

Landscape heterogeneity and metapopulation dynamics

5.1 Introduction

Landscape ecologists became interested in how landscape structure affects ecological responses during the mid-1980s (Risser *et al.* 1984). One ecological response of interest to landscape ecologists is population dynamics. In the mid-1980s, metapopulation ecology, the study of habitat spatial structure in population dynamics, had already been in existence for 14 years (Levins 1970). It was therefore natural for landscape ecologists with an interest in population dynamics to take the metapopulation ecology perspective as a starting point in developing a landscape-scale population ecology.

In this chapter I review the original metapopulation model and describe how the spatial structure incorporated in metapopulation models has changed over the past 35 years. I then discuss limitations of the classical metapopulation framework for predicting population dynamics in heterogeneous landscapes, and I argue for continued development of landscape population models.

5.2 Levins' metapopulation model

Levins' metapopulation model is arguably the first model of population dynamics devised for the "study of population processes in a heterogeneous environment" (Levins 1969). This model represents a population existing in T patches (called "sites" by Levins.) The number of these patches that is occupied by the species is N , and the rate of change of occupied patches is

$$\frac{dN}{dt} = mN \left(1 - \frac{N}{T} \right) - EN$$

Key Topics in Landscape Ecology, ed. J. Wu and R. Hobbs.

Published by Cambridge University Press. © Cambridge University Press 2007.

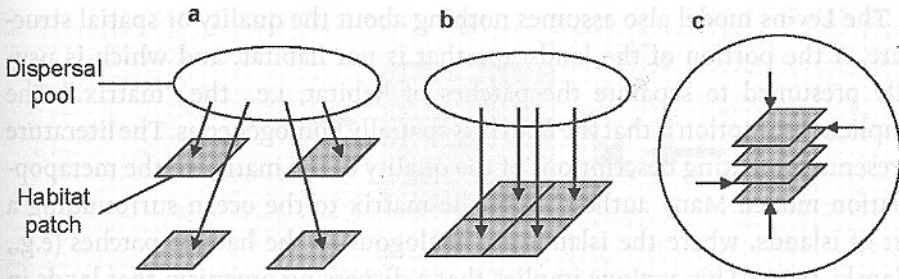


FIGURE 5.1

Three equally valid illustrations of spatial heterogeneity as represented in the Levins (1969) model. All patches have the same colonization probability. (a) patches are disjunct; (b) patches are contiguous (one patch); (c) patches are superimposed

where m is the rate of colonization of empty patches (called “migration” by Levins) and E is the rate of extinction of occupied patches. The model is analyzed to give the number of occupied patches at equilibrium: $T(1 - E/m)$. Therefore, the number of occupied patches increases with increasing colonization rate and with decreasing extinction rate. Note that the local populations within patches are not represented in the model; there is no explicit consideration of births, deaths, emigration, or immigration. Instead, patches are simply either occupied or not occupied, and the only two processes considered are establishment of new populations (colonization) and extinction of existing populations. The original metapopulation model and its derivatives have therefore also been called “patch occupancy” models (Higgins and Cain 2002, Ovaskainen and Hanski 2003) or “presence–absence” models (Baguette and Schtickzelle 2003) or “extinction–colonization” models (Fahrig 2002).

The Levins metapopulation model includes landscape spatial structure in the sense that the habitat in the model is assumed to be divided into T pieces. However, since the colonization and extinction rates are the same for all patches, the model implicitly assumes that all patches are identical in every sense. Of particular importance is that, since the pieces of habitat are all equally likely to be colonized, the model does not include spatial relationships among the habitat pieces. All pieces of habitat are assumed to be in the same location relative to potential colonists. This is sometimes envisioned as a “dispersal pool” in which dispersing individuals mix and then are randomly redistributed among the patches (Fig. 5.1). However, there is in fact nothing in the model that requires the “patches” to be spatially disjunct from each other (Fig. 5.1). In some ways the most realistic way of viewing the model is to think of all the patches as being in the same location (Fig. 5.1). Therefore, although the Levins model subdivides the environment into T pieces, there is no explicit spatial structure to the habitat.

