MATRIX STRUCTURE OBSCURES THE RELATIONSHIP BETWEEN INTERPATCH MOVEMENT AND PATCH SIZE AND ISOLATION

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Abstract. Metapopulation models assume that local population size (in a habitat patch) and therefore local extinction probability, is a function of patch size, and that interpatch movement rate and therefore recolonization of local extinctions is a function of both patch size and patch isolation. We hypothesized that the predictive power of models that relate patch immigration rate to patch size and isolation will be reduced when spatial structure in the landscape matrix (the nonhabitat portion of the landscape) affects organism movement through the landscape. We used a simulation model to evaluate this hypothesis for three different aspects of matrix spatial structure (contrast among matrix cover types, number of matrix cover types, and grain of matrix spatial pattern) and for two different types of movement behavior, representing a specialist and a generalist species. We tested the hypothesis for one aspect of matrix structure (number of matrix cover types) in a translocation field study of the eastern chipmunk (*Tamias striatus*, a habitat specialist) and the white-footed mouse (*Peromyscus leucopus*, a habitat generalist). When the matrix was composed of a small number of cover types, patch size and isolation accounted for up to 75% of the variation in patch immigration rate in the simulation study, and for 61% of the variation in interpatch movement in the field study. However, when the matrix was composed of a large number of cover types, the amount of explained variation dropped to as little as 33% for the simulation study and to 17% in the field study. Our results suggest that patch characteristics, such as patch size and isolation, may be poor predictors of interpatch movement when the landscape matrix is heterogeneous and when the organism responds to boundaries between different matrix cover types. These results imply that habitat patch-based models, such as those based on current metapopulation theory, will perform poorly in these situations.

Key words: immigration; interpatch movement; landscape composition; landscape configuration; landscape matrix; landscape pattern; landscape structure; metapopulation; patch isolation; patch size; small mammals; spatially explicit model.

INTRODUCTION

The metapopulation paradigm has become widespread in ecology and conservation biology. Within this paradigm, an organism's environment is described as a set of habitat patches within a uniform non-habitat "matrix." Patch size and patch isolation are considered to be the important determinants of population distribution. Local population size (within a patch) and therefore local extinction probability is assumed to be a function of patch size, and interpatch movement rate and therefore recolonization of local extinctions is assumed to be a function of both patch size and patch isolation (e.g., Hanski 1994, Day and Possingham 1995, Frank and Wissel 2002).

However, empirical relations between population responses and patch size and/or patch isolation are often weak or even absent (Bender et al. 1998, Mazerolle and Villard 1999, Debinski and Holt 2000). Such results are usually explained in one of two ways. First, if the scale of habitat pattern does not match the scale of movement of the organism in question, there will be no relation between patch isolation and the abundance or distribution of the species (Doak et al. 1990, Levin 1992, Malmer and Enckell 1994, Kareiva and Wennergren 1995, Gustafson 1998). Second, if there is high variability among patches in habitat quality, this may be the over-riding factor determining abundance and distribution, and the effects of patch size and isolation on extinction and colonization may be relatively weak or undetectable (Danielson 1992, Danielson and Anderson 1999).

A third reason why patch size and isolation may poorly predict species abundance and distribution in nature is that spatial structure in the non-habitat ("matrix") portion of the landscape could obscure relationships between interpatch movement and habitat patch size and isolation (Gustafson and Gardner 1996, Wiens 1997). If the species shows different movement responses to different matrix cover types, the movement

paths that individuals take through the landscape will depend on the occurrence and pattern of these cover types in the matrix. This will ultimately influence the rate of interpatch movement (Jonsen et al. 2001, Ricketts 2001, Cooper et al. 2002, Gobeil and Villard 2002, Goodwin and Fahrig 2002*a*, Schooley and Wiens 2003). If all areas of the matrix are the same cover type, or if there is a regular, fine-grained pattern of different cover types in the matrix then interpatch movement should be predictable by patch size and isolation. However, these situations are probably rare (Wiens 1995).

We hypothesized that models based only on habitat patch characteristics such as patch size and isolation will have lower predictive power when applied in situations where the landscape matrix contains a variety cover types, than in situations where the matrix is spatially homogeneous. The predictive power should be further reduced if the cover types are highly contrasting, in terms of the response of the organism to them, and if the pattern of cover types in the matrix is coarse. We used a simulation model to evaluate the logic of this hypothesis and to estimate the degree to which matrix structure is expected to mask the relationship between interpatch movement and patch size and isolation. We did this for three different aspects of matrix structure—contrast among matrix cover types, number of matrix cover types, and grain of matrix spatial pattern—and for two different types of movement behavior, representing a specialist and generalist species. Finally, we tested the hypothesis for one aspect of matrix structure (number of matrix cover types) in a field study of two common species of woodland small mammals in the Ottawa area, the eastern chipmunk (*Tamias striatus*, a habitat specialist) and the white-footed mouse (*Peromyscus leucopus*, a habitat generalist), using return rates from between-patch translocations as a surrogate for interpatch movement rate (Bowman et al. 2002). We predicted that small mammal return rates would be more predictable from patch size and isolation in landscapes with a small number of cover types in the matrix than in landscapes where the matrix contains a diversity of cover types.

