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Research article

Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers

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Abstract

We examined the effects of matrix structure and movement responses of organisms on the relationships between 7 patch isolation metrics and patch immigration. Our analysis was based on simulating movement behaviour of two generic disperser types (specialist and generalist) across mosaic landscapes containing three landcover types: habitat, hospitable matrix and inhospitable matrix. Movement, mortality and boundary crossing probabilities of simulated individuals were linked to the landcover and boundary types in the landscapes. The results indicated that area-based isolation metrics generally predict patch immigration more reliably than distance-based isolation metrics. Relationships between patch isolation metrics and patch immigration varied between the two generic disperser types and were affected by matrix composition or matrix fragmentation. Patch immigration was always affected by matrix composition but not by matrix fragmentation. Our results do not encourage the generic use of patch isolation metrics as a substitute for patch immigration, in particular in metapopulation models where generic use may result in wrong projections of the survival probability of metapopulations. However, our examination of the factors affecting the predictive potential of patch isolation metrics should facilitate interpretation and comparison of existing patch isolation studies. Future patch isolation studies should include information about landscape structure and the dispersal distance and dispersal behaviour of the organism of interest.

Introduction

Inspired by the theory of island biogeography (MacArthur and Wilson 1967), and as a fundamental component of metapopulation theory (Levins 1969; Hanski 1991), patch isolation has been a subject of numerous studies over the past 2 decades. Many empirical studies have examined statistical relationships between a variety of patch isolation metrics and response variables such as abundance or presence/absence of species (Bender et al. Appendix 1). Patch isolation metrics have also been used to infer patch colonization probabilities in metapopulation models (e.g., Verboom et al. (1991) and Adler and Nuernberger (1994), Hanski (1994), Hanski and Thomas (1994), Lindenmayer and Lacy (1995), Moilanen and Hanski (1995), Hess (1996), Lindenmayer and Possingham (1996)). Most spatially explicit metapopulation simulators, such as RAMAS (Boyce 1996; Swart and Lawes 1996), VORTEX (Lindenmayer et al. 1995; Lindenmayer and Lacy 1995) or ALEX (Lindenmayer et al. 1995; Lindenmayer and Possingham 1996) require patch isolation metrics as input. These metrics are usually derived from GIS maps. These models assume that patch isolation metrics equate to immigration and/or colonization rates, but this assumption is usually untested and may often be unfounded (see Haig et al. (1998) for discussion).

The results of studies investigating the effects of patch isolation are quite variable (see Bender et al. Appendix 1). This may be largely due to the unreliability of some of the most popular patch isolation metrics. The purpose of the current paper was to examine how the performance of patch isolation metrics is affected by (i) variation in non-habitat or “matrix” structure in the landscape, and (ii) the movement responses of the organism to landscape structure. Performance was determined as the correlation between patch immigration and the patch isolation metric, where immigration was derived from an individual-based simulation model of animal movement through virtual or “neutral” landscapes (e.g. With (1997)).

