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Patch quality and landscape connectivity effects on patch population size: implications for metapopulation sizes and studies of landscape value

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ABSTRACT

Question: How do patch population sizes vary as a function of patch quality and landscape connectivity within heterogeneous landscapes?

Model: We developed a population dynamics model to compare relative population size within patches as a function of patch quality and landscape connectivity, defining these variables from an organism's perspective. We used differences between birth and death rates as measures of patch quality and immigration rates into patches as measures of landscape connectivity.

Results: An interaction between immigration and patch quality resulted in a more positive influence on population sizes in high-quality patches than in low- or intermediate-quality patches. We also found that patch quality had much greater positive effects on patch population size than immigration.

Predictions: For any given species, the proportion of high-quality patches in a landscape will be a more important determinant of metapopulation size than landscape connectivity. Thus landscapes with high proportions of high-quality patches will be of greater value to populations than landscapes with high connectivity and few high-quality patches. We present a predictive framework that can serve as a springboard for empirical work about metapopulation sizes, landscape value, and conservation strategies for species in heterogeneous landscapes.

Keywords: landscape connectivity, landscape value, metapopulation, patch population size, patch quality.

INTRODUCTION

Empirical studies suggest that patch population persistence and the distribution of populations among patches depend in large part on patch quality and landscape connectivity (Sarre *et al.*, 1995; With and Crist, 1995; Mazerolle and Villard, 1999; Fleishman *et al.*, 2002; Wiens, 2002; Bossuyt *et al.*, 2004; Franken and Hik, 2004; Williams and Kremen, 2007; Jaquiéry *et al.*, 2008). However, little

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previous work has considered the relative importance of these variables to patch demographic outcomes, which are key influences on patch and metapopulation sizes. The dynamics of populations within patches determine the size of the population summed across all patches in the landscape. Here, we use the term 'metapopulation' to refer to the total abundance (i.e. the sum) of all populations across all patches in a landscape. To date, a general framework linking habitat patch quality and landscape connectivity to metapopulation size has yet to be articulated. Such a framework would provide *a priori* hypotheses that would advance understanding of species–environment relationships more rapidly than examination of relationships *post hoc* (MacNally and Bennett, 1997). Testing the predictions of such a framework also would facilitate the development of conservation, management, and/or restoration strategies for declining species.

We begin development of such a framework by first constructing a population dynamics model that incorporates patch quality and landscape connectivity effects on patch population sizes. We address two issues that have received limited attention to date. First, patch quality has received less emphasis than variables such as patch size, although patch quality clearly affects population dynamics within patches (e.g. Jaquiéry *et al.*, 2008). Second, previous studies have emphasized patch occupancy dynamics rather than population dynamics within patches (e.g. Fleishman *et al.*, 2002). Population dynamics determine patch population sizes and population sizes determine the relative likelihood of extinction. Hence, by relating population dynamics to landscape connectivity and habitat patch quality we should be able to refine our understanding of what factors are important in determining patch population persistence in heterogeneous landscapes. We then use the insights gained from this perspective to develop a framework that generates testable predictions about how metapopulation sizes vary across landscapes with different degrees of connectivity and proportions of high-quality patches.

DEMOGRAPHIC CORRELATES OF PATCH QUALITY AND LANDSCAPE CONNECTIVITY: MODEL ASSUMPTIONS

For species with active or passive dispersal, once an organism ceases to disperse and settles at a specific location, subsequent survival and/or reproductive outcomes depend on the ecological conditions within the patch. Patch quality is typically quantified by measurements of the nature and abundance of required resources, for example the abundance of plants used by animals for shelter, foraging or oviposition (e.g. Sarre *et al.*, 1995). To understand how patch quality affects population dynamics, we focus our analysis on the outcome of resource use across individuals within a population. In a high-quality patch, we assume resources are in great abundance and/or of high quality and that individuals are able to extract more energy from the resources than are individuals in low-quality patches, leaving individuals in high-quality patches with more energy for reproductive activities. Thus greater patch quality leads to greater average fitness of individuals in a population, with birth rates exceeding death rates by a larger margin.