METHODS

Simulation model

We used a modified version of the model in Bender et al. (2003), which is a stochastic, spatially explicit model that represents a landscape as a spatial grid of cells. Patches are defined as spatially contiguous cells of the same type. The model simulates movement of individual organisms among patches, and records the number of successful immigrations to each patch in each run. To define the spatial structure of habitat in the current study, we used 95 maps, each representing a 10 × 10 km landscape in southern Ontario, Canada (described in Trzcinski et al. 1999). In these maps,

"habitat" is forest, and the remainder of the landscape (mainly agricultural lands) is matrix. The landscapes represented a range of forest cover from 2.5% to 55.8% and, independently, a range of fragmentation levels from many small patches to fewer large patches. All landscapes were 512 × 512 cells in size.

Movement.—We conducted identical, independent simulations using two different types of movement behavior: random and directed. We used random movement behavior to represent a generalist species that had little aversion to the matrix, and directed movement behavior to represent a habitat specialist that tended to move quickly and directly between habitat patches (Matter 1996, Charrier et al. 1997). Directed movement was never applied within habitat patches. Rather, movement behavior within habitat was always random to simulate searching behavior that is typical within habitat patches (McIntyre and Wiens 1999). Further details of the simulation model are described in the Appendix.

Matrix spatial structure.—Each matrix cover type was assigned a "perceived hospitality" value, which refers to the level of potential threats (e.g., predation, road mortality, restricted or energetically costly movement) perceived by an animal that is confronted with a decision of whether or not to move into that matrix cover type. The relative perceived hospitality values of two adjacent cells then determined the "permeability" of the boundary between them, i.e., the likelihood that moving animals would move from one cell to the other (see the Appendix for implementation details). For example, if an animal were to begin its movement path in a habitat patch or a matrix patch with high perceived hospitality, it would be unlikely to move into an adjacent patch that had a very low perceived hospitality value, whereas it would always enter an adjacent patch with a higher perceived hospitality value (that is, if its movement path directed it there). Thus, the model simulates realistic paths an animal might take when encountering a variety of matrix cover types when moving between habitat patches (see Gardner and Gustafson [2004] for a somewhat similar movement algorithm). Note that for our model, one should not confuse "perceived hospitality" with the concept of patch permeability. Perceived hospitality is an attribute of the cover type as perceived by the organism, while permeability is an attribute of the boundary between two cover types.

We systematically varied three aspects of matrix spatial structure (Li and Reynolds 1994), to determine their relative effects (Fig. 1). Preliminary simulations using homogeneous matrices (one matrix cover type only) indicated that the fit of the relationship between immigration rate and patch size and isolation was not affected by the average perceived hospitality value of the matrix. Nevertheless, in designing the landscapes with spatially structured matrices we attempted to maintain an average perceived hospitality value
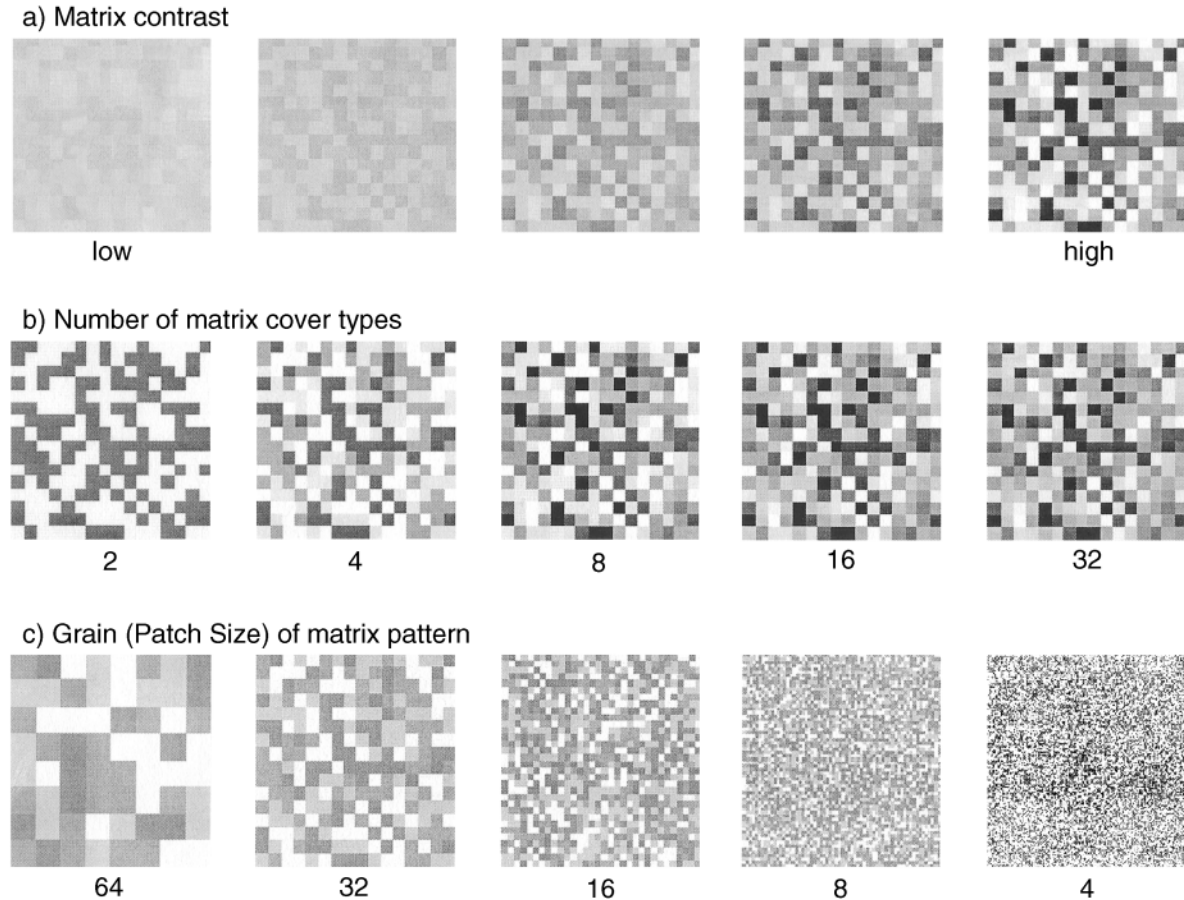
FIG. 1. Graphical representations of three components of matrix spatial structure that were systematically varied in the simulated landscapes.