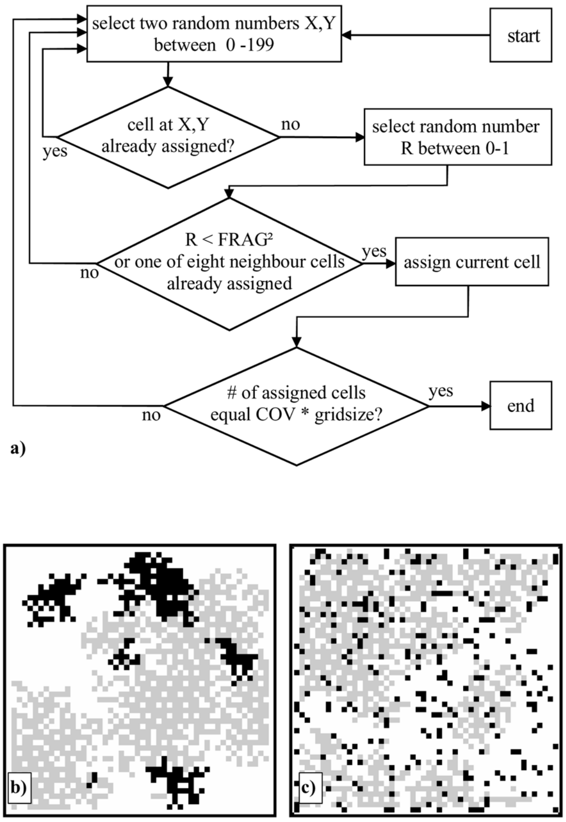

Figure 1. a) Algorithm to generate the mosaic landscape models. b,c) Examples for the generated mosaic landscapes at a resolution of 50 × 50 cells. Both landscapes contain 10 percent habitat (black squares) and 40 percent hospitable matrix area (gray squares). Habitat area is aggregated in a) (H_FRAG = 0.05) and randomly distributed in b) (H_FRAG = 0.81). Hospitable matrix area is aggregated in both landscapes (HM_FRAG = 0.05).

Methods

Model description

Landscape structure

Isolation metrics and immigration for habitat patches were calculated in simulated mosaic landscapes comprised of 3 landcover types. The landscape models corresponded to a square grid of 40,000 cells, where each cell was assigned to one of the 3 landcover types: habitat (H), hospitable matrix (HM), and inhospitable matrix (IM). The assignment of each landcover type was governed by two parameters: COV and FRAG. The proportion of a landcover type in the landscape was defined by COV. FRAG influenced the size and shape of patches by defining the spatial aggregation of assigned cells. A placement algorithm was used to first assign H and subsequently HM to cells of the grid (Figure 1a). The remaining cells were then assigned to IM. The values of the parameters for cover types H and HM used in the simulation experiment are shown in Table 1. The algorithm used to simulate these mosaic landscapes is also described in Fahrig (1997, 1998) and Tischendorf and Fahrig (2000), Tischendorf (2001).

Finally, patches were built by joining adjacent (orthogonal and diagonal) cells of the same landcover type. In the final landscape model, each cell of the grid belonged to one patch, which was uniquely defined by its cover type and an identification number.

Movement behaviour

The movement behaviour of two generic disperser types, a specialist and a generalist, was modelled. We assumed that a specialist disperser has (i) a low probability of crossing boundaries from habitat to matrix (Mader 1984; Wiens et al. 1985; Bakowski and Kozakiewicz 1988; Merriam et al. 1989; Duelli et al. 1990; Mader et al. 1990; Frampton et al. 1995; Mauremooto et al. 1995; Charrier et al. 1997; Sakai and Noon 1997; Haddad 1999), (ii) a high risk of mortality while in matrix (high dispersal mortality) (e.g., Lidicker (1975) and Gaines and McGlenaghan (1980), Krohne and Dubbs (1984), Krohne and Burgin (1987), Garrett and Franklin (1988), Henein and Merriam (1990), Johansen (1994), Fahrig et al. (1995), Schippers et al. (1996), Charrier et al. (1997), Poole (1997), Sakai and Noon (1997), Bonnet et al. (1999), Beaudette and Keppie (1997)), and (iii) fast movement and high inter-step movement correlation, i.e., small turning angles between consecutive movement steps, in matrix (e.g., Baars (1979) and Rijnsdorp (1980), Wallin and Ekbom (1988), Wegner and Merriam (1990), Hansson (1991), Andreassen et al. (1996), Matter (1996), Charrier et al. (1997), Collins and Barrett (1997), Rosenberg et al. (1997)). In con-

Table 1. Parameters used to create landscapes for simulation experiments, and their factorial combinations. Each cell in the landscape was one of 3 types: habitat, hospitable matrix, and inhospitable matrix. Only parameters for habitat and hospitable matrix were explicitly controlled because these parameters completely constrain the amount and pattern of inhospitable matrix. "Range" indicates the range over which the parameter was varied, "step" is the step size for parameter selection within the range and "variations" is the resulting number of levels for that parameter. The number of levels of HM_COV is constrained by H_COV. All factorial combinations result in 1,554 landscapes.

