Forestry Commission

Research Note

Biodiversity in fragmented landscapes: reviewing evidence on the effects of landscape features on species movement

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Maintaining species' movement around landscapes is considered important if we are to conserve populations of many species and help them adapt to climate change. Particular features in the landscape have the potential to hinder or facilitate species movement. As each species interacts with the landscape differently, it can be hard to extract general patterns to include in planning and management guidance. This Research Note draws information together to look for such patterns. Firstly, we conducted a systematic review of the scientific literature. This relatively new technique in environmental sciences allowed a quantitative meta-analysis of specific types of evidence, as well as a traditional qualitative synthesis of the wider information available on UK species. Our review confirmed that, for those species for which there is evidence, most prefer to move through landscape features similar in structure to their breeding habitat. For example, woodland species tend to prefer to move through habitats which have some elements of vertical structure. However, we also established that species are idiosyncratic and their responses have various behavioural causes. For example, some landscape features that have a contrasting structure with a species' breeding habitat may provide better shelter from predators, while others may act as good visual cues for navigation. Secondly, we summarise species-based landscape ecological studies carried out by Forest Research over the past few years.

Forest Research

Introduction

Habitat fragmentation and the subsequent increasing isolation of populations is one of the major contributing factors to the loss of biodiversity. The movement of individuals among small, isolated populations is therefore an important ecological process in fragmented landscapes (Tischendorf and Fahrig, 2000). These movements may maintain genetic diversity, rescue declining populations, re-establish populations, and maintain networks of populations through metapopulation dynamics (Hanski, 1998). In addition, climate change is likely to mean species will need to move polewards, to higher elevations or to different areas with suitable microhabitats. Some species will have difficulty keeping up with the movement of areas with suitable climates if their habitat is fragmented and the intervening landscape impedes their progress.

In the previous Information Notes on 'Evaluating biodiversity in fragmented landscapes' (Watts *et al.*, 2005; Watts *et al.*, 2007 and Eycott *et al.*, 2007) we showed how features in the wider landscape could potentially impact on species movement, for example by modelling species–landscape interactions. However, many of these modelled interactions were based on limited empirical evidence, expert opinion and general principles. There was interest in seeking to support models and concepts used in policymaking with a thorough review of the evidence base.

Landscape features and species movement

Various features in the landscape, for example hedgerows and woodlands, are increasingly recognised as impacting on species movement and exacerbating or relieving the impacts of habitat fragmentation (Kupfer *et al.*, 2006). The effect of a landscape feature on movement is species-specific and depends upon species' dispersal abilities combined with the composition of the surrounding landscape. The same set of landscape features may allow free movement for some species, while hindering movement for others. Given the countless combinations of landscape features and species, there is unlikely to be adequate evidence available for every situation. Therefore the aim of this review was to draw general conclusions from a range of landscape and species studies.

A review of the evidence

We utilised a systematic review technique in order to consider the quantitative and qualitative evidence for the impact of landscape features on species movement. This technique was recently developed for conservation and environmental management from the medical evidence review model (NHS Centre for Reviews and Dissemination, 2001; Pullin and Stewart, 2006). Systematic review strives to minimise error and bias through an exhaustive search of peer-reviewed journal publications, grey literature and unpublished research findings. The process is planned beforehand and a protocol written with any assumptions and generalisations made clear, so that the review can be repeated at a later date if necessary.

Our research question was, '**Which landscape features affect species movement?**' Within this question, we focused on the features comprising the landscape between patches (the matrix), and species movement that was measured directly (e.g. by continuous observation, radio-tracking or marking individuals). This focus meant that all the studies we considered were on animals, mostly vertebrates and winged insects.

We performed a keyword search of online journal databases, internet search engines and research agency websites (see Box 1

Box 1 – Keywords and search terms

The keywords we used were organised into Boolean searches, which make use of AND and OR clauses to make the search narrower or wider. The formulation of subsets of spatial and subject context words helped to ensure that only the most relevant studies were identified. The search terms were as follows:

Intervention:

corridor*	link*	connect*
barrier*	network*	mosaic*
bridge*	"buffer zone*"	"spatial pattern*"
"stepping stone*"	patch*	heterogen*
highway*	edge*	permeab*

Outcome:

movement	migration	immigration
dispersal	coloni*	emigration
isolation	invasion	

Spatial context:

habitat	matrix
landscape	fragment*

Subject context:

biodiversity	species	metapopulation*
conservation	population*	

An asterisk (*) indicates a 'wildcard', which allows the database or search engine to look for multiple words that have different endings, e.g. connect* captures [connect OR connected OR connection OR connectivity OR connectedness]. Speech marks (" ") around two words restricts the search to where that phrase occurs (for example, "buffer zone*" picks up 'buffer zone' and 'buffer zones' but not 'buffer the zone'.

for keywords and search terms). We retrieved references to 11 270 articles, reports and web pages, which were then examined for relevance. First we rejected over 4000 from their titles, having inadvertently retrieved articles on palaeontology, chemistry and molecular biology. Over 6000 references were then rejected after reading the abstracts or summaries as many were reviews of other papers, or were about modelling with no original data in them. 525 articles remained, of which 315 were found to fit the inclusion criteria set at the start of the project.