across all matrix cells of approximately 0.5 for all landscapes (Fig. 1).

The first aspect of matrix structure that we varied was the contrast among different matrix cover types with respect to their perceived hospitability values, i.e., the variability of the perceived hospitability values around the mean value of about 0.5. For example, low matrix contrast might occur where habitat patches are wetlands and the matrix types are different seral stages of forest, which have rather similar perceived hospitability values for an amphibian moving between wetlands. High matrix contrast might occur in a landscape where the matrix types are forest, pasture, and different types of crop fields, which have very different perceived hospitability values for the amphibian.

For the contrast comparison, we kept the pattern of matrix constant and the number of matrix types constant at four, and then varied the four matrix perceived hospitability values (h) from very similar ($h \in \{0.43, 0.48, 0.53, 0.58\}$, 1 SD = 0.07) to very dissimilar ($h \in \{0.05, 0.35, 0.65, 0.95\}$, 1 SD = 0.40; Fig. 1a). We predicted that in landscapes with low contrast matrices, there would be fewer attempts to avoid matrix patches

with low perceived hospitability, because the perceived hospitability values for matrix cover types were all relatively similar. Therefore, there would be less influence of the matrix on animal movement, and movement would be more easily predicted by patch size and isolation in landscapes with low contrast matrices than in landscapes where the contrast among matrix cover types was high (see also Gustafson and Gardner 1996).

The second aspect of matrix spatial structure that we varied was the number of cover types in the matrix. We hypothesized that in landscapes with more matrix cover types there will be more potential decisions an organism must take as it finds a route between patches. Therefore, the number of possible routes should increase with increasing number of cover types, making the prediction of that route more difficult. This should reduce the strength of the relationship between interpatch movement and patch size and isolation.

The third aspect of matrix structure that we varied was the grain of the matrix pattern, from coarse-grained (patch size in the matrix = 64 cells) to fine-grained (patch size in the matrix = 4 cells; Fig. 1c). We hypothesized that if two habitat patches are close together
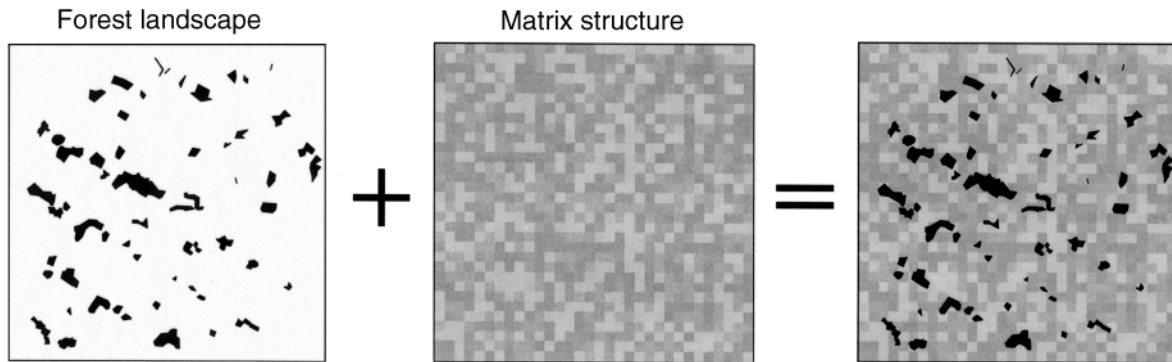
Forest landscape   Matrix structure

Fig. 2. Illustration of how matrix structure was introduced into the 10×10 km forest landscapes for the simulation experiment. Each of the 95 habitat maps was combined with each of the 31 matrix patterns to produce 2945 landscapes.

and the pattern of the matrix is very coarse-grained, then the matrix between those two habitat patches has a high likelihood of being homogeneous. However, another pair of habitat patches in the same landscape that are close together might also be separated by a homogeneous matrix, but by a different matrix cover type (e.g., one that is considerably less hospitable to movement). Therefore, when the matrix pattern is coarse, the predictability of interpatch movement from patch size and isolation should be low. In contrast, the average perceived hospitability of the matrix between two neighboring patches embedded in a fine-grained matrix should be more similar for all pairs, because between patches there will be a large number of different matrix cover types. This should result in a stronger relationship between interpatch movement and patch size and isolation in landscapes with a fine-grained matrix than in landscapes with a coarse-grained matrix. The effect of the grain of matrix spatial pattern might also depend on how many cover types exist in the matrix, i.e., interpatch movement should be less predictable when there are many matrix cover types. Therefore, we simultaneously varied grain and number of matrix cover types (while holding contrast constant) in a factorial design (five levels of grain $\times$ five levels matrix cover types) to assess a potential interaction between these two variables.