Parameter Name	Parameter Description	Range	Step	Variations
H_COV	amount of habitat (proportion of grid)	0.1–0.7	0.1	7
H_FRAG	fragmentation of habitat	0.05–1	0.19	6
HM_COV	amount of hospitable matrix	0 – (1-H_COV)	0.1	10, 9..., 3
HM_FRAG	fragmentation of hospitable matrix	0.05–1	0.19	6

Table 2. Model parameters defining the specialist and generalist disperser types. Each type is defined by a set of parameters for each of the three different cover types in the landscape model (habitat, hospitable matrix and inhospitable matrix). Step length determines the distance moved per movement step, and is the expected value of a negative exponential distribution (individual step lengths are drawn from the distribution). Step angle is drawn from a uniform probability distribution within the range of angles shown. Boundary crossing probability defines the probability that an individual crosses that boundary type, on each encounter.

Disperser Type	Parameters	Cover Type		
		Habitat (H)	Hospitable Matrix (HM)	Inhospitable Matrix (IM)
Specialist	mortality (rate per 1000 movement steps)	0.1	0.5	1
	step length	1	3	5
	step angle	± 180°	± 45°	± 5°
	boundary crossing probability	H → HM: 0.3 H → IM: 0.1	HM → H: 1 HM → IM: 0.2	IM → H: 1 IM → HM: 1
Generalist	mortality (rate per 1000 movement steps)	0.1	0.2	0.5
	step length	1	1	2
	step angle	± 180°	± 180°	± 135°
	boundary crossing probability	H → HM: 0.9 H → IM: 0.7	HM → H: 1 HM → IM: 0.7	IM → H: 1 IM → HM: 1

trast, generalist dispersers have a higher probability of leaving habitat, lower dispersal mortality while travelling through matrix, and less directed movement paths in matrix (i.e., larger turning angles between consecutive movement steps).

The disperser types' responses to landscape structure were implemented by linking movement, mortality and boundary crossing of individuals to cover and boundary types in the landscape model. The actual value of a dispersal parameter experienced by an individual in a time step therefore depended on the individual's position on the modeled landscape at that time (Table 2). Individual movement was defined by two parameters: step length, drawn from an exponential distribution, and step angle, drawn from a uniform distribution. The expected value of the exponential distribution and the range of the uniform distribution depended on the landcover type (Table 2). Decisions on mortality (per time step) and boundary crossing were made by comparing the current value of these parameters (depending on the individual's position) to random numbers between 0 and 1. If the random number was smaller than the parameter value, the individual 'died' in the case of mortality or, in the case of boundary crossing, it crossed into the other landcover type. If the individual did not cross the boundary, it returned to the previous patch, by adding 180° to the direction of the next movement step. Individuals who left the landscape re-entered at the opposite border, resulting in no net losses or gains due to emigration from or immigration into the landscape (Haefner et al. 1991).

Simulations

Simulations were conducted on 1,554 landscapes models (see Table 1) for each of the 2 disperser types. Each landscape model represented a different configuration of the three cover types, as a result of a factorial combination of the four landscape parameters

(Table 1). Each simulation run comprised 1,000 movement steps for each of 800 individuals. The individuals were initially randomly distributed across the habitat cells. Each simulation run was repeated 10 times for each of the two disperser types on the same landscape model.

Analysis of model output

Immigration was defined as the first time an individual entered a habitat patch; any re-entry into a habitat patch previously visited by that individual was not counted as immigration. The response variable, patch immigration, was the average (over 10 simulation runs) of the total number of immigrations to a habitat patch.