A landscape that presents no obstacles to movement for some individuals may be difficult to traverse for others, resulting in different landscape connectivity due to different levels of mobility (e.g. Sarre *et al.*, 1995; Travis and Dytham, 2002; Goheen *et al.*, 2003). Thus it is important to consider landscape connectivity from an organismal perspective (Pearson *et al.*, 1996). The greater the mobility of individuals in a landscape (or aquatic environment), the greater the connectivity among patches within a landscape. The major demographic impact of high connectivity is to increase the migration rate among different patch populations of a species within a heterogeneous landscape. High connectivity should reduce the extent to which local habitats must provide resources that increase individual fitness and maintain patch populations in the face of environmental variation. In what follows, we use immigration into patches as an index of landscape connectivity. We vary immigration rate in a stochastic, individual-based population model to examine the impact of landscape connectivity on population dynamics.

THE MODEL

Consider a typical patch nested within a larger landscape. We assume that the patch is composed of a limited number of sites at which individuals can establish themselves, obtain resources, produce offspring, and survive. At the start of each generation, there are a fixed number of adult females, each of which obtains one breeding site. We assume site selection has a random element to it in that it is not possible for females to definitively predict their reproductive output at a site. During breeding season t, each of N_t individuals raises b_{it} offspring to maturity ($i = 1, 2, \ldots, N_t$) and survives until generation $t + 1$ with probability $1 - d_{it}$. Because of the stochastic nature of the environment and breeding success, b_{it} and d_{it} are considered random variables. Each succeeding generation represents an independent sample of the range of possible birth and death outcomes described by these two random variables. We also assume that the birth and death process is stationary, i.e. the statistical distribution describing the random variables does not change from one generation to the next. Finally, since for many organisms investment of energy in reproduction decreases the probability of surviving to the next generation (e.g. Stjernman *et al.*, 2004; Descamps *et al.*, 2009), we assume that birth and death rates are drawn from a bivariate distribution where b_{it} and d_{it} have a positive covariance.

Suppose further that each individual in the population encounters a fraction of the total number of individuals in the population f_i while breeding and attempting to survive. Each individual encountered has a small negative effect on birth probability and a small positive effect on death probability, say b_0 and d_0, respectively. If these effects vary little among individuals, they can be considered constants. The total negative effects on birth rate for individual i in generation t would then be $b_0 f_i N_t$. Similarly, the total positive effects on death rate for individual i in generation t would be $d_0 f_i N_t$. We can now create a recursion equation that describes population change from one generation to the next:

$$N_{t+1} = N_t + \Sigma_i (b_{it} - b_0 f_i N_t) - \Sigma_i (d_{it} + d_0 f_i N_t) \tag{1}$$

The term $(b_{it} - b_0 f_i N_t) - (d_{it} + d_0 f_i N_t)$ is the fitness of individual i in the population at time t. Given the assumptions above, the average and variance of individual fitness in the population at time t (W_t) are respectively

$$W_t = E(b_{it}) - E(d_{it}) - N_t (b_0 + d_0) \tag{2a}$$

$$\mathrm{var}(W_t) = \mathrm{var}(b_{it}) + \mathrm{var}(d_{it}) - 2\,\mathrm{cov}(b_{it}, d_{it}) \tag{2b}$$

Note that because the stochastic birth–death process is stationary, all the expectations in equation (2) will be constants. If $\mu_b = E(b_{it})$, $\mu_d = E(d_{it})$, $\sigma_b^2 = \mathrm{var}(b_{it})$, $\sigma_d^2 = \mathrm{var}(d_{it})$, and $\sigma_{bd} = \mathrm{cov}(b_{it}, d_{it})$, the constant variance in fitness is

$$\sigma_W^2 = \sigma_b^2 + \sigma_d^2 - 2\sigma_{bd} \tag{3}$$

Because the population has an implicit 'carrying capacity' due to the effects of density dependence (b_0 and d_0), the population will persist over time when the average rate of change (N_{t+1}/N_t) approaches one. In deterministic population dynamics (i.e. no variances in birth/death rates among individuals), the equilibrium population size would be