The Levins model also assumes nothing about the quality or spatial structure of the portion of the landscape that is not habitat, and which is usually presumed to separate the patches of habitat, i.e., the “matrix.” The implicit assumption is that the matrix is spatially homogeneous. The literature presents conflicting descriptions of the quality of the matrix in the metapopulation model. Many authors liken the matrix to the ocean surrounding a set of islands, where the islands are analogous to the habitat patches (e.g., Hanski 1994). This analogy implies that a dispersing organism that lands in the matrix will inevitably “drown;” the matrix is therefore viewed as a hostile environment and dispersal mortality is implicitly high. However, the original metapopulation model and its derivatives do not actually include the processes of emigration from patches or dispersal mortality. The potential effects of these processes on population dynamics are not obtainable from the models. Therefore, it may be more accurate to describe the matrix in metapopulation models as being “sufficiently benign to allow passage of dispersing organisms” (Vandermeer and Carvajal 2001).

5.3 Spatially realistic metapopulation models

In the 35 years since Levins first introduced his model, hundreds of papers have analyzed and expanded on its basic structure. Current metapopulation models represent additional spatial structure beyond that represented in the Levins model, in two important respects: patches are assumed to vary in size and in location relative to each other. Metapopulation models that include patch sizes and relative locations have been termed “spatially realistic” metapopulation models (e.g., Wahlberg *et al.* 1996) and are reviewed in Hanski and Ovaskainen (2003). There are many different possible ways of formulating such models. As a particular example, in the metapopulation model presented by Drechsler *et al.* (2003), colonization of an empty patch i is both: (1) a decreasing function of the distances from i to the occupied patches in the metapopulation, on the assumption that immigration increases with decreasing distance, and (2) an increasing function of the sizes of the occupied patches, on the assumption that larger occupied patches produce more potential colonists (Fig. 5.2). The probability of extinction of occupied patch i is assumed to be both: (1) a decreasing function of the size of i , on the assumption that larger occupied patches contain larger populations, which have lower extinction probabilities, and (2) a decreasing function of the colonization probability of i , on the assumption that colonization probability is correlated to immigration rate, and increasing immigration rate should decrease extinction probability through the rescue effect. Since colonization probability is a function of patch

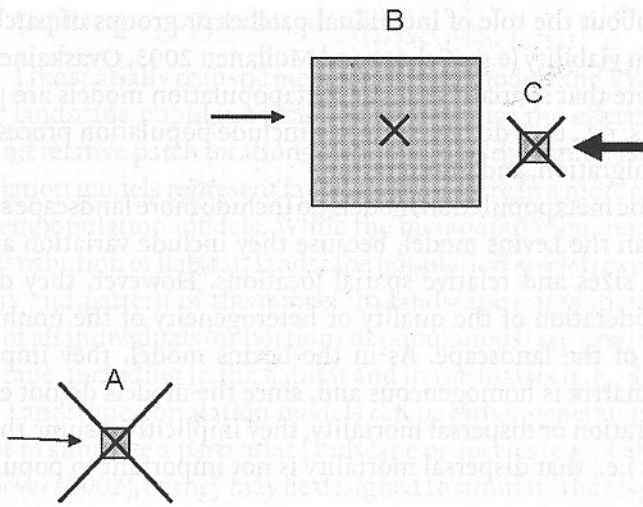


FIGURE 5.2

Illustration of the relationships between patch size and interpatch distance and extinction and colonization probabilities in a “spatially realistic” metapopulation model (Drechsler *et al.* 2003). The size of the \times over each patch represents the probability of location extinction when the patch is occupied. The thickness of the arrow entering each patch represents the probability of colonization when the patch is unoccupied. Patch A has the lowest colonization rate because of the large distance to potentially occupied patches such as patch B. Patch A also has the highest extinction probability because it is a small patch (with a presumed small population) that is far from other occupied patches, thus reducing the chance of rescue. Patch B also has a low colonization rate; however, it is higher than the colonization rate of patch A, because patch B is close to patch C which is likely to be occupied (due to its proximity to a large patch, B). Patch B has the lowest extinction probability because it is very large (which implies a large population). Patch C has the highest colonization probability because it is close to a patch that is highly likely to be occupied and to produce many potential colonists because of its large size (patch B). Patch C has an intermediate extinction probability; its extinction probability based on only its patch size would be high, but it should be frequently rescued from extinction by immigration from patch B

size and interpatch distance, extinction probability is therefore also a function of patch size and interpatch distance in this model (Fig. 5.2).