Seven patch isolation metrics were calculated for a set of patches from each landscape model (Table 3). The calculation of patch isolation metrics was restricted to focal patches ranging between 50 and 150 cells in size, to reduce effects of patch size and shape on the isolation metrics. Our results are based on analyzing patch isolation metrics and patch immigration for a random sample of 2500 habitat patches in this size range. Patches used in the calculation of the metrics, however, were not limited to the restricted patch sizes of the focal patches.

The landscape was treated as a torus when calculating patch isolation metrics, i.e., the spatial neighbourhood of each habitat patch was never cut off at a landscape border, but was linked to the opposite side of the landscape. This approach avoids biases of patch isolation metrics near landscape borders and is consistent with the torus implementation of the individuals' movement. The mean of the dispersal distance over all individuals (summed for each individual over its 1000 movement steps) was used for calculating the 2 patch isolation metrics that depended on dispersal distance (DDIST, DPROX, see Table 3).

Analyses began with patches from landscape models containing ten percent habitat (i.e., H_COV = 0.1, Figure 1b, 1c and Table 1), since this proportion of habitat results in very patchy landscapes (e.g., Gardner et al. (1987) and With et al. (1997)). Correlation coefficients between all patch isolation metrics and patch immigration were calculated, for the generalist and specialist disperser types. In a second step the correlation coefficients were calculated separately for all other levels of habitat amount, i.e., for increasingly less patchy landscapes.

To examine the influence of matrix structure on the ability of the isolation metrics to predict patch immigration, an ANCOVA (SAS Institute 1990) was conducted with patch immigration as the dependent variable, HM_COV and HM_FRAG as independent class variables and patch isolation metrics as covariates. The interaction effects between each of the two class variables HM_COV and HM_FRAG and the patch isolation metric indicated the degree to which the relationship between the isolation metric and patch immigration depended on the amount or fragmentation of hospitable matrix. Correlation coefficients were also calculated between the patch isolation metrics and patch immigration separately for each level of the variable HM_COV.

Results

Figure 2 shows the correlation coefficients between the patch isolation metrics and patch immigration for the generalist and specialist disperser types. Patch isolation metrics predicted patch immigration consistently better for the generalist disperser type (compare Figures 2a and 2b). For the generalist disperser type, correlation coefficients were slightly higher when (i) information was included on the mean dispersal distance (i.e., DDIST and DPROX) and (ii), the metric was based on amount of habitat in a buffer zone (BUFFER and PROX). DPROX performed best for the generalist disperser type. In contrast, for the specialist disperser type the dispersal distance dependent isolation metrics DDIST and DPROX did not result in higher correlations between patch immigration and patch isolation metrics. In fact, DPROX predicted patch immigration worse than PROX, in particular with increasing buffer distance (compare DPROX_10 and DPROX_50 in Figure 2b).

For both disperser types buffer distance did not affect the fit of the proximity index (PROX). Increasing buffer distance did, however, result in poorer fits of the BUFFER metric for the generalist disperser type. For the specialist disperser type, correlations between DPROX and immigration rate declined with increasing buffer distance (Figure 2b).

To summarize, metrics based on the amount of habitat area surrounding the focal habitat patch (PROX, DPROX, BUFFER) predicted patch immigration rates generally more reliably than did metrics based on inter-patch distances (NDIST, DDIST). The comparison between the two disperser types revealed

Table 3. Patch isolation metrics used in this study. The metrics belong to one or more of three categories. 1) distance-based measures (e.g., NDIST); 2) area-based measures (e.g., BUFFER_B) and 3) dispersal distance dependent measures (e.g., DDIST). Complexity and assumed performance increase from NDIST to DPROX_B, the latter belonging to all three categories.