$$N^* = (\mu_b - \mu_d)/(b_0 + d_0) \tag{4}$$

The average population abundance over time when the population is stationary is

$$E(N) = N^* + \mu_W/(b_0 + d_0) \tag{5}$$

where $\mu_W = (\mu_b - \mu_d)$. That is, average abundance in the stochastic model will differ from the equilibrium population size of the corresponding deterministic system, depending on the average fitness of individuals when the population is near carrying capacity (μ_W). The amplitude of the fluctuations of the population near carrying capacity is related to the variance of abundance in the patch region (σ_N^2), given by

$$\sigma_N^2 = \sigma_W^2/(b_0 + d_0)^2 \tag{6}$$

Average individual fitness, then, is closely linked to the dynamical behaviour of a stochastically varying population.

Immigration is included in the population model given in equation (1) by including a stochastic immigration rate term. If $I(t)$ is the rate of individuals entering the population between generation t and $t + 1$, then equation (1) becomes:

$$N_{t+1} = N_t + \Sigma_i\,(b_{it} - b_0 f_i\, N_t) - \Sigma_i\,(d_{it} + d_0 f_i\, N_t) + I(t) \tag{7}$$

Here we assume that $I(t) \geq 0$ and has a variance of σ_I^2. The inclusion of an immigration term means that population growth could still be positive even if $W_t < 0$. In fact, the population could persist indefinitely when $W_t < 0$ if the variance in fitness was sufficiently low and the expected immigration rate was sufficiently high. This provides a demographic mechanism for the 'rescue effect' (Brown and Kodric-Brown, 1977; Gonzalez *et al.*, 1998; Jaquiéry *et al.*, 2008).

Using equation (7), we examined how landscape connectivity and patch quality interact to affect the behaviour of patch populations. For simplicity, we assumed the primary demographic effect of inhabiting high-quality patches is to allow individuals to raise more offspring. The conclusions we draw from this analysis would not change qualitatively if we assumed that the demographic effect was to lower death rate, or more generally, to increase the difference between per capita birth and death rates.

Each simulation consisted of numerical iteration of equation (7) for 200 time steps. For most simulations, transient dynamics were resolved after the first 20 generations. For each simulation, average per capita death rate was set at 0.5, and average birth rate was given a value of 0.475, 0.5 or 0.525 to simulate three levels of patch quality. Density-dependent effects for birth and death were set at 0.007. The variances for birth and death rate were both 0.75, and the correlation between birth and death rate was 0.70. We used three levels of immigration, the first being no immigration. Immigration rate was then increased (from 0 to 0.5 and then to 1) by increasing the variance of a normal distribution centred at 0; immigration occurred only when the value drawn from the normal distribution exceeded 0. We kept as many parameter values as possible constant so that the results would primarily reflect landscape connectivity and patch quality effects, as we defined them. The values for birth, death, and immigration rates were chosen to produce a range of outcomes. Results were qualitatively similar for different values.

Simulations began with an initial population size of 10. For each of nine sets of parameter values (three patch qualities multiplied by three immigration rates), 100 simulations were done. Average population size was calculated for each simulation, and a two-way analysis of variance was performed on the resulting set of simulations ($n = 900$).

RESULTS

When birth rate was less than death rate (i.e. low patch quality), 44% of populations with no immigration went extinct after 200 generations. In contrast, no extinctions occurred when immigration took place. Immigration succeeded in maintaining small population sizes (Fig. 1). When birth rate was equal to or exceeded the death rate (intermediate and high patch quality, respectively), populations always persisted (Fig. 1), regardless of immigration rate. (Given the birth and death rates, and variances used in the model, extinctions for these groups were unlikely.)

Immigration rate and patch quality had positive, interacting effects on average population size (Table 1). A 100% increase in immigration (from 0.5 to 1.0) increased average patch population size approximately 1.5 times when birth rate was 0.5 and 1.3 times when birth rate was 0.525 (Fig. 1). In contrast, a 2.5% increase in average birth rate (from 0.500 to 0.525) increased average patch population size approximately 2.7 times when immigration was 0.5 and 2.3 times when immigration was 1.0 (Fig. 1). Thus, the effects of patch quality are much stronger than those of immigration on average patch population size (Fig. 1).

