with strong powers of dispersal (for example, generalist woodland birds) and more ubiquitous mammals will move to new habitat with little regard for the nature of the matrix in between. Species with very limited dispersal powers, and confined to very specialist habitats within mature woodland, would have little likelihood of movement to new patches for a variety of reasons, not just linked to weak dispersal powers (discussed in more detail in Section 7.2). Moreover, should such species use new links, the resources or conditions required for successful establishment might well be missing. It is the species of intermediate dispersal ability, hindered by hostile matrix (i.e., intensive land uses) surrounding patches, but with the ability to disperse through new woodland and other semi-natural habitats that should be the target of 'reversal'. This cohort of species must also be able to move in sufficient numbers and have sufficiently catholic habitat requirements that colonisation occurs with sufficient frequency for movement to be beneficial. These species would also be likely to be able to survive in, and develop a metapopulation structure at the landscape scale. Key questions for landscape planners should be; which species fall into this category? How many of them are there?, and are they of such conservation significance that they justify the attention and resources they are *de facto* receiving?

Fragmentation can selectively affect different species (Kruess and Tscharntke, 1994; Zabel and Tscharntke, 1998); for example, differential dispersal rates can result in a simplified community membership (Jacquemyn et al., 2001; Butaye et al., 2001). Many examples of work from restoration ecology indicate that once community modification has occurred, a shift back to the original membership may not be likely even if a diversity of habitats develop. For example, disturbance in habitats during restoration has been shown to lead to a change in ecological structure and functioning of aquatic communities (Carlson et al., 1990; Spence et al., 1996). Disturbance can result in species replacement and adjustments of the functional characteristics in the community (Minshall et al., 1983; Power et al., 1995; Rader, 1997; Hershey and Lamberti, 2001). Muotka and Laasonen (2002) studied streams in Finland that had been restored following channalization. The streams failed to support expected communities after significant recovery time, because mosses, necessary to trap resources required by parts of the community had been negatively affected by restoration. Community structure remained simplified, similar to its pre-restoration state. It would appear that even if physical habitat structure is in place, and assuming that species are able to reach the new habitat, a functional community may take quite some time to develop. To understand implications of fragmentation for community functioning much information on demography and interactions within patches (Harrison and Bruna, 1999) and new and newly restored patches is required.

7.2. Negative effects of increasing connectivity

Networks, especially those with corridors, may function as conduits for undesirable species or disease spread (Hess, 1994),

before woodland species are able to utilise them. For example, there is concern that invasive non-natives might gain access to previously isolated strong holds of native species (e.g., grey squirrel colonising red squirrel strong holds and transmitting squirrelpox). Furthermore, concentrating woodland species into corridors may make them more vulnerable to predation (King, 1989), stranding through rapidly changing environmental conditions, edge effects or isolation through careless corridor design (e.g., encountering gaps or barriers, roads).

Guidance in network design is therefore critical to their success, yet cannot be given without an indication of properties the most vulnerable species require. To date, guidance on network development, including corridors, is sparse. If corridors are to meet the requirements of most woodland species then design must be based upon the requirements of the most sessile species. It is acknowledged that corridors must be sufficiently wide to maintain interior habitat quality if they are likely to be used by poor dispersers (Noss, 1983). Buckley et al. (2002) suggest that edge effects will penetrate about 50 m into woodlands, so a corridor should be over 100 m wide before it is likely to contain some interior habitat. The unique landscape context into which the corridor or network is to be located will also influence species requirements. In the absence of firm guidance ‘as wide as possible’ is the most common rule of thumb for corridor design (Bennett, 2003) to increase likelihood of resource provision for dispersing individuals (Lindenmayer et al., 1993).