Altogether there were 31 different matrix patterns: five levels of each of the three aspects of matrix structure, an additional 15 patterns needed to analyze the interaction between matrix grain and number of matrix cover types, and a homogeneous "control" matrix (perceived hospitability = 0.5) for comparison. We combined each of the 95 habitat maps with each of the 31 matrix patterns (Fig. 2), resulting in 2945 landscapes. For each of these landscapes we conducted 50 replicate runs, using each of the two movement behaviors, resulting in a total of 147 250 simulation runs. In each run, we simulated movement of 250 individuals and their descendents (as described in the Appendix) and the simulation output was the number of immigration

events into each patch occurring over 1000 time steps. These were averaged for each patch over the 50 replicate runs for each landscape.

Analysis of simulation output.—We compared the R^2 value of the model relating patch immigration rate to patch size and isolation across the different levels of each of the three aspects of matrix structure, and each of the factorial levels for the interaction between the number of matrix cover types and the grain of matrix pattern. Patch isolation was estimated from the amount of habitat within a 15-cell buffer area around each patch, which was demonstrated to be a reliable patch-level estimate of isolation (at least for this model) by Bender et al. (2003). We compared the R^2 values from the "control" landscapes (with homogeneous matrices) to the results from landscapes with spatially structured matrices to evaluate (1) our prediction that immigration rate should be more predictable from patch size and isolation in the homogeneous matrix landscapes than in the landscapes with spatial structure in the matrix and (2) the relative effects of the different components of matrix structure (contrast, number of cover types, and grain) on the relationship between immigration rate and patch size and isolation.

Small mammal field study

The purpose of the field study was to test the prediction that the relationship between interpatch movement rate and patch size and isolation would be stronger when the landscape matrix contains few cover types than when it contains many matrix cover types. Unlike the simulation study, it was impossible for us to separate the independent effects of the three components of matrix structure (contrast, number of matrix types, and grain) because we were unable to manipulate the spatial structure of our landscapes in the field. Instead, we used the two extremes that occur in our region: (1) landscapes where the matrix was composed mainly of one land cover type (usually corn fields or pasture fields), and (2) landscapes where the matrix was composed of a great diversity of matrix cover types. Note

that in our landscapes contrast among matrix cover types is not necessarily greater in landscapes with more cover types, and field sizes (grain of matrix pattern) in our area are relatively consistent. Therefore, our field study represented mainly a comparison of the effect of the number of matrix cover types on the relationship between interpatch movement and patch size and isolation. Hereafter, we refer to the landscapes dominated by one matrix cover type as having ''homogeneous matrices'' and landscapes characterized by a high diversity of cover types in the matrix as having ''heterogeneous matrices.''

We translocated woodland small mammals (*Peromyscus leucopus*, ''mice'' and *Tamias striatus*, ''chipmunks'') between forest patches in landscapes with homogeneous vs. heterogeneous matrices and then estimated the probability of return to the patch in which they were captured. We compared the fit of the relationship between the probability of return and patch size and isolation for patches in landscapes with homogeneous vs. landscapes with heterogeneous matrices, to test our hypothesis that patch size and isolation should be better predictors of interpatch movement in landscapes with few matrix cover types than in landscapes with many matrix cover types.

Study area and site selection.—The study was conducted in 20 landscapes south and west of Ottawa, Ontario. The landscapes contained forest patches embedded in a matrix of predominantly agricultural fields, mainly corn, soybean, alfalfa/hayfield, and pasture, as well as abandoned agricultural fields, early-successional forest, and human developed/built-up areas. These land cover types are quite different based on their structural characteristics (e.g., vegetation height and density), and we assumed that our study species also viewed these as distinct types with different perceived hospitability levels (M'Closkey 1975, M'Closkey and Fieldwick 1975, Dueser and Shugart 1978, Vandruff and Rowse 1986). Across the region, some areas are dominated by one type (e.g., corn fields, pastures), whereas other places have many different cover types interspersed. We capitalized on this variation by selecting 2.5 × 2.5 km landscapes that differed in their number of matrix cover types. Ideally, we would have chosen landscapes that varied across a gradient of number of matrix cover types, and then related this measure of matrix structure to the fit of the relationship between animal movement rates and patch size and isolation. However, we were unable to obtain recent classified maps of the landscapes that would allow us to identify and quantify land cover composition accurately. So instead, we chose pairs of nearby landscapes that represented two extremes of matrix structure: those with a rather homogeneously composed matrix (i.e., predominated by corn, hay, or pasture fields) vs. landscapes containing a very high diversity of matrix cover types. We sampled for small mammals at each pair of landscapes (one characterized by a homogeneous ma-
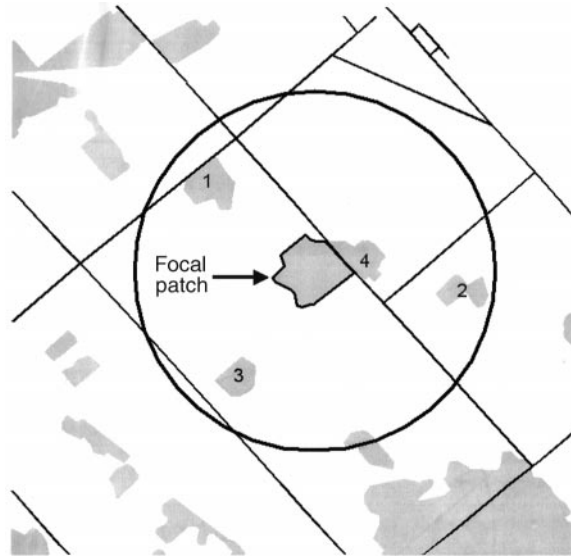