These 315 articles were then classified according to the experimental design and landscape feature tested. From this classification we were able to select groups of studies which had designs similar enough for statistical testing using meta-analysis. The studies we included were very variable and so only relatively small groups could be analysed together.

Summaries of all the studies used in the meta-analyses are provided in Appendix 1 of the full systematic review report, published at www.environmentalevidence.org/SR43.

Quantitative meta-analyses

Meta-analysis is a set of statistical techniques that can be used to combine and summarise quantitative results from individual studies within a systematic framework. This provides greater statistical power* and scope for exploring the factors explaining variation in the results (Lipsey and Wilson, 2001). Meta-analysis is more than just 'vote-counting' the numbers of studies reporting positive or negative outcomes. To work out the overall effect, the size of each study is also taken into account. The method does not utilise the absolute difference in the number of individuals responding to the 'treatment' (like a new hedgerow, or a field headland), but the relative number compared with how many were tested in each group. This is termed a risk ratio. Figure 1 illustrates how the effect of different landscape features on species movement is calculated. A risk ratio of 1 equals no effect, whereas a risk ratio greater than 1, as in Figure 1 where it is 1.1, indicates that the landscape feature more similar to the habitat is the one where there is more movement.

Within our overall research question '**Which landscape features affect species movement?**', we were able to answer three specific sub-questions, each related to a particular experimental design and landscape feature.

(A) Do corridors increase the number of animals that move between patches?

If individuals can move from one patch to another, they can colonise new habitat and recolonise vacant patches, as well as exchange genes which may help them adapt to changes in their environment. By corridors, we referred only to linear patches of the same vegetation as the breeding patch but *too small or narrow to act as a breeding patch itself*. This was a relatively strict definition compared with some reviews.

Figure 1 An example of the calculation of a risk ratio, where four out of the six mice initially marked in one woodland are then found to have crossed the surrounding plantation, and three out of the five mice initially marked in another woodland are then found to have crossed the surrounding corn field, making a risk ratio of (4/6)/(3/5) = 1.1

We analysed nine studies and found that, as the mean risk ratio is greater than 1, there was a significant increase in the number of animals that move between two patches if there is a corridor between them (Figure 2). This effect was stronger if the animals had to choose between moving through a corridor or whatever else (i.e. the matrix) was surrounding the patch, rather than experiments where pairs of patches with corridors were compared with pairs of patches without.

(B) Do matrix features that are structurally similar to the breeding habitat increase the number of animals that move between patches?

This question is similar to that of Question A, but in this case the vegetation between the patches was not the same vegetation as the breeding patch; this is the situation portrayed in Figure 1. Studies included in the analysis for this question had two (or more) pairs of patches, with each pair separated by different vegetation. For example, Baum *et al.* (2004) looked at planthoppers, which live on native prairie grass in the USA, and tested whether the they were more likely to move from one patch of prairie grass to another if there was non-native grass or bare mud between the two. We were testing the hypothesis that as species may be adapted to move within their breeding habitat, they may prefer to move through matrix that has a similar structure to their breeding habitat.

The different matrix types tested did not significantly affect the number of animals that moved between patches, in the ten experiments we analysed (Figure 3), as the mean confidence interval (diamond) crosses the line of no effect (risk ratio 1).

*Power, in statistical terms, refers to the effect that increasing the number of samples has on the likelihood of detecting a significant effect.

(C) Do matrix features that are structurally similar to the breeding habitat increase the number of animals that emigrate from a breeding patch?

Analysis C was intended as an expansion of Analysis B, in order to expand the number of studies included and so gave the analysis more 'power'. Emigration is the act of leaving a patch, so many of the studies in this group observed individuals within the surrounding matrix rather than in other patches.