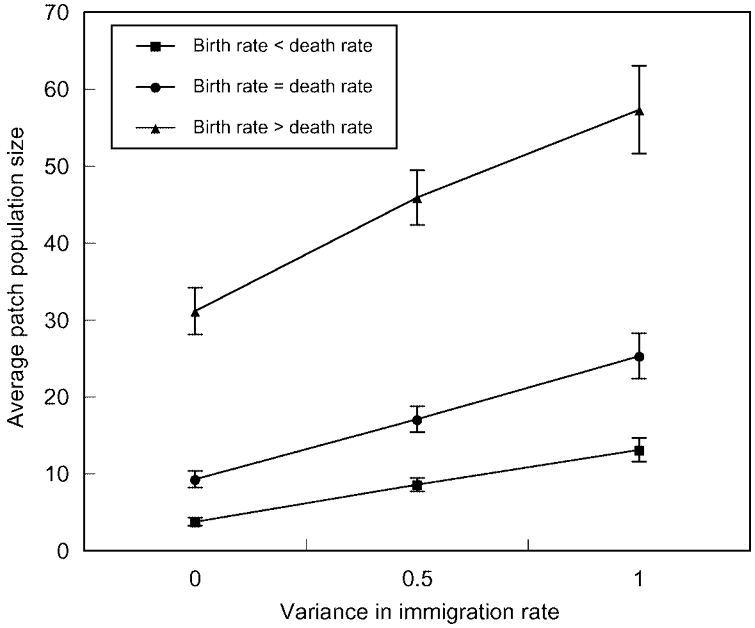

Fig. 1. The relationships between average population size, average birth rate, and rate of immigration for 100 simulations of stochastic populations using equation (7). Variance in immigration rate is a measure of the amount of expected immigration from a half normal distribution; higher variance translates into a higher average rate of immigrants entering the population each generation. Symbols represent averages of 100 simulations after transient dynamics ended. Error bars represent ± one standard deviation.

Table 1. Analysis of variance of average population sizes obtained from 900 simulations: 100 simulations for each of nine patch quality/landscape connectivity combinations using the model given in equation (7)

Source	d.f.	SS	MS	*F*	*P*
Immigration rate	2	44305	22152.00	2835	<0.0001
Birth rate	2	215326	107663.00	13779	<0.0001
Interaction	4	7291	1822.00	233	<0.0001
Error	891	6961	7.81		
Corrected total	899	273884			

DISCUSSION

Our results indicate that (1) the interaction between immigration and patch quality has a more positive influence on population sizes in high-quality patches than in low- or intermediate-quality patches, and (2) patch quality has much greater positive effects on patch population size than immigration. These results provide intriguing suggestions about the importance of ecological context to demographic outcomes.

The significant interaction between landscape connectivity and patch quality resulted in substantially higher population sizes in high-quality patches than in low- and intermediate-quality patches (Fig. 1). We believe that the interaction results from the relatively greater per capita fecundity of any individual that immigrates into a high-quality patch, compared with an individual that immigrates into a lower-quality patch. Each immigrating individual has a greater likelihood of positively influencing population size in high-quality patches than in other patch types. In essence, individuals immigrating into intermediate- and low-quality patches are worth less than individuals immigrating into high-quality patches. These results suggest that improving both patch quality and connectivity may have more than additive effects on patch population sizes within landscapes.

However, our results also indicate that patch quality has a much stronger effect on patch population size than immigration rate. Low- and intermediate-quality patches, even in well-connected landscapes, may have lower population sizes than isolated high-quality patches (Fig. 1). Thus, with regard to metapopulation size, high landscape connectivity is unlikely to compensate for high proportions of low- and intermediate-quality patches across a landscape.

We now consider how our results can be used to construct a predictive framework of metapopulation responses to landscapes that vary in connectivity and proportion of high-quality patches. We assume that a larger metapopulation size increases the likelihood of metapopulation persistence and so consider landscapes with higher metapopulation sizes to be of higher value.