Spatially realistic metapopulation models are typically analyzed for persistence probability of the metapopulation. Persistence probability increases with increasing colonization rates and decreasing extinction probabilities, and with increasing variance in patch sizes and interpatch distances. Increasing variance in patch sizes implies some large patches which have very low probabilities of extinction, and increasing variance in isolation values implies spatial contiguity of patches, i.e., groups of patches within the landscape that are close together and therefore have high colonization rates (Ovaskainen *et al.* 2002, Ovaskainen and Hanski 2003). These models can also be used to

study questions about the role of individual patches or groups of patches in overall population viability (e.g., Cabeza and Moilanen 2003, Ovaskainen and Hanski 2003). Note that spatially realistic metapopulation models are patch-occupancy models, i.e., they do not explicitly include population processes of births, deaths, emigration, and immigration.

Spatially realistic metapopulation models do include more landscape spatial heterogeneity than the Levins model, because they include variation among patches in patch sizes and relative spatial locations. However, they do not include any consideration of the quality or heterogeneity of the nonhabitat (matrix) portion of the landscape. As in the Levins model, they implicitly assume that the matrix is homogeneous and, since the models do not explicitly include emigration or dispersal mortality, they implicitly assume that the matrix is benign, i.e., that dispersal mortality is not important to population dynamics.

5.4 PVA tools based on the metapopulation framework

Most applied ecologists who deal with real-world conservation problems encounter metapopulation theory indirectly, through tools for population viability analysis (PVA) such as "ALEX", "RAMAS-space" and "VORTEX" (reviewed in Lindenmayer *et al.* 1995). These models are different from the classical metapopulation theory discussed above in that the population dynamics within patches are included in the models. This is an important distinction; several authors have shown that by collapsing the population processes of births, deaths, emigration, and immigration into the two processes of local colonizations and extinctions, classical metapopulation models can lead to large errors in prediction (Amaresekare and Nisbet 2001, Higgins and Cain 2002, Léon-Cortés *et al.* 2003).

On the other hand, PVA metapopulation models do adhere to the assumptions of classical metapopulation theory in their representation of habitat and landscape structure. Specifically, these models are habitat-patch based; each local population is assumed to occur within a habitat patch. Similar to the spatially realistic metapopulation models (above), patch sizes and interpatch distances are included in the PVA metapopulation models. Like other metapopulation models, the PVA metapopulation tools do not model the movement of organisms in the matrix, and they do not include dispersal mortality. The number of individuals moving from patch A to patch B is a function of the size of the population in patch A and the distance from A to B. There is no accounting for individuals that emigrate from patches but fail to reach other patches, i.e., dispersal mortality. Therefore, the PVA metapopulation models, like classical metapopulation theory, assume a benign, homogeneous matrix.

5.5 Landscape population models

Like spatially realistic metapopulation models and PVA metapopulation tools, landscape population models incorporate the effects of habitat-patch size and relative patch locations on population dynamics. However, landscape population models represent landscape structure in a more complete way than do metapopulation models. While the metapopulation models consider only the distribution of habitat, landscape population models explicitly include the quality and pattern of the matrix. In landscape population models the locations of all individuals (or portions of populations) are simulated on the entire landscape, including in the habitat and in the matrix (e.g., dispersing individuals). Landscape population models can be either general in that they are not meant to simulate a particular landscape or species (e.g., Fahrig 1998, Flather and Bevers 2002), or they may be designed to simulate the response of a particular species to landscape structure (e.g., Topping and Sunderland 1994, Henein *et al.* 1998). Inclusion of the effects of matrix quality and heterogeneity on population dynamics can have important effects on model predictions. In fact, landscape population models can produce very different model predictions than one would get using a metapopulation model, as discussed in the following two sections.

5.5.1 Matrix quality

As discussed above, metapopulation models do not explicitly include the matrix. There is no effect of dispersal mortality on population persistence in metapopulation models. This is an important omission; in reality not all emigrants from a patch will successfully find a new patch; some proportion of them will die. This means that emigration can reduce overall population persistence because it adds to mortality. This mortality will be balanced to some extent by the positive colonization and rescue effects of successful emigrants (i.e., immigrants) on overall population persistence. However, metapopulation models only include the positive effects of immigration on population persistence and neglect the possible negative effects of emigration, i.e., dispersal mortality.