7.3. Long distance dispersal

Another consideration for the utility of reversing fragmentation by increasing links is the significance of rare long-distance movements made by individuals (Cain et al., 1998; Jacquemyn et al., 2003). Such long distance dispersal events may play a key role in allowing species to keep pace with shifting ranges in fragmented landscapes (Ozinga et al., 2004), for example, as a result of climate change (Opdam and Wascher, 2004; Smithers, 2004; Pearson and Dawson, 2005). Such events may be especially important for the survival of sedentary species associated with ancient woodland, especially plants (Takahashi and Kamitani, 2004). Observations of these extreme long distance dispersal events remain elusive (Clark et al., 1999; Higgins and Richardson, 1999; Nathan et al., 2003; Dolman and Fuller, 2003) often due to the inability to detect such events through experimental design (Schneider, 2003). However, there are some notable exceptions. At least four species of saproxylic insects, previously considered to have poor dispersal powers, have experienced a rapid expansion of their range. This has been due to more favourable habitat becoming available as a result of climate change in the last few decades (Alexander, 2003, 2004), rather than a concerted effort to improve habitat connectivity.

Long distance dispersal events may have implications for community composition, illustrated by changing community composition along environmental gradients (Ozinga et al., 2004). If such movements are, as limited evidence suggests, more important for dispersal than initially anticipated, then the

value of the work to improve connectivity, based on short to medium distance movements, has to be reviewed.

7.4. Colonisation and habitat quality

Reaching a new location is only the first stage in the colonisation process; habitat requirements still need to be met sufficiently that viable populations will develop (Honnay et al., 1999; Baguette et al., 2000; Dolman and Fuller, 2003). Otherwise, small population sizes when combined with isolation effects have been found to increase extinction through stochastic events (Newman and Pilon, 1997). Thus, attempts to increase connectivity must also consider the role of habitat quality (including the role of habitat management). New woodlands will lack complex habitat structure of more established habitats, providing fewer niches in which a complex woodland community can develop. Previous land-uses may reduce quality of newly created or restored woodland for some time. For example, Honnay et al. (1999) found that enriched soil chemistry (phosphate) formed a barrier to woodland plants colonising reforested abandoned agricultural land.

8. Discussion

This review has indicated a lack of firm empirical evidence that species increase following attempts to increase connectivity in fragmented woods and also an over-emphasis of the importance of habitat fragmentation per se as a threat to biodiversity. Biodiversity losses are most likely a result of the amount of regional habitat loss rather than fragmentation (Harrison, 1994; Fahrig, 1998, 2001, 2003; Harrison and Bruna, 1999; Rosenberg et al., 1997; Trzcinski et al., 1999). The small effect of fragmentation per se suggests that biodiversity loss cannot be significantly reduced by adjusting habitat pattern (Fahrig, 2001). Species may well benefit from actions intended to increase connectivity, but the current lack of evidence needs addressing. The process of addressing evidence gaps could also include an examination of possible alternative strategies for reducing biodiversity loss.

The conservation and expansion of existing woodland by establishing new woodland next to mature woodlands may increase survival probabilities of existing populations particularly of more sessile species (Forman, 1995; Woodland Trust, 2000; Jacquemyn et al., 2002; Smithers, 2004; Watts et al., 2005) thus increasing the probability of dispersal. The consolidation and enhancement of the resilience of biologically valuable woodlands can also be achieved through managing surrounding habitats less intensively (Smithers, 2004). By increasing the quality of the matrix, isolation effects (Carroll et al., 2004), extinction rates and edge effects in fragments (Ricketts, 2001; Rodewalde, 2003) can also be reduced. Dispersal is also more likely by increasing the availability of resources required by woodland species, increasing cover to avoid predation, and developing a moderated microclimate to improve the survival rate of dispersers (Fahrig, 2001). Semi-natural habitats such as stream-sides and riparian strips,

meadows, bracken, hedges, ungrazed pasture and scrub have been shown to provide suitable conditions for woodland species (Boycott, 1934; Eden and Eden, 1999; Peterken, 2002). Improving matrix quality in fragmented landscapes by reducing land use intensity, increasing cover of semi-natural habitats, protecting existing semi-natural habitats, connectivity and refugia and increasing heterogeneity are often achievable through agri-environment schemes (AES) (Donald and Evans, 2006). The precautionary stance of protecting existing connectivity will also ensure a basis for networks exists should a firm evidence base develop. Furthermore, other fragmented habitats are also likely to benefit, by not becoming further fragmented by new links and intensive land uses.