From an organismal perspective, connectivity and the proportion of high-quality patches within a landscape result from interactions between a species' biology and landscape and patch characteristics (With and Crist, 1995). Landscape connectivity results from landscape configuration and a species' mobility. The proportion of high-quality patches results from resource distributions within patches and the resource requirements of species. Thus, different species will perceive any one landscape differently. For example, a given landscape

Table 2. Predicted features of metapopulations inhabiting landscapes that vary in connectivity and the proportion of high-quality patches

	Landscape connectivity	
Proportion of high-quality patches	Low	High
Low	*Type A: Low-value landscape* Small metapopulation size, high extinction risk	*Type B: Moderately low-value landscape* Moderately small metapopulation size, moderately high extinction risk
High	*Type C: Moderately high-value landscape* Moderately large metapopulation size, moderately low extinction risk	*Type D: High-value landscape* Large metapopulation size, low extinction risk

is likely to have a lower proportion of high-quality patches for species with highly specialized resource requirements than species with more generalized requirements. Keeping this organismal perspective in mind, metapopulation sizes should be greatest in well-connected landscapes with high proportions of high-quality patches and smallest in poorly connected landscapes with low proportions of high-quality patches. Predictions are less straightforward when landscapes are well connected with low proportions of high-quality patches or poorly connected with high proportions of high-quality patches. Our simulation results indicate that patch quality is a more important positive influence on metapopulation size than landscape connectivity. Thus we predict that metapopulation sizes will be greater in poorly connected landscapes with high proportions of high-quality patches than in well-connected landscapes with low proportions of high-quality patches (Table 2).

The framework in Table 2 can serve as a springboard for future empirical work on metapopulation sizes in landscapes that vary in connectivity and proportions of high-quality patches. As an example, we compare predicted responses of species with specialized or generalized resource requirements and different levels of mobility to a given landscape. Highly specialized requirements for food or habitat have repeatedly been associated with limited distributions and increased extinction risk (Sarre *et al.*, 1995; With and Crist, 1995; Fisher *et al.*, 2003; Bossuyt *et al.*, 2004; Charrette *et al.*, 2006; Jones *et al.*, 2007; Devictor *et al.*, 2008). Specialists typically show higher rates of population increase and/or greater resource use efficiency than generalists when preferred resources are abundant, but show greater negative impacts when resources are sparse (e.g. Steffan-Dewenter and Tscharntke, 2000; Ostergard and Ehrlen 2005; Sorensen *et al.*, 2005a, 2005b; Rand and Tscharntke, 2007). In a patch with their required resources, higher average fitness of individuals in a population of specialists will lead to a higher population size than a population of generalists, all else being equal (i.e. density-dependent effects are equivalent). Note, however, that this local abundance pattern holds only for patches where appropriate resources are available for the specialist population. A specialist species is likely to experience more local patches where the expected difference between birth and death rates will be close to zero or negative, i.e. a landscape is more likely to have a low proportion of high-quality patches for specialist species than generalist species. When the abundance of a specialist is averaged across space, it is likely that its average abundance will be lower than that of a more generalized species because it attains high densities in relatively few locations (Hanski, 1982).

If a specialized species also has poor mobility, a landscape is more likely to be perceived as poorly connected than for a more mobile species, and thus be of low value (Type A landscape; Table 2). Average abundance across the landscape will be low, and there will be little chance for 'rescue effects' to maintain patch populations tending towards zero (Fig. 1). Such demographic profiles may be typical of many rare or endangered species. For example, the specialist gecko species *Oedura reticulata* was much less widely distributed in a patchy Australian landscape than a generalist gecko *Gehyra variegata*, despite both species being relatively poor dispersers (Sarre *et al.*, 1995). For poor-mobility specialist species, increasing both the proportion of high-quality patches and the quality of matrix habitat to improve survivability of immigrating individuals should maximize landscape value, metapopulation size, and the likelihood of metapopulation persistence. However, given that land-management resources are often limited, we suggest that, given our simulation results, increasing the proportion of high-quality patches should be a higher priority than increasing landscape connectivity for specialist, low-mobility species. Increasing the proportion of high-quality patches could potentially transform landscapes for these species from Type A (low-value) to Type C (moderately high value; Table 2).