Landscape population models explicitly include emigration, dispersal mortality, and immigration (Fig. 5.3). In these models, population persistence is generally found to be a declining function of emigration rate, except at low emigration rates (Fig. 5.4). At very low emigration rates, an increase in emigration rate causes an increase in persistence, due to rescue and recolonization of local populations. However, at higher emigration rates, further increases in emigration rate result in decreasing persistence probability of the

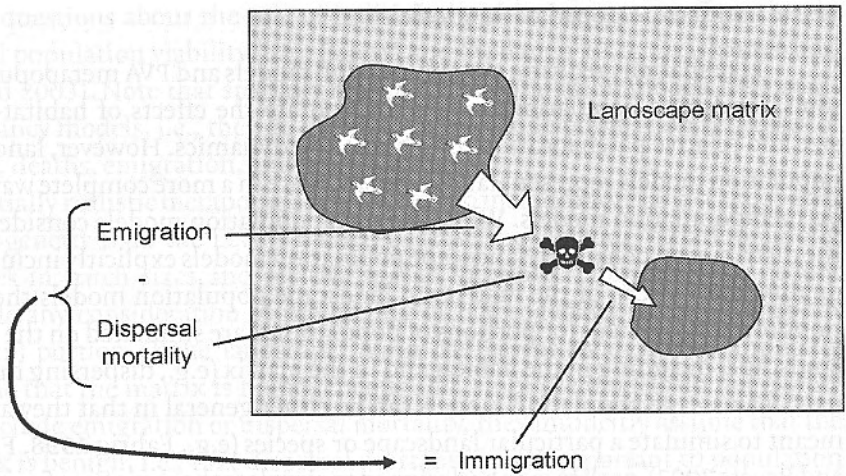


FIGURE 5.3

Illustration of the effect of matrix quality on immigration rate. Immigration is the result of emigration minus dispersal mortality. The lower the matrix quality, the higher the dispersal mortality. The net effect of an increase in emigration rate on overall population persistence in the landscape depends on the balance between the negative effect of dispersal mortality and the positive effects of immigration (i.e., colonization and rescue)

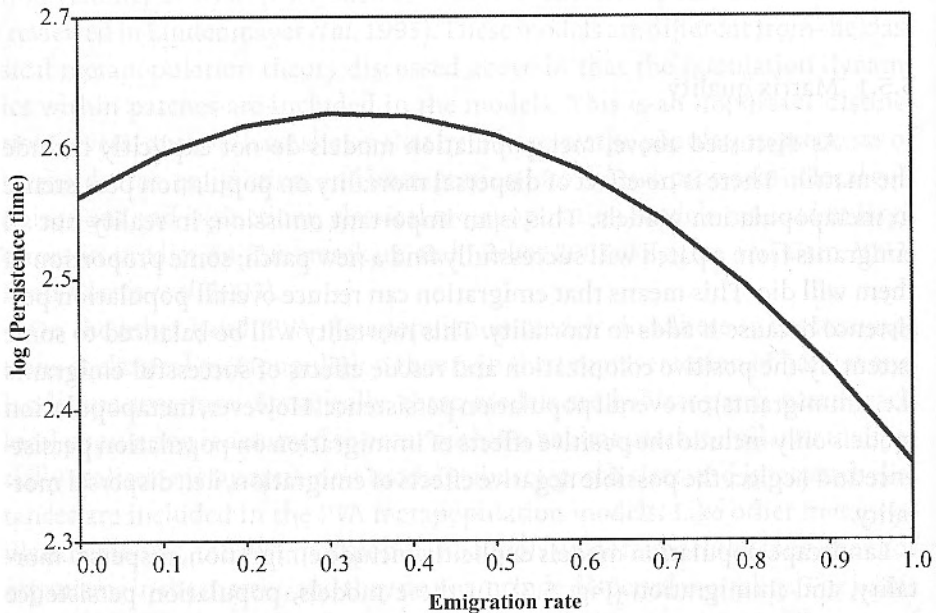


FIGURE 5.4

Relationship between emigration rate and log (population persistence time), based on simulations using a landscape population model (Fahrig 1998). Note that the location of the maximum and the steepness of the curve change with changing model parameters (e.g., reproductive rate, disturbance probability)

population due to the added dispersal mortality (Fahrig 1990, Casagrandi and Gatto 1999).