FIG. 3. An example landscape (circle) and surrounding area illustrating a focal patch where small mammals were trapped, and relocation patches (numbered) that were selected from accessible adjacent woodlots. Gray polygons indicate forest patches, and lines indicate roads. White areas are a mixture of agricultural fields, mainly corn, soybean, alfalfa/hayfield, and pasture, as well as abandoned agricultural fields, early-successional forest, and human habitations. The circle indicates a 1250 m radius from the center of the focal patch. Twenty focal patches were sampled, 10 situated in landscapes with homogeneous matrices and 10 in landscapes with heterogeneous matrices.

trix and the other a heterogeneous matrix) for a 1-wk period each between July and October of 1999. The paired design was adopted to control for the increase in small-mammal density that was predicted to occur as the season progressed (Fahrig and Merriam 1985, Wegner 1995, Henein 1995).

We trapped small mammals in a focal patch (Brennan et al. 2002) in the center of each landscape (Fig. 3). All sampled patches were deciduous forest with similar vegetation characteristics, and patches ranged in size from 0.40 to 50 ha (mean = 7.0 ha, 1 SD = 7.8 ha). In each focal patch, two pairs of parallel transects of aluminum Sherman box traps (i.e., four transects in total) were laid out. Each transect began 15 m from the forest edge, and, within each transect, traps were spaced at 5-m intervals. Up to 15 August, 100 traps were used per patch. After that date, the number of traps was reduced to 75 because it became logistically impossible to process the increased number of trapped animals. Traps were baited with birdseed (primarily millet and sunflower seed) and provided with Dacron wool for bedding material. Traps were run continuously for a 6-d period, and checked and rebaited one to three times per day, as necessary. All new captures and recaptures were noted, and some animals were selected for translocation (see next paragraph). On the seventh day of sampling, traps were checked, recovered, and

redeployed to the next pair of sampling sites. We did not sample beyond seven days at a site because we never captured new individuals after the initial four days of trapping, and most (>94%) of the recaptured animals were trapped within 48 hours of their initial capture.

Captured mice and chipmunks were uniquely identified with sequentially numbered Monel ear tags, except for females that were pregnant or lactating, small juveniles, or individuals that did not appear healthy, which were immediately released. Tagged animals were relocated to other forest patches of similar habitat to the focal patch. All but two relocation patches were less than 1000 m from the focal patch, which is the farthest distance a mouse or chipmunk might reasonably move in a day or two (Merriam and Lanoue 1990, Henein 1995, Bowman and Fahrig 2002). However, an abundance of relocation patches were not always available, necessitating placement of one relocation patch at 1210 m and another at 1360 m (different landscapes). Generally speaking, mice and chipmunks in this study area will attempt to return to their home patch following a relocation (K. Henein and J. Wegner, *personal communication*). We capitalized on this behavior, and assumed that animals returning to their home patch would encounter the same landscape features that an animal might encounter when moving naturally between patches in the same landscape. Therefore, we believed that our translocation experiment would simulate movements typical of other movement events, such as seasonal or dispersal movements among forest patches in the landscape. This is supported by Bowman et al. (2002), who showed that in small mammals maximum return distances following translocations are similar to maximum dispersal distances. Although we could not measure the actual rate of movement directly, we were able to measure the proportion of individuals that returned, and used this as a surrogate measure of interpatch movement rate for each species.

Analysis of recapture data.—There were two stages in our analysis of the field data. First, we regressed the percentage of translocated individuals (by species) that returned to each focal patch on focal patch size and average relocation distance (i.e., an index of patch isolation, measured as the mean distance between the focal patch and all relocation patches in that landscape). Note that this index of isolation is performed at the landscape level and differs from the patch-level measure used in the simulation study. We adopted a different isolation index in the field study because we felt that the exact distance of translocation (averaged across all relocation patches in a landscape) was the most precise measure of isolation obtainable, and did not require estimation by means of a metric such as a proximity index. Because more individuals were captured and translocated at some sites than others, the regression was weighted by the number of translocations in each landscape. The term ''species'' (mice or chipmunks) was also included

in the model, as were all first-order interaction terms. Once the regression model was built, our second step was to perform further analysis on the outcome (i.e., the residuals) to determine whether there were differences in the fit of the model with respect to the two landscape types. We used a paired-sample t test to determine if the mean absolute size of the residuals differed between the two types of landscapes. Based on our hypothesis, we predicted that the residuals of the model relating the rate of return to patch size and isolation should be smaller for the homogeneous matrix landscapes than the heterogeneous matrix landscapes. Note that we could not evaluate our hypothesis by simply including landscape type in the regression model, because the hypothesis predicts an effect of landscape type on the fit of the relationship between interpatch movement and patch size and isolation; it does not make any prediction about the effect of landscape type on interpatch movement itself. We also performed separate regressions of return rate on patch size and isolation for the data from each type of landscape (homogeneous and heterogeneous), and then directly compared the R^2 values to quantify the difference in the fit of the two regressions. Finally, we also partitioned the residuals by species and recalculated the regression equations to examine whether there was a difference in the effect of matrix heterogeneity on the fit of the relationship between return rate and patch size and isolation for the generalist species and the specialist species (mouse and chipmunk, respectively).