For a specialized species with high mobility, a landscape is more likely to be perceived as better connected. However, this species will still face the likelihood that the landscape has a low proportion of high-quality patches because of its specialized resource requirements (Type B landscape; Table 2). For example, the South African butterfly, *Orachrysops ariadne*, is highly mobile and highly specialized. Although *O. ariadne* is a strong flier, its required habitat of native grasslands covers only 1% of its original extent. Consequently, it is very rare and investigators estimated a substantially lower population size for it than its congener, *O. subravus*, which has much less specialized resource requirements (Samways and Lu, 2007). The almost complete absence of suitable patches for *O. ariadne* overrides the high landscape connectivity, resulting in a small metapopulation size. Increasing the proportion of high-quality patches could potentially transform *O. ariadne*'s landscape from Type B (moderately low value) to Type D (high value; Table 2).

Generalist species are more likely to experience a higher proportion of the patches in a landscape as being of high quality (birth rate > death rate) than specialist species. However, generalist species with low mobility are less likely to inhabit high-value landscapes because they are more likely to perceive any given landscape as poorly connected (Type C landscape; Table 2). Increasing the quality of matrix habitat should increase metapopulation sizes for these species, although, given the minor effects of immigration on population size in our simulations, the response may be modest. Generalists with high mobility (Type D landscape; Table 2) should achieve the highest metapopulation sizes. Such characteristics typify 'weedy' species that can move across the landscape easily and find appropriate habitat in most patches.

The above examples demonstrate how the framework can be used to predict and compare the responses of various species to one landscape, given the species' different natural history characteristics, including levels of specialization and mobility. The framework can also be used to generate predictions for one species across different landscapes that vary in connectivity and proportion of high-quality patches.

As described above, two assumptions of this framework are: (1) landscape connectivity influences patch population sizes primarily through effects on individuals being able to move through a landscape, and (2) patch quality influences population size through effects on population growth rates. In some cases, landscape influences may affect population growth rates within patches, such as where a range of necessary resources is widely distributed throughout a landscape (e.g. Dennis *et al.*, 2006). However, to keep this initial framework simple and testable these potential effects are not included.

Like all frameworks, the one presented in Table 2 is a simplification of reality. Despite the simplifications, our framework provides general principles to guide investigations of metapopulation responses to landscape that vary in connectivity and proportions of high-quality patches. The framework builds on previous work by providing testable predictions that will advance understanding of species–landscape relationships. This is particularly important in the face of land-use change (Huston, 2005), global climate change (Debinski *et al.*, 2006), and biological invasions (Nesslage *et al.*, 2007) that are altering the landscapes in which species have evolved.

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REFERENCES

Bossuyt, B., Honnay, O. and Hermy, M. 2004. Scale-dependent frequency distributions of plant species in dune slacks: dispersal and niche limitation. *J. Veg. Sci.*, **15**: 323–330.

Brown, J.H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**: 445–449.

Charrette, N.A., Cleary, D.F.R. and Mooers, A.O. 2006. Range-restricted, specialist Bornean butterflies are less likely to recover from enso-induced disturbance. *Ecology*, **87**: 2330–2337.

Debinski, D.M., VanNimwegen, R.E. and Jakubauskas, M.E. 2006. Quantifying relationships between bird and butterfly community shifts and environmental change. *Ecol. Appl.*, **16**: 380–393.

Dennis, R.L.H.T., Shreeve, T.G. and Van Dyck, H. 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodivers. Conserv.*, **15**: 1943–1966.

Descamps, S., Boutin, S., McAdam, A.G., Berteaux, D. and Gaillard, J.-M. 2009. Survival costs of reproduction vary with age in North American red squirrels. *Proc. R. Soc. Lond. B*, **276**: 1129–1135.

Devictor, V., Julliard, R. and Jiguet, F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**: 507–514.