The negative effect of emigration on population persistence in landscape population models leads to conclusions that are opposite to those normally drawn from a metapopulation analysis. For example, based on their landscape population model of a rare butterfly species, León-Cortés *et al.* (2003) concluded that "contrary to most metapopulation model predictions, system persistence declined with increasing migration rate, suggesting that the mortality of migrating individuals in fragmented landscapes may pose significant risks to system-wide persistence." Similarly, Gibbs (1998) and Carr and Fahrig (2001) found in empirical studies that more mobile amphibian species are more strongly negatively affected by human-caused landscape changes than are less mobile species. Gibbs (2001) points out that this is in contrast to the "widely held notion" that more dispersive species should perform better in human-modified landscapes. This notion is taken from the metapopulation prediction that higher colonization rates lead to higher population persistence, which has been incorrectly interpreted to mean that increasing dispersal (emigration) always has a positive effect on population persistence. Landscape population models, which explicitly include the matrix, do not lead to this erroneous prediction.

Elsewhere I have also argued that the lack of explicit consideration of the matrix in metapopulation models has led to an over-estimate of the effect of habitat subdivision or fragmentation per se relative to the effect of habitat loss on population persistence (Fahrig 2002). In metapopulation models habitat loss reduces population persistence by an assumed reduction in colonization or immigration rate with decreasing habitat amount. In landscape population models, loss of habitat increases the proportion of the population that spends time in the matrix, where reproduction is not possible and where mortality rate is usually assumed to be higher than in breeding habitat. Habitat loss therefore decreases the overall reproduction rate and increases the overall mortality rate in landscape population models. I have argued that this imposes a constraint on the potential for reduced habitat fragmentation to mitigate effects of habitat loss in landscape population models (Fahrig 2002).

In fact, the critical role of dispersal mortality in population persistence was anticipated over 20 years ago in theoretical studies of the evolution of optimal emigration rate, using evolutionary stable strategy (ESS) models (Comins *et al.* 1980, Levin *et al.* 1984, Klinkhamer *et al.* 1987; Fig. 5.5). Optimal emigration rate was shown to be a decreasing function of dispersal mortality rate. Therefore, as matrix quality decreases (i.e., dispersal mortality rate increases), the optimal emigration rate should decrease. This means that, in the face of human alterations to the landscape that reduce matrix quality, such as addition