RESULTS

Simulation study

Overall, the most remarkable result from the simulation study was that the introduction of even a small degree of spatial structure in the matrix (e.g., two matrix types with moderate contrast) reduced the fit of the statistical model relating immigration rate to patch size and patch isolation. Approximately 70% of the variation in immigration rate from simulation runs conducted in landscapes with homogeneous matrices could be accounted for by patch size and isolation (represented by the dashed line in Fig. 4). In contrast, immigration rate in the simulations in landscapes with varying matrix structures often had a much weaker relationship with patch size and isolation (bars in Fig. 4). The grain of matrix pattern had the largest effect on the fit of the statistical model, and the number of matrix types also had an effect (Fig. 4). When the number of matrix cover types was high and the grain of pattern was coarse (i.e., large grain), patch size and isolation could only account for approximately one-half of the variation that they explained in landscapes with homogeneous matrices. This pattern was consistent for both random and directed movement simulations (Fig. 4). The influence of number of matrix cover types appears to depend on the grain of matrix
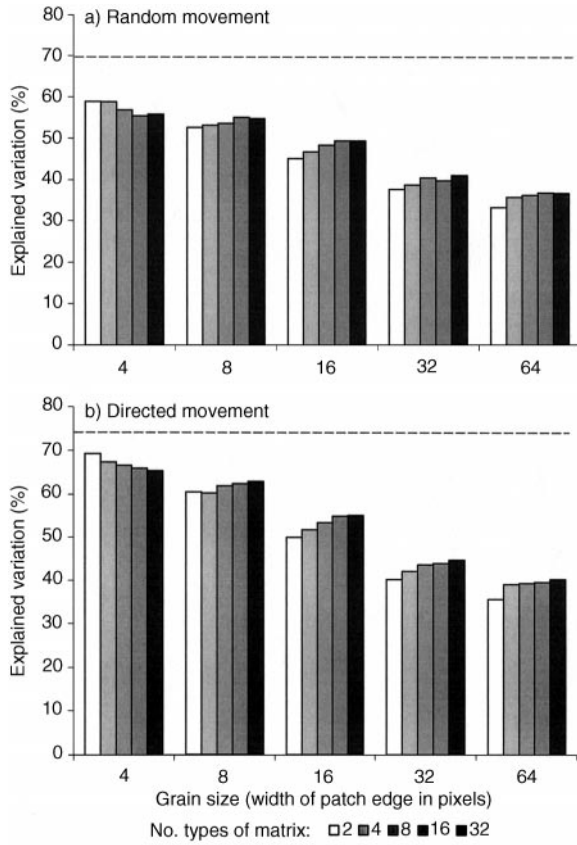
FIG. 4. Amount of variation in immigration rate explained by patch size and isolation for varying degrees of grain size and varying number of matrix cover types constituting the matrix (see Fig. 1). The dashed line indicates the amount of variation that was explained by patch size and isolation in the absence of matrix structure (a homogeneous matrix).

pattern; the number of matrix types was positively related to model fit for coarse patterns, and negatively related to model fit for the fine-grained matrices (Fig. 4).

The degree of contrast in perceived hospitability of the matrix cover types had surprisingly little effect on the fit of the statistical model relating immigration rate to patch size and isolation. The R^2 value decreased only slightly with increasing contrast, and the trend was nearly identical for both random movement (decline in R^2 from 0.39 to 0.37) and directed movement (decline in R^2 from 0.43 to 0.40).

Overall, there were small but consistent differences between simulations using random movement and directed movement, with respect to the fit of the model relating patch immigration to patch size and isolation. For all combinations of landscape patterns, the simulations using random movement patterns (generalist species) had slightly lower fits than the simulations using directed movements (specialist species; see *Methods: Analysis of recapture data*).

Small mammal study

In total, we captured 274 mice and 193 chipmunks. Of these, 180 mice and 103 chipmunks were suitable for relocation. Most of the relocated animals were males because the majority of females captured were lactating and/or visibly pregnant and were therefore not relocated. The overall return rate of relocated animals was approximately 20% (22% for mice and 18% for chipmunks). The return rate did not differ significantly between landscapes with relatively homogeneous matrices and heterogeneous matrices, for either species (Table 1). Therefore, the overall permeability of the two landscape types was similar, so we were able to directly compare the predictability of return rates to patches, from patch size and isolation, between the homogeneous and heterogeneous landscapes.

Prior to analysis of the movement data, we conducted an assessment of data quality. The two landscapes in week four were troublesome because return rates were anomalously low, mainly because all individuals were initially captured on the second-to-last day of trapping, which did not leave sufficient time to retrap returning animals. Using the DFFITS method of PROC GLM in SAS, the return rates (for both species) in week four were identified as strongly influential outliers, and therefore removed from all subsequent analyses. Further, chipmunks were not captured in one of the heterogeneous landscapes, so there is one record with missing data in our analyses.

The first step in the analysis was to construct and evaluate a regression model of return rates (the surrogate for movement rates) based on patch size, isolation, and species. The ANOVA table for the multiple regression model is presented in Table 2. There was a highly significant effect of isolation and a smaller significant effect of patch size on return rate (Fig. 5). There was no effect of species or its interaction terms on return rate, indicating that the nature of the relationship between return rate and patch size and isolation did not differ between mice and chipmunks. We also examined whether there was a correlation between the residuals for mice and chipmunks, but there was none ($r = 0.164$, $P = 0.560$).