Abbreviation	Definition	Description
NDIST		Edge to edge distance to the nearest habitat patch – This metric defines isolation by the distance of a focal patch to its nearest neighbour without considering the size of the nearest neighbour patch nor other patches in the vicinity of the focal patch. Isolation is expected to decrease with increasing values of NDIST.
DIST_5	$\sum_{j=1}^{5}\frac{DIST_j}{5}$	Average distance to the five nearest patches – This metric defines isolation by the average of the distances to the five nearest neighbours. Considering more neighbour patches in the vicinity of the focal patch might lead to a better prediction of the actual isolation of the focal patch. Isolation is expected to decrease with increasing DIST_5.
DDIST	$e^{-DIST/d}$	Exponential, dispersal distance (d) weighted edge to edge distance to nearest patch – This metric weights the distance to the nearest habitat patch by the dispersal distance of an organism. Isolation is expected to increase with increasing DDIST.
DDIST_5	$\sum_{j=1}^{5}\frac{e^{-DIST_j/d}}{5}$	Average of DDIST to five nearest patches (j) – This metric averages the weighted edge to edge distances to the five nearest neighbours. Isolation is expected to increase with increasing DDIST_5.
BUFFER_B: B = 10, 30, 50		Sum of all habitat cells within a buffer distance (B) – This metric defines isolation by the total amount of habitat located within a buffer area surrounding the focal habitat patch. Isolation is assumed to decrease with increasing habitat area, i.e., with increasing values of BUFFER.
PROX_B: B = 10, 30, 50	$\sum_{j=1}^{N}\frac{A_j}{DIST_j}$	Sum of the ratio between area (A) and DIST for all patches (N) within a buffer distance (B) around a patch – This metric weights the area of all patches within a buffer distance by the edge to edge distance of these patches to the focal patch. Large patches, which are close to the focal patch have a stronger effect on reducing isolation than small remote patches. Isolation is expected to decrease with increasing PROX_B.
DPROX_B: B = 10, 30, 50	$\sum_{j=1}^{N}e^{-DIST_j/d}A_j$	Sum of the product between area (A) and DDIST for all patches (N) within a buffer distance (B) – This metric weights the area of all patches within a buffer distance by the distance of these patches to the focal patch and by the dispersal distance of an organism. Isolation is expected to decrease with increasing DPROX_B

contradicting effects of buffer distance and the inclusion of dispersal distance in the isolation metrics, on their correlations with patch immigration.

The effect of matrix structure on the statistical relationships between the isolation metrics and patch immigration is shown in the interaction terms between the isolation metrics and HM_COV and HM-_FRAG in Table 4. There were significant interaction effects between matrix composition and all proximity metrics (PROX) and some buffer metrics (BUFFER) for both disperser types (Table 4a, 4b). The effect of matrix composition on the relationship between patch isolation metrics and patch immigration is also reflected in the range bars in Figure 2. The range bars are the minima and maxima of the correlation coefficients, when calculated separately for the different values of HM_COV, i.e., different amounts of hospitable matrix area. Matrix fragmentation affected relationships between two DPROX metrics and one BUFFER metric and patch immigration for the generalist disperser type (Table 4a). In contrast, matrix fragmentation affected relationships between two