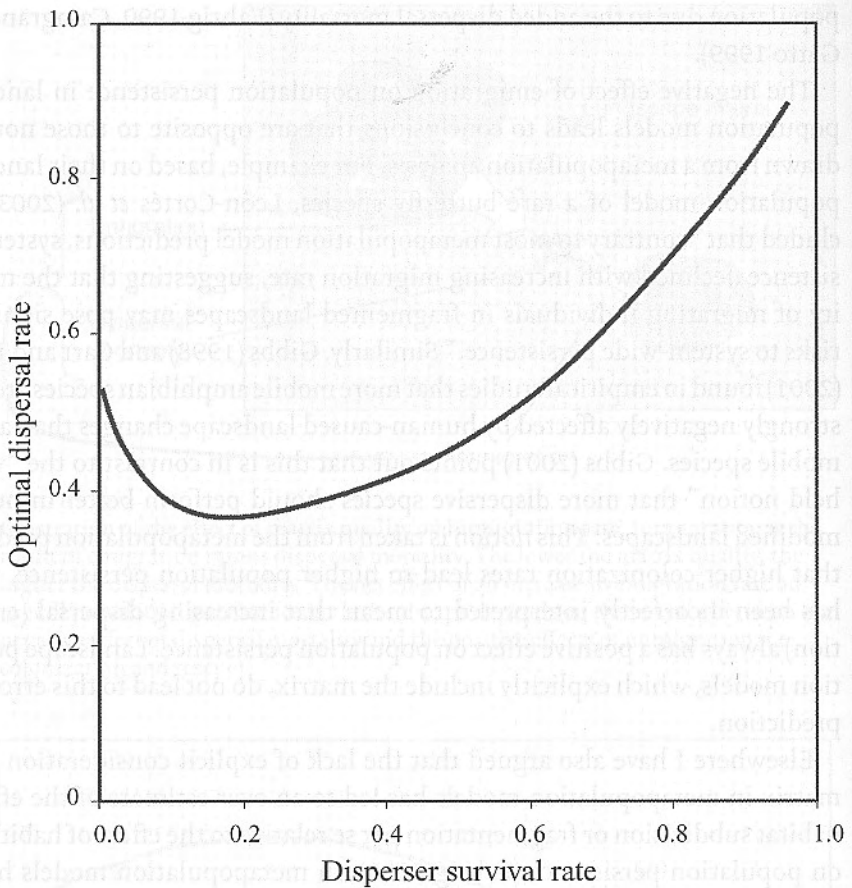


FIGURE 5.5

Optimal dispersal rate as a function of disperser survival rate, based on an evolutionary stable strategy (ESS) analysis of a stochastic spatially implicit patchy population model with random local extinctions (Comins *et al.* 1980). The curve is redrawn from Figure 5.4 in Comins *et al.*, where local extinction probability was 0.1

of roads or pesticide-laden crop fields, species with low emigration rates are more likely to persist than species with high emigration rates, despite the fact that, in the short term, they will have lower rates of colonization of empty patches. The negative effect of emigration is due to an overall increase in mortality rate of the population, which reduces overall population size. This reduction in population size eventually also reduces the probability of recolonization of local extinctions, leading to a downward spiral to extinction (Venier and Fahrig 1996).

5.5.2 Matrix heterogeneity

In addition to overall matrix quality (affecting dispersal mortality), some landscape population models include different types of landcover in the

matrix. Since metapopulation models (including spatially realistic metapopulation models and PVA metapopulation tools) do not include the matrix, they also do not include matrix heterogeneity. Does matrix heterogeneity alter metapopulation predictions of population persistence? Theoretical work has not yet directly addressed this question. However, simulation studies (Gustafson and Gardner 1996, Tischendorf *et al.* 2003) have shown that patch size and isolation are good predictors of patch immigration rates only when the matrix is homogeneous. Bender and Fahrig (2005) conducted spatially explicit simulations and a field study of small mammal movement. They found that when the matrix was homogeneous, patch size and isolation accounted for up to 75 percent of the variation in patch immigration rate in the simulation study, and for 61 percent of the variation in patch immigration rate in the field study. However, when the matrix was heterogeneous, the amount of variation explained by patch size and isolation dropped to as little as 35 percent in the simulation study and to 17 percent in the field study. In an empirical study, Walker *et al.* (2003) found that patch sizes and interpatch distances did not adequately predict the distribution of a rock-dwelling rodent; presence of movement barriers in the landscape (rivers) needed to be included for the model to successfully predict distribution. Similarly, Cronin (2003) found that interpatch movement of an insect parasitoid depended on the type of matrix between the two patches. Therefore, metapopulation predictions, which assume that patch colonization rates are a function of interpatch distances, are likely to be poor when the matrix is heterogeneous. A landscape population model is needed in this situation.

5.5.3 When should population models include matrix quality and heterogeneity?

The more spatial structure that is incorporated into population models, the less feasible they are to parameterize for real species. Therefore, it is important to delineate the situations in which information on landscape structure is needed and when it is not needed. Due to the large potential effect of dispersal mortality on population persistence (Fahrig 2001), information on overall matrix quality is almost certainly always necessary.

This leaves the question: when does the heterogeneity of the matrix (independent of its average quality) affect population persistence? There are two situations in which matrix heterogeneity should matter. First, it seems obvious that information on matrix heterogeneity will be needed if the risk of mortality differs among different types of cover in the matrix. For example, predators may favour certain matrix-cover types, which will result in higher risk of mortality for prey when they travel through them than when they travel through