TABLE 1. Summary of return rates for white-footed mice and eastern chipmunks in landscapes with relatively homogeneous matrix composition vs. heterogeneous matrix composition.

Species	Matrix type	Returned	Not returned	Return rate (%)
Mice	heterogeneous	21	68	24
	homogeneous	18	73	20
Chipmunks	heterogeneous	7	30	19
	homogeneous	12	54	18

Note: Neither species had significantly different return rates between the two types of landscape matrices (mice, $\chi^2 = 0.39$, df = 1, $P = 0.54$; chipmunks, $\chi^2 = 0.01$, df = 1, $P = 0.93$).

TABLE 2. ANOVA of the relationship between proportion of individuals returning to a patch, and patch size, isolation, and species (mice vs. chipmunks).

Source	df	MS	F	P
Model	5	2.145	4.16	0.005
Patch size	1	2.336	4.54	0.041
Patch isolation	1	7.084	13.75	<0.0001
Species	1	0.170	0.33	0.569
Patch size × species	1	0.105	0.20	0.655
Patch isolation × species	1	0.528	1.02	0.319
Error	31	0.515		

The second step in the analysis was to then compare the fit of the relationship between return rate and patch size and isolation for the two landscape types (homogeneous vs. heterogeneous matrices). We decomposed the residuals from the regression model in step one above, and examined whether the mean absolute value of the residuals differed between landscapes with a homogeneous vs. a heterogeneous matrix. A paired-sample t test revealed that the size of the residuals was significantly different between the two landscape types ($t = 1.84$, $n = 18$, $P = 0.042$). The absolute value of
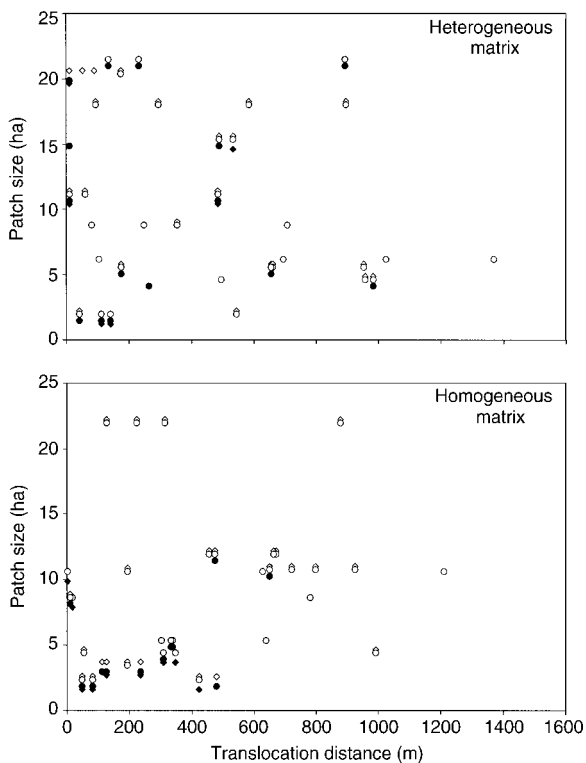

FIG. 5. Plot of individual mice (circles) and chipmunks (diamonds) that returned (solid symbols) or did not return (open symbols) to their patch of capture following translocation to a different patch, as a function of patch area and patch isolation (i.e., distance of translocation). The upper panel shows animals translocated in landscapes with heterogeneous matrices. The lower panel shows animals translocated in landscapes with homogeneous matrices.

TABLE 3. Summary of the fit of the multiple regression of the proportion of returning individuals on patch size and isolation, for landscapes with homogeneous and heterogeneous matrices separately.

Matrix type	R^2	F	df	P
Homogeneous	0.61	12.51	2, 18	<0.001
Heterogeneous	0.17	1.61	2, 17	0.232

the residuals in the landscapes with heterogeneous matrices were more than twice the size of those in the landscapes with homogeneous matrices. Table 3 illustrates this difference: the fit of the relationship between return rate and patch size and isolation is considerably higher for landscapes with a homogeneous matrix than for those with a heterogeneous matrix. Although mice and chipmunks responded to patch size and isolation in a qualitatively similar fashion, the return rates of chipmunks appeared to be more strongly related to patch size and isolation (Table 4).

Although it would have been interesting to further decompose the data by landscape type and species to determine whether, for example, chipmunk return rates were most predictable in landscapes with homogeneous matrices, the sample size of the field data (nine homogeneous and nine heterogeneous landscapes) prohibited this analysis.

DISCUSSION

Our simulation study and empirical results suggest that habitat patch size and isolation can be poor predictors of interpatch movement when the landscape matrix contains many different cover types (heterogeneous matrix) in a coarse-grained pattern. When the matrix was homogeneous (only or mainly one cover type), patch size and isolation accounted for up to 75% of the variation in patch immigration rate in the simulation study, and for 61% of the variation in return rate of translocated animals in the field study. However, when the matrix was heterogeneous, the amount of explained variation dropped to as little as 33% for the simulation study and to 17% in the field study. Although these two studies are not directly comparable because different measures of movement and isolation were used in each case, the consistent pattern is certainly suggestive that matrix structure obscures the influence of patch size and isolation on movement.

Coarsely grained patterns of many matrix cover types obscured the influence of patch size and isolation

TABLE 4. Summary of the fit of the multiple regression of the proportion of returning individuals on patch size and isolation for a habitat generalist (white-footed mouse) and specialist (eastern chipmunk), separately.