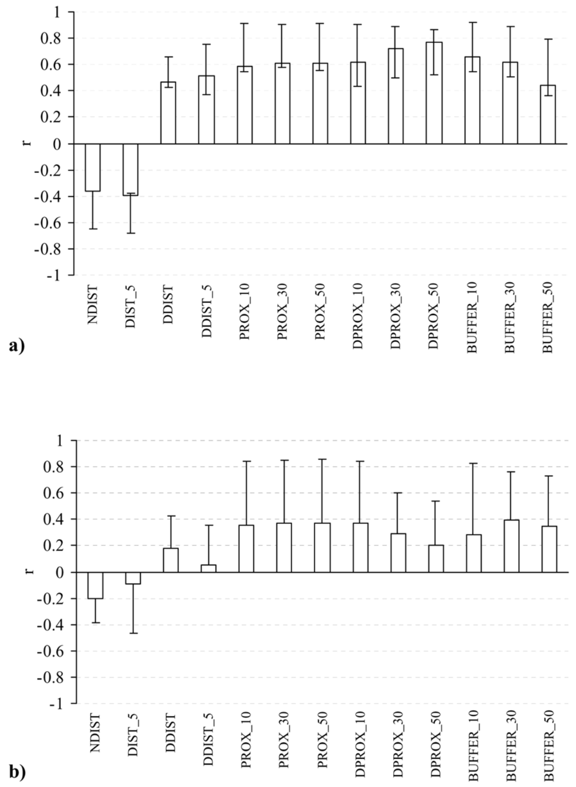

Figure 2. Correlation coefficients between the patch isolation metrics (see Table 3) and patch immigration for (a) generalist and (b) specialist disperser types. Bar heights correspond to the correlation coefficients obtained from model landscapes with 10 percent habitat. The range bars show the range of the correlation coefficients when calculated separately for different amounts of hospitable matrix (HM_COV).

nearest neighbour metrics and patch immigration for the specialist disperser type (Table 4b). Main effects of HM_COV on patch immigration were significant in all statistical models and main effects of HM-_FRAG on patch immigration were not significant in any of the models.

Table 4. Effects of matrix composition (HM_COV) and matrix fragmentation (HM_FRAG) on the relationships between the patch isolation metrics and patch immigration. Presented are the F-values for the interaction effects of patch isolation metrics (column 1) and (i) matrix composition (column 2) and (ii) matrix fragmentation (column 3), on patch immigration.

Isolation Metric	F-value for Isolation Metric *HM_COV (df=8)	F-value for Isolation Metric *HM_FRAG (df=5)
a) generalist disperser type		
NDIST	0.77 ns	0.46 ns
DIST_5	0.84 ns	0.32 ns
DDIST	0.95 ns	0.59 ns
DDIST_5	1.21 ns	0.36 ns
PROX_10	2.44*	0.76 ns
PROX_30	2.64*	1.12 ns
PROX_50	2.46*	0.97 ns
DPROX_10	0.95 ns	2.94*
DPROX_30	1.89 ns	2.97*
DPROX_50	1.61 ns	2.21 ns
BUFFER_10	1.55 ns	3.19**
BUFFER_30	2.43*	0.84 ns
BUFFER_50	2.08*	1.89 ns
b) specialist disperser type		
NDIST	0.44 ns	2.52*
DIST_5	1.12 ns	1.53 ns
DDIST	0.41 ns	2.46*
DDIST_5	1.08 ns	1.71 ns
PROX_10	2.97**	2.01 ns
PROX_30	3.07**	2 ns
PROX_50	3.08**	2.09 ns
DPROX_10	1.19 ns	1.09 ns
DPROX_30	0.56 ns	0.66 ns
DPROX_50	0.91 ns	1.29 ns
BUFFER_10	2.55*	1.98 ns
BUFFER_30	0.49 ns	0.44 ns
BUFFER_50	1.27 ns	0.96 ns

ns = not significant
* $p < 0.05$
** $p < 0.01$

The results presented in Figure 2 and Table 4 are based on patchy landscape models containing 10 percent habitat area, i.e., a subset of all simulated mosaic landscapes. A correlation analysis with data pooled over all 1,554 landscape models produced results that we were not able to interpret. The main reason for this was that the relationships between the patch isolation metrics and patch immigration were non-linear (Figure 3). Changes in patch immigration become smaller with increasing distance to another patch (Figure 3a) or with increasing habitat amount in a buffer zone (Figure 3b). Since habitat amount in the neighbourhood of the patch was the main determinant of all the isolation metrics, the performance of the metrics depends on where in the range of habitat amount they are applied. Increasing habitat amount results in larger values of the buffer and proximity metrics and in shorter inter-patch distances. Figure 4 shows how the correlation coefficients and slopes of the relationships between patch isolation metrics and patch immigration changed with increasing habitat amount in the landscape. Both correlation