Buffering existing woodlands and enhancing matrix quality are likely to take less time to yield conservation benefit than forest network development as habitats involved will mature more quickly (Mortimer et al., 2000; Webb, 2002; Buckley et al., 2002; Walker et al., 2004). This is an important consideration in the light of the predicted impact of climate change on isolated species. Yet the habitats concerned are still only likely to benefit species with intermediate dispersal powers, for example, reptiles, amphibians, mammals and some invertebrates (Donald and Evans, 2006). Solutions are not apparent for species more restricted to woodlands, especially to the pressing issue of 'enhanced isolation' through climatic factors (Pearson and Dawson, 2003). Increasing connectivity is however, unlikely to be of benefit (Hulme, 2005).

I would recommend that research areas below are considered to develop the evidence base prior to directing resource into the development of networks that focus extensively on increasing links (With, 2002):

- (1) Understanding mechanisms with which taxa with low dispersal (for instance ancient woodland specialists) move needs particular attention, specifically:
 - What difference does source population size make to dispersal curves?
 - How many individuals are required to disperse to avoid (meta) population decline?
 - What can we deduce/observe about rare long distance dispersal events for these species?
- These insights would enable judgements to be made on the likelihood of species using new linkages and thus the utility of incorporating their requirements into designs.
- (2) How, and how frequently do individuals (representing species and taxa of a range of dispersal abilities and woodland specialisation) utilise new woodland and semi-natural habitats for dispersal in fragmented landscapes? How mature do new landscape elements need to be for different taxa to use them for dispersal?
 - (3) An evaluation of the role of increased links in mitigating against climate change impacts is vital (Pearson and Dawson, 2005), as findings are likely to suggest further adjustment of policy to prevent future biodiversity loss.
 - (4) An understanding of the level of community complexity present in established woodlands representative of the

desired end-point of habitat restoration/creation. The development of models to predict likely community structure in these new and restored habitats and landscapes may be possible in the future.

- (5) Management guidelines need to be developed to ensure suitable habitat and niches are available in newly created/restored woods, so colonisation rates are maximised. This is critical especially in habitat networks that incorporate new woodlands.
- (6) Observational and experimental studies, and monitoring of landscapes where connectivity is being increased would enable the development of empirically motivated theory, beginning with real fragmentation scenarios and the explanation of real observations as their goal (Harrison and Bruna, 1999). Time taken for species to move through restored landscapes (using woodland links versus increased semi-natural cover and heterogeneity) and for viable populations to develop, plus the legacy of on-going declines from previous fragmentation need to be monitored. Well designed monitoring programmes will identify which species are colonising naturally, which may need introduction, whether undesirable species are also colonising (Newton and Smith, 1998) and the role of existing semi-natural habitats in enhancing dispersal. Recommended methodologies already exist (for example, Beier and Noss, 1998).
- (7) Information from (6) would ensure expectations of land managers are informed and sufficient time is allowed for project evaluation. Also, when coupled with climate change data and associated habitat change projections, movement rate data would enable an evaluation of network utility for different species groups in face of climate change. A greater understanding of the persistence of (meta) populations through time and space is also vital to enable landscape planners to develop robust networks in light of range shifts (Opdam and Wascher, 2004). Of special importance is an understanding of the role of spatio-temporal connectivity in species persistence in fragmented landscapes (e.g., Hope and Humphrey (2004).
- (8) It is plausible that species dispersal may differ between edge and centre of ranges. Long distance dispersal events at invasion fronts need to be understood in relation to spatio-temporal habitat availability and in the presence of environmental stress (e.g., climate change). For example, are mechanisms that previously aided dispersal, identifiable and able to persist now and in the future? The likelihood of genetic bottleneck development would also need to be evaluated in these and other studies.

These recommendations require re-focussing on autecological and community ecology studies. This need for a shift of focus is becoming more apparent as this and other reviews indicate (Harrison and Bruna, 1999; Bailey and Pryor, 2004; Davies and Pullin, 2006). Models are evolving into more and more sophisticated, multi-parameter tools, yet are unable to increase in predictive power and accuracy until the paucity of data required to parameterise and validate them is addressed.

They will provide land managers a realistic time frame within which benefit to biodiversity is likely through restoring connectivity.