Species	R^2	F	df	P
Generalist (mouse)	0.17	1.97	2, 18	0.170
Specialist (chipmunk)	0.74	19.71	2, 17	<0.001

on movement rates the most in the simulation model. This result is consistent with our hypotheses, suggesting that interpatch movement rates are most unpredictable when animal movement paths are influenced by features in the matrix, e.g., they avoid cover types that are perceived to be inhospitable or impermeable by going around them. In comparison to the grain of the matrix pattern and the number of matrix types, the contrast among matrix types had relatively little effect on the relationship between interpatch movement and patch size and isolation in our simulation study. This agrees with Gustafson and Gardner (1996) who simulated interpatch movement in three landscapes, and found only small effects of matrix contrast on the correlation between immigration rate and patch isolation. This result still surprised us because increasing the contrast of matrix types should have increased the number of times movement paths were diverted. It is possible that the range of values we used for varying grain and number of matrix cover types was large in comparison to natural variation in real landscapes. This may have inflated the effect of these factors relative to the effect of contrast among cover types.

Several studies have suggested that interpatch movement of organisms can be affected by the types and pattern of land cover in the matrix (Ricketts 2001, Cooper et al. 2002, Gobeil and Villard 2002, Goodwin and Fahrig 2002a, Tischendorf et al. 2003). Nevertheless, the use of metapopulation-type models that ignore matrix structure remains popular in species management (e.g., McCullough 1996, Lawes et al. 2000, Rodríguez and Delibes 2003). In one sense, this is understandable, because adding matrix structure to a model generally requires more information about movement behavior and habitat use than is available. On the other hand, our results suggest that applying metapopulation-type models in situations where the matrix is heterogeneous and/or coarse-grained may result in a false sense of confidence in the model predictions.

We modeled two types of movement behavior (generalist and specialist) using random movement and directed movement (respectively) to determine whether movement behavior might influence the results. We found that there was a small (<10%) difference between the results for the two movement types, and that interpatch movement rates using random movement were consistently less predictable from patch size and isolation than were interpatch movement rates using directed movement (Fig. 4). In the field study, we observed that generalist (mice) movement was considerably less predictable from patch size and isolation than was specialist (chipmunk) movement (Table 4). Taken together, these results suggest that the movement of habitat generalists may be harder to predict than specialists, especially in landscapes with a heterogeneous matrix. Unfortunately, our data do not allow us to understand why generalists do not respond as predictably to patch size and isolation as specialists. One

plausible explanation is that generalists and specialists respond differentially to matrix cover types while moving between habitat patches. By definition, generalists interact with a larger number of land cover types than specialists, and therefore, they may also respond quite differently to cover types in the matrix when they are moving from patch to patch. If one overlooks this response, predicting movement from information about habitat structure alone (e.g., habitat patch size and isolation) may be insufficient. We did not record and analyze the individual movement paths of our simulated or real animals to confirm this suggestion, but this could be done in a follow-up study.

There are some movement behaviors for which patch size and isolation may be strong predictors of patch immigration, even when the matrix is heterogeneous and coarse grained. For example, Serrano and Tella (2003) suggested that the effects of patch size and isolation are accentuated for animals that display conspecific attraction. Therefore, for such animals, patch size and isolation effects might still be prevalent even when the matrix is heterogeneous. This hypothesis needs to be tested. A second situation where matrix structure may not affect the relationship between interpatch movement and patch size and isolation is when the organism does not display differential responses to the boundaries between different matrix cover types. Goodwin and Fahrig (2002b) studied the effect of matrix structure on interpatch movement. In their model and field system (a beetle), the organism displayed different movement behaviors within different matrix cover types, but did not show any aversion to crossing between cover types. In this situation, the structure of the matrix had very little effect on interpatch movement (see also Fahrig and Nuttle, *in press*).

The implication of our results is that it may often not be appropriate to apply habitat patch-based models, such as those based on metapopulation theory, to populations in patches that are situated in landscapes with spatially heterogeneous matrices, particularly for habitat generalists. Such models implicitly assume that the matrix has either a negligible, or at least a spatially homogeneous effect on animals moving through the landscape. This assumption is violated when animals respond to boundaries between matrix cover types, and we have demonstrated that this response can greatly diminish the capability of a model based on patch size and isolation to predict the relative rates of movement among patches. Under these conditions, it is questionable whether a patch-based approach is appropriate because it may be expected to have low predictive power. Unfortunately, there is no "easy fix" because accounting for the effects of matrix structure on interpatch movement adds considerable complexity to a model (e.g., Ferreras 2001, Goodwin and Fahrig 2002b, James et al. 2002, Sutcliffe et al. 2003, Gardner and Gustafson 2004). Parameterization of such a model requires estimates of mortality and movement behavior, often rep-

resented as values of ''friction'' or ''cost'' associated with each cover type in the landscape. Since the uncertainty in parameterization of such a model will almost always be very high, adding such complexity usually results in only a small improvement to model fit (e.g., R^2 increased from 0.33 to 0.46 in Ferreras [2001]). Whenever matrix structure is expected to have a large effect on movement paths, ''the idiosyncratic nature of each landscape will play a significant role in the fate of dispersing animals'' (Gardner and Gustafson 2004). In this situation, inferring immigration rates from landscape structure may not be feasible; direct empirical estimates of interpatch movements may be required.

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APPENDIX

A description of the simulation model is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-056-A1.