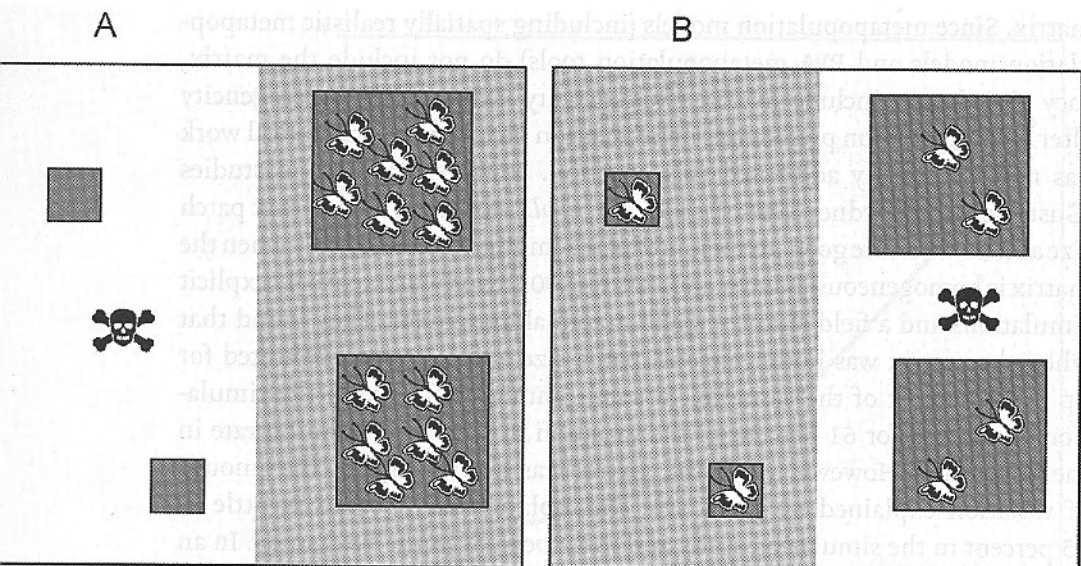


FIGURE 5.6

Illustration of the effect of matrix pattern relative to the habitat pattern, on population size and persistence. Dispersal mortality is high in the white matrix cover type and low in the grey matrix cover type. A and B have the same average matrix quality (averaged over the landscape). However, the overall population size and persistence probability is higher in A than in B because in A most dispersing individuals (i.e., those from the large patches) encounter high-quality matrix, whereas in B most dispersing individuals encounter low-quality matrix. The latter situation results in a higher overall mortality rate for the population

other cover types. In this situation the rate of movement between patches will depend on the cover type(s) that separates them (Fig. 5.6).

The second situation in which matrix heterogeneity will affect population persistence is when the species shows different affinities for different matrix cover types. Landscape population models can incorporate this by using different boundary crossing probabilities for different cover types, such that the probability of a disperser crossing into a benign cover type is high and out of a benign cover type is low, relative to the same probabilities for a more risky matrix-cover type. This type of movement behavior was included in the simulation models of Tischendorf *et al.* (2003) and Bender and Fahrig (2005), and led to a large predicted effect of matrix heterogeneity on interpatch movement. In contrast, Goodwin and Fahrig (2002) simulated a species that showed different movement behaviors within different matrix-cover types, but no difference in mortality among the matrix-cover types and no differential boundary crossing probabilities among matrix-cover types. In this model, matrix heterogeneity had very little effect on interpatch movement.

5.6 Conclusions

Levins' model was an important development in population ecology because it represented a transition from a spatially homogeneous to a heterogeneous representation of habitat. Major changes in metapopulation models over the past 35 years include: (1) the development of spatially realistic metapopulation models, which incorporate the effects of habitat patch sizes and relative locations on extinction and colonization rates, and (2) the development of PVA metapopulation tools which incorporate local population dynamics into a realistic metapopulation modeling framework.

These metapopulation models are useful in some situations. However, they are likely to fail in situations where: (1) the landscape matrix is not benign, i.e., dispersal mortality is potentially important to population dynamics, and (2) the matrix is heterogeneous, resulting in low predictability of colonization from habitat structure (i.e., patch sizes and locations) alone. For many organisms, human alterations to the landscape (e.g., urban and agricultural development) increase the probability of dispersal mortality, thus reducing matrix quality. In addition, these alterations create a heterogeneous landscape matrix from the perspective of dispersing organisms. Therefore, the conditions that compromise the predictive ability of metapopulation models are likely to occur for species of conservation concern in human-dominated landscapes. In these situations, further development of landscape population models will be needed to improve predictions of the effects of landscape structure on population dynamics. Application of landscape population models to species conservation problems will require collection of information that is not currently available in the literature for most species, including rates of emigration from habitat, and movement rates and mortality rates in various matrix-cover types.

Acknowledgments

I thank members of the Landscape Ecology Laboratory at Carleton for comments on and discussion of an earlier draft of this chapter. Two anonymous reviewers provided helpful comments. This work was supported by the Natural Sciences and Engineering Research Council of Canada.

References

- Amarasekare, P. and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *American Naturalist* 158, 572–84.
- Baguette, M. and N. Schtickzelle. 2003. Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Animal Ecology* 40, 404–12.