In contrast to Analysis B, the presence of a matrix type more similar to the breeding habitat did increase the emigration rate (Figure 4). This difference was particularly strong in experiments where the two matrix types tested were very different. However, it is not clear whether there is a difference between Analysis B and Analysis C because more studies could be included (20 instead of 10, though this did lead to a wider range of species studied), or because matrix land cover affects whether individuals leave a patch but does not affect whether they go on to find new patches.

Figures 2–4 Forest plots of the different studies included in each meta-analysis compared with one another on the same scale. Solid boxes represent data points (studies) and the larger the box, the more replicates there were in the study. Horizontal lines are each study's associated 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and where boxes lie to the right of that line, corridors increased the rate of movement between patches (in boxes lying to the left of the solid line, corridors actually decreased movement). The dashed vertical line represents the mean risk ratio (the diamond represents mean confidence limits) and as the mean risk ratio is greater than 1, overall species are more likely to move between patches with a corridor than without a corridor. Superscript numbers indicate the sources of original data – see References (pages 7–8).

Figure 2 Corridor studies included in Meta-analysis A. Note that the study of bees moving between forest clearings had a small sample size which is why it had a very high standard error.

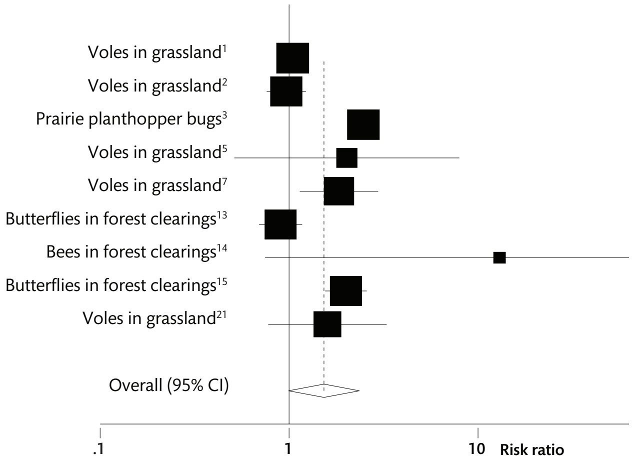


Figure 3 Individual movement data for Analysis B, showing rates of movement between patches separated by matrix more or less similar to their 'home' habitat.

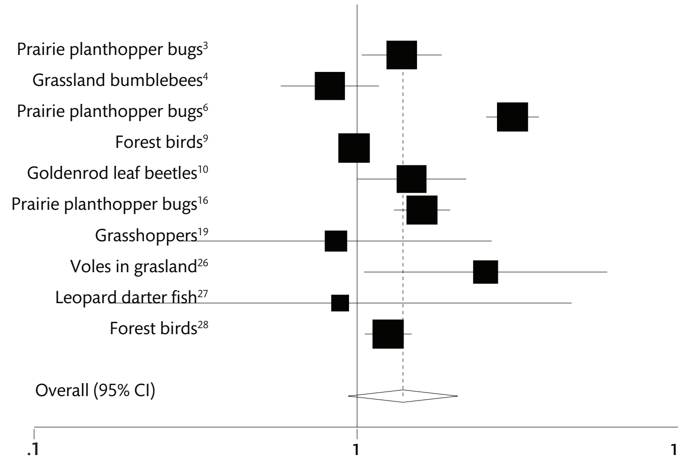
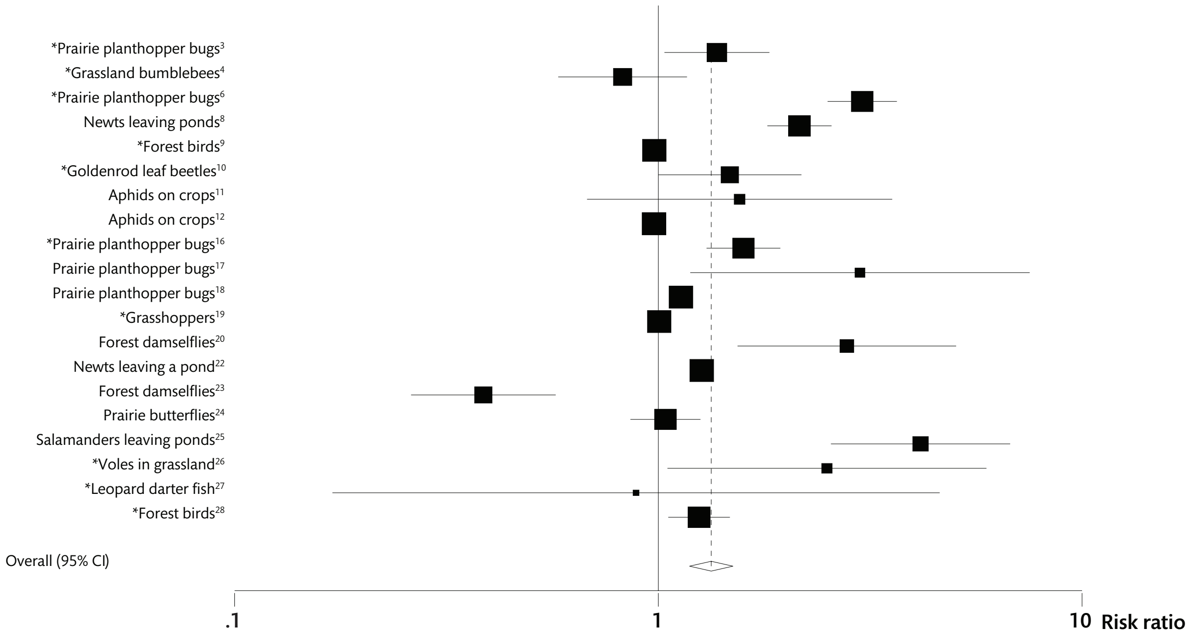