Fisher, D.O., Blomberg, S.P. and Owens, I.P.F. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. R. Soc. Lond. B*, **270**: 1801–1808.

Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C.L. and Murphy, D.D. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conserv. Biol.*, **16**: 706–716.

Franken, R.J. and Hik, D.S. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *J. Anim. Ecol.*, **73**: 889–896.

Goheen, J.R., Swihart, R.K., Gehring, T.M. and Miller, M.S. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos*, **102**: 95–103.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. and Evans-Freke, I. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, **281**: 2045–2047.

Hanski, I. 1982. Patterns of temporal and spatial variation in animal populations. *Ann. Zool. Fenn.*, **19**: 21–38.

Huston, M.A. 2005. The three phases of land-use change: implications for biodiversity. *Ecol. Appl.*, **15**: 1864–1878.

Jaquiéry, J., Guélat, J., Broquet, T., Berset-Brändll, L., Pellegrini, E., Moresi, R. *et al.* 2008. Habitat-quality effects on metapopulation dynamics in greater white-toothed shrews, *Crocidura russula. Ecology*, **89**: 2777–2785.

Jones, M.M., Rojas, P.O., Tuomisto, H. and Clark, D.B. 2007. Environmental and neighbourhood effects on tree fern distributions in a neotropical lowland rain forest. *J. Veg. Sci.*, **18**: 13–24.

MacNally, R. and Bennett, A.F. 1997. Species-specific predictions of the impact of habitat fragmentation: local extinction of birds in the box-ironbark forests of central Victoria, Australia. *Biol. Conserv.*, **82**: 147–155.

Mazerolle, M.J. and Villard, M.A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience*, **6**: 117–124.

Nesslage, G.M., Maurer, B.A. and Gage, S.H. 2007. Gypsy moth response to landscape structure differs from neutral model predictions: implications for invasion monitoring. *Biol. Invasions*, **9**: 585–595.

Ostergard, H. and Ehrlen, J. 2005. Among population variation in specialist and generalist seed predation – the importance of host plant distribution, alternative hosts and environmental variation. *Oikos*, **111**: 39–46.

Pearson, S.M., Turner, M.G., Gardner, R.H. and O'Neill, R.V. 1996. An organism- based perspective of habitat fragmentation. In *Biodiversity in Managed Landscapes: Theory and Practice* (R.C. Szaro and D.W. Johnston, eds.), pp. 77–95. Oxford: Oxford University Press.

Rand, T.A. and Tscharntke, T. 2007. Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos*, **116**: 1353–1362.

Samways, M.J. and Lu, S.-S. 2007. Key traits in a threatened butterfly and its common sibling: implications for conservation. *Biodivers. Conserv.*, **16**: 4095–4107.

Sarre, S., Smith, G.T. and Meyers, J.A. 1995. Persistence of two species of gecko (*Oedura reticulata* and *Gehydra variegata*) in remnant habitat. *Biol. Conserv.*, **71**: 25–33.

Sorensen, J.S., McLister, J.D., and Dearing, M.D. 2005a. Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecology*, **86**: 125–139.

Sorensen, J.S., McLister, J.D. and Dearing, M.D. 2005b. Novel plant secondary metabolites impact dietary specialists more than generalists. *Ecology*, **86**: 140–154.

Steffan-Dewenter, I. and Tscharntke, T. 2000. Butterfly community structure in fragmented habitats. *Ecol. Lett.*, **3**: 449–456.

Stjernman, M., Raberg, L. and Nilsson, J. 2004. Survival costs of reproduction in the blue tit (*Parus caeruleus*): a role for blood parasites. *Proc. R. Soc. Lond. B*, **271**: 2387–2394.

Travis, J.M.J. and Dytham, C. 2002. Dispersal evolution during invasions. *Evol. Ecol. Res.*, **4**: 1119–1129.

Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biol.*, **47**: 501–515.

Williams, N.M. and Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol. Appl.*, **17**: 910–921.

With, K.A. and Crist, T.O. 1995. Critical threshold in species' responses to landscape structure. *Ecology*, **76**: 2446–2459.