The purpose of restoring connectivity must be clearly defined. At this point we enter a philosophical debate regarding what is we are trying to restore. Frequently documents state that it is the restoration of biodiversity that we are striving towards. Yet, biodiversity can only become a target when it is clearly defined (Failing and Gregory, 2003). If we use the most widely accepted definition used by the Convention of Biological Diversity (CBD, 2003) then it is likely we would be aiming for a wide diversity of species and habitats within woodlands. But, I would argue that what we are really seeking to achieve is a compliment of species that will develop into a functioning woodland community with the full range of natural processes and associated structural diversity represented (Ormerod, 2003). New woodlands will quite quickly develop high numbers of the ‘usual woodland suspects’ (Honnay et al., 2002a), both native and non-native that are not suppressed by fragmentation. Yet this does not seem to be a satisfactory end point for policy implimentation (Simberloff, 2004). If success is measured by inventory of species present, which is often the case in post-restoration monitoring, care must be taken that species richness does not become a surrogate for woodland biodiversity (*sensu* Heilmann-Clausen and Christensen, 2005). If increasing connectivity is to benefit those species most at risk from fragmentation and therefore develop full community membership, more complex strategies such as expanding existing woodlands, even importing specific habitats (e.g., deadwood (Honnay et al., 2002a; Smithers, 2004)) may also be required. Differential dispersal rates alone may ensure that community membership will unlikely reflect that of a ‘representative community’ within the foreseeable future (20–50 years), unless dispersal vectors are also fully restored (Ozinga et al., 2004). Therefore, I would argue that restoring functional woodland community should become the goal rather than biodiversity gain. For this to be achieved we need to draw on community ecology, to define the features required in woodland restoration and develop benchmarks with which we can measure success (see Ruez-Jaén and Mitchell Aide, 2005).

Appendix A

Empirical studies of fragmentation effects on European woodland species.

Effects included in study	Species	Duration of study	Effects found	Reference
Birds				
Abundance and woodland area	Eight breeding bird species	7 years	Higher numbers in smaller woods for seven spp.	Bellamy et al. (2000)
Habitat quality, landscape structure and area	Breeding birds	3 years	Woodland species breeding governed by wood size and isolation	Hinsley et al. (1995a,b), Bellamy et al. (1996)
Habitat quality, landscape structure	Nuthatch	6 years	Isolation, absent from small woods	Bellamy et al. (1998)
Isolation	Nuthatch	3 years	Isolation and area effects, prefer larger patches	van Langevelde (2000)
Fragmentation and habitat quality	Six forest breeding species	2 years	Three species associated with unfragmented woods	Lauga and Joachim (1992)
Area	Bird species	7 years	Area effects	Moore and Hooper (1975)
Area and isolation	Bird species	3 years	Slight area effect, no isolation effect. Hab quality more important	Helliwell (1976)

In conclusion, I would like to underline that I am not arguing that the detrimental processes associated with habitat loss and fragmentation should not be addressed, but that we need to scientifically demonstrate the benefits to biodiversity of increasing connectivity through the development of networks and corridors (Bennett, 2003). This review has highlighted the paucity of research currently available to provide this evidence, but also summarises the many projects that are already developing networks, plus alternative approaches that may be a more risk averse use of limited resources until the evidence base is developed. Monitoring projects described could start to provide important indications to ensure informed application in the future. Through the research areas described it should be possible to further inform the development of habitat connectivity for biodiversity gain.

Interest in increasing habitat connectivity has been catalysed by pioneering research in landscape ecology, but now the resulting discussions are producing far more questions for researchers to address. Policy needs to be evidence-based and delivery needs to be directed by well-founded best practice. However, we have to be realistic and accept that there is such a high level of interest in landscape-scale approaches, and given the pressure to find solutions to biodiversity loss under predicted climate change scenarios, that neither policy nor practice can wait for all the questions raised in this paper to be answered. This means that in the short-term land managers will have to adopt two tactics. Firstly, they will need to rely on ‘first principles’ to guide and underpin strategy development. Secondly, they will need to take an adaptive approach to implementation, and with associated monitoring, modify strategies if outcomes appear not to reflect desired endpoints.

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Appendix A (Continued)

Effects included in study	Species	Duration of study	Effects found	Reference
Fragmentation	Tawny owls	3 years	Change in behaviour, home range size increase, higher turnover in fragments	Redpath (1995a,b)
Area, isolation, habitat quality	Woodland interior specialists	1 year	Isolation and area effects for interior species	Opdam et al. (1985)
Isolation and area	Breeding forest birds	2 years	Isolation effects forest interior spp. Predicted by area.	van Dorp and Opdam (1987)
Area, isolation, vegetation	All birds	1 year	Residents increased with area	Ford (1987)
Fragmentation and habitat quality	All birds	1 year	Isolation effects for woodland specialists	McCollin (1993)
Fragmentation and habitat quality on juvenile dispersal	Nuthatch	2 years	Fragmentation increased dispersal rate	Matthysen et al. (1995), Matthysen and Currie (1996)
Mammals				
Patch size	Mammals and raptors	5 years	No area effect for mammals	Loman (1991)
Habitat age*, and isolation	Dormouse	–	Size effects found	Bright and Morris (1992)
Area, isolation and age*	Dormouse	2 years	Area and isolation effects.	Bright et al. (1994), Bright (1996)
Fragmentation genetic variation	Red squirrel	4 years	Some genetic effects associated with isolation through decreased immigration	Wauters et al. (1994a)
Fragmentation	Red squirrel	2 years	Small, unconnected woods avoided	Wauters et al. (1994b)
Fragmentation	Red squirrel	–	Area effects	Verboom and Apeldoorn (1990)
Fragmentation and area	Red squirrel	1 year	Area effect in unfragmented landscape, isolation in frag.	Celada et al. (1994)
Fragmentation	Red squirrel**	3 years	Gender influence but age of stand best predictor	Andrén and Delin (1994)
Area and isolation	Wood mouse, bank vole	–	Isolation effects	Fitzgibbon (1997)
Isolation and area	Wood mouse, bank voles	–	No isolation effects	Zhang and Usher (1991)
Habitat quality, area isolation, age*	Yellow-necked mouse	2 years	Habitat quality most important	Marsh and Harris (2000)
Invertebrates				
Isolation and area	Woodland specialists	1 year	Area effects found, Isolation effects found for vagile sp.	Shreeve and Mason (1980)
Isolation and area	Woodland moths	1 year	Area and isolation effect found	Usher and Keiller (1998)
Size, isolation and shape	Spiders Beetle	–	Isolation effects found Shape effects found	Usher et al. (1993)
Isolation and area	Coleoptera	–	Strong isolation effects	Welch (1990)
Isolation and area	Carabidae	–	Strong isolation effects in weak dispersers	Opdam et al. (1993)
Age and isolation	Carabidae	16 years	Local extinctions increased by isolation	den Boer (1990)
Age of woodland*	Ground beetles	7 years	Spp. richness higher in ancient woods. No area effects	Assmann (1999)
Area and age of wood*	Molluscs	1 year	Weak area effect found and association with ancient woodland	Wardhaugh (1995)
Plants				
Patch size	Woodland sp.	–	<1.5 ha no woodland species, no isolation effects	Usher et al. (1992)
Isolation, woodland age*	Woodland sp.	2 years	Some isolation effects	Dzwonko (1993)
Isolation, woodland age	–	2 years	Some area and isolation effects, plus patch quality	Dzwonko and Loster (1992)
Hab quality, soils, isolation and area	All species	1 year	No area or isolation effects	Helliwell (1976)
Area, isolation and wood age*	Woodland vascular plants	10 years	Isolation effects	Peterken and Game (1984)
Colonisation rates of recent woodlands	Vascular plants	>100 years records	Failure to colonise by some wood species	Harmer et al. (2001)
Area, past landscape change and dispersal rates	Vascular plants	1 year	Dispersal influences community composition, age and area related.	Jacquemyn et al. (2001, 2003), Butaye et al. (2001)
Colonisation rates of recent woodlands*	Vascular plants	1 year	v. slow colonisation of recent woods	Brunet and von Oheimb (1998)

(–) Information not available, (*) ancient woodland status of woodlands explicitly considered, (**) radiotelemetry was used to determine movement of individuals.

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