Figure 4 Risk ratios for Analysis C, comparing individual emigration rates from patches surrounded by more favourable or less favourable matrix, aggregated into each study. Studies marked with a * are also in Analysis B.



Qualitative analysis of UK species data

In order to look at more than just the 29 papers that were included in the meta-analysis, we also looked at the 67 papers which included data on UK species. They were summarised into tables and sorted according to different attributes: species group, home habitat, landscape feature, and experimental design.

This revealed that most studies picked up by the systematic search were on winged insects (followed by large herbivores and then rodents) and very few were on freshwater invertebrates or reptiles. The papers included information on 20 UK Biodiversity Action Plan priority species and ten 'recent arrival' non-native species. Woodland species accounted for nearly half of the studies, and wetland and marsh habitats were under-represented.

There was no single landscape feature that dominated the papers though many studies compared two different matrix types, in a similar fashion to Analyses B and C in the meta-analysis. There was no single most common experimental design either, with each design adapted to suit the species and situation.

Table 1 summarises the findings by landscape feature. This is a useful general guide, but note that unlike the meta-analysis, the summary is based the conclusions provided by the papers' authors, with no accounting for the size or rigour of the studies. A list of all the studies used and detail of the methods and outcomes is provided in Appendix 3 of the report at www.environmentalevidence.org/SR43. Table 2 summarises just the data for forest or woodland species.

The information we retrieved during the review suggests that matrix elements that are more structurally similar to the breeding patches of the species do provide increased likelihood of movement or dispersal. Exceptions occur, in particular where the species:

- is very mobile and does not react to the matrix (e.g. large birds);
- uses more permeable features if present but still disperses at the same rate (e.g. some beetles);
- uses features structurally dissimilar to their home habitat for cover (e.g. some amphibians) or because they do not impede physical locomotion (also noted in amphibians).

Table 1 A qualitative summary of 67 papers which looked at the impact of different matrix features on the movement of UK-resident species. The summary is based on the conclusions provided by the authors.

Landscape feature	Outcome summary
Corridors (same vegetation as home habitat)	**Positive** outcomes reported (few studies but all well controlled).
Barriers built by people	**Negative** impacts of roads on movement are more likely for larger/multiple roads. Many different types of weirs have **negative** impacts on fish movement.
'Animal crossings' and tunnels under roads	Often avoided, but their presence can reduce animal–vehicle collision rates. The type of tunnel preferred depends on species.
Linear matrix features similar to home habitats	Mostly **positive** outcomes over a range of studies. Some species seem to follow linear elements to navigate (this includes elements of a dissimilar structure to their home habitat).
Patch edge shapes	Little evidence found in this review. Edge impacts on dispersal have been reviewed elsewhere, e.g. Parker *et al.* (2005).
Direct comparisons of matrix types (not including linear features)	**Positive** responses to matrix types more similar to the home habitat reported for butterflies and amphibians. Preferences may be based on protection from predation. Localised movement of mammals less impacted by matrix. Evidence for other invertebrates is a mixture of **positive** and neutral.
Studies of complex landscapes which include a range of matrix features	Animals making large-scale movements respond to matrix: evidence from deer and birds. These movements may be related to resource availability or perceived threat.
Matrix heterogeneity (how mixed-up the different features are)	Less evidence. Deer and bush crickets moved further and were more likely to move in more fragmented landscapes.

Table 2 A qualitative summary of a subset from the 67 papers used for Table 1 which looked at the impact of different matrix features on the movement of UK-resident woodland or forest species. The references for the statements can be found in the original report at www.environmentalevidence.org/SR43.