- Bender, D.J. and L. Fahrig. 2005. Matrix heterogeneity can obscure the relationship between inter-patch movement and patch size and isolation. *Ecology* **86**, 1023–33.
- Cabeza, M. and A. Moilanen. 2003. Site-selection algorithms and habitat loss. *Conservation Biology* **17**, 1402–13.
- Carr, L. W. and L. Fahrig. 2001. Impact of road traffic on two amphibian species of differing vagility. *Conservation Biology* **15**, 1071–8.
- Casagrandi, R. and M. Gatto. 1999. A mesoscale approach to extinction risk in fragmented habitats. *Nature* **400**, 560–2.
- Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionary stable dispersal strategies. *Journal of Theoretical Biology* **82**, 205–30.
- Cronin, J. T. 2003. Matrix heterogeneity and host-parasitoid interactions in space. *Ecology* **84**, 1506–16.
- Drechsler, M., K. Frank, I. Hanski, R. B. O'Hara, and C. Wissel. 2003. Ranking metapopulation extinction risk: from patterns in data to conservation management decisions. *Ecological Applications* **13**, 990–8.
- Fahrig, L. 1990. Interacting effects of disturbance and dispersal on individual selection and population stability. *Comments on Theoretical Biology* **1**, 275–97.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**, 273–92.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* **100**, 65–74.
- Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* **12**, 346–53.
- Flather, C.H. and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist* **159**, 40–56.
- Gibbs, J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* **13**, 263–8.
- Gibbs, J.P. 2001. Demography versus habitat fragmentation as determinants of genetic variation in wild populations. *Biological Conservation* **100**, 15–20.
- Goodwin, B. J. and L. Fahrig. 2002. How does landscape structure influence landscape connectivity? *Oikos* **99**, 552–70.
- Gustafson, E. J. and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**, 94–107.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* **9**, 131–5.
- Hanski, I. and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. *Theoretical Population Biology* **64**, 119–27.
- Henein, K., J. Wegner, and G. Merriam. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. *Oikos* **81**, 168–86.
- Higgins, S. I. and M. L. Cain. 2002. Spatially realistic plant metapopulation models and the colonization–competition trade-off. *Journal of Ecology* **90**, 616–26.
- Klinkhamer, P. G., T. J. de Jong, J. A. J. Metz, and J. Val. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical Population Biology* **32**, 127–56.
- Léon-Cortés, J. L., J. J. Lennon, and C. D. Thomas. 2003. Ecological dynamics of extinct species in empty habitat networks. 1. The role of habitat pattern and quantity, stochasticity and dispersal. *Oikos* **102**, 449–64.
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* **26**, 165–91.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237–40.
- Levins, R. 1970. Extinction. Pages 77–107 in M. Gerstenhaber (ed.). *Lecture Notes on Mathematics in the Life Sciences* 2. Providence, RI: American Mathematics Society.

- Lindenmayer, D.B., M.A. Burgman, H.R. Akçakaya, R.C. Lacy, and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS-space and VORTEX for modelling the viability of wildlife metapopulations. *Ecological Modelling* **82**, 161–74.
- Ovaskainen, O. and I. Hanski. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? *Theoretical Population Biology* **64**, 481–95.
- Ovaskainen, O., K. Sato, J. Bascompte, and I. Hanski. 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. *Journal of Theoretical Biology* **215**, 95–108.
- Risser, P.G., J.R. Karr, and R.T.T. Forman. 1984. *Landscape Ecology: Directions and Approaches*. Special Publication Number 2. Champaign, IL: Illinois Natural History Survey.
- Tischendorf, L., D.J. Bender, and L. Fahrig. 2003. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* **18**, 41–50.
- Topping, C.J. and K.D. Sunderland. 1994. A spatial population dynamics model for *Leptyphantes tenuis* (Araneae: Linyphiidae) with some simulations of the spatial and temporal effects of farming operations and land-use. *Agriculture, Ecosystems and Environment* **48**, 203–17.
- Vandermeer, J. and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* **158**, 212–20.
- Venier, L. and L. Fahrig. 1996. Habitat availability causes the species abundance–distribution relationship. *Oikos* **76**, 564–70.
- Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. *Science* **273**, 1536–8.
- Walker, R.S., A.J. Novaro, and L.C. Branch. 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). *Landscape Ecology* **18**, 187–94.