Feature	Response
Barriers built by people, 'animal crossings' and tunnels under roads	Rodents cross fewer wide roads than narrower ones. Generally, mustelids and foxes will only use wider, vegetation covered tunnels. Badgers, hedgehogs and deer either rarely enter or entirely avoid tunnels. Breeding birds disperse away from roads and further where roads are present. One small study suggested localised movements of bank voles were not influenced by presence of gravel roads.
Linear features similar to home habitats.	A large study shows that woodland birds have preference for woody linear features (hedges) in the matrix. Carnivorous mammals also use woody linear features for movement. Grey squirrels cross hedge gaps but dormice do not.
Patch edge shapes	Smaller passerines dislike crossing edges more than larger ones.
Direct comparisons of matrix types (not including linear features)	Birds do respond to the matrix, with a reluctance to cross rivers. Woodland beetles respond to matrix structure, preferring shady habitats, but can go through quite open habitats, for example meadow, and often move faster over more open ground. One small study suggested localised movements of bank voles were not influenced by the matrix.
Studies of complex landscapes which include a range of matrix features	Deer, owls and voles and woodmice all avoid crossing arable, red squirrels less so.

New evidence from research projects

There is clearly some scope for more analysis of the review data, but it is clear that there are many gaps in the information available from existing studies. Forest Research are involved in a number of projects investigating how species interact with the landscape. The research has focused on woodland species or species of open habitats within woodland. Some of these projects are included in the table of evidence from the systematic review, and others begin to fill the evidence gaps. Some of the preliminary findings are summarised over the next few paragraphs.

For example, we have found in collaboration with Butterfly Conservation that the small pearl-bordered fritillary butterfly operates as a metapopulation within a large conifer plantation in north Wales, breeding in and moving between small patches of wet grassland scattered throughout the forest. This may have implications for future forest planning and management.

On the Isle of Wight, we have used wood crickets as a representative for fragmentation-sensitive deciduous woodland species. Wood crickets are found in discrete populations within woodlands, in suitable patches of dappled shade and leaf litter. A joint project with a PhD student from Bournemouth University (Brouwers, 2008) confirmed that there was limited recorded movement of wood crickets between fragmented populations: studies of dispersal and perceptual range revealed movements of around 50–60 m from the woodland edge through favourable habitats (e.g. semi-natural landscape features). At Forest Research we are evaluating the genetic similarity of these discrete wood cricket populations to investigate the degree to which landscape features may have either promoted or impeded their movement in the past.

Technological advances have been a great help in understanding species movement. The use of PIT tags (similar to those used for 'chipping' pets) and radio-tracking have revealed that the edible dormouse is spreading through the Chilterns and can travel over a kilometre between nesting and hibernation sites. Lesser horseshoe bats were radio-tracked by a PhD student from Bristol University, in a project partly funded by the Forestry Commission, in different parts of southwest England and south Wales. This work has confirmed the importance of linear, woody features to bat movement in landscapes ranging from intensive agricultural to upland marginal (Knight, 2006).

Current projects aimed at filling other evidence gaps include a collaboration with the University of Cumbria to investigate the impact of the landscape on the movement of grey squirrels through the use of historical records, genetics and micro-GPS units. Publication of these studies should help future reviewers fill some of the evidence gaps.

Conclusions

There is evidence that matrix features similar in structure to breeding habitat patches increase species movement. The evidence base is broad and heterogeneous. The overall strength of the evidence is fairly low, which may be at least partly accounted for by the variability in individual species' responses to landscape features, and also by the relative infrequency of dispersal events. Some of the most abundant evidence was for the relative importance of linear features to movement. The evidence supports assumptions made in a range of modelling studies (described in Watts *et al.*, 2005).

For those involved in designing and planning landscapes, it is worth considering whether the design should account for many species or only a small number of protected or priority species. Population size can be increased by improving, buffering and extending existing habitat patches or creating new ones (Watts *et al.*, 2005). Our review suggests that for a range of species, a variety of linear features with similar vegetation structures to the habitat patches should be created or maintained, in order to increase movement rates between those patches. This review has therefore supported many of the types of actions already used in practice, such as maintaining shelterbelts between woodlands, or creating wide grassy rides through plantations in heathland areas. However, if the focus is on a few species, the existing literature should be searched specifically for relevant information on likely responses to landscape action. Current research projects should continue to fill the evidence gaps highlighted by this review.

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Superscript numbers indicate references linked to data in Figures 2, 3 and 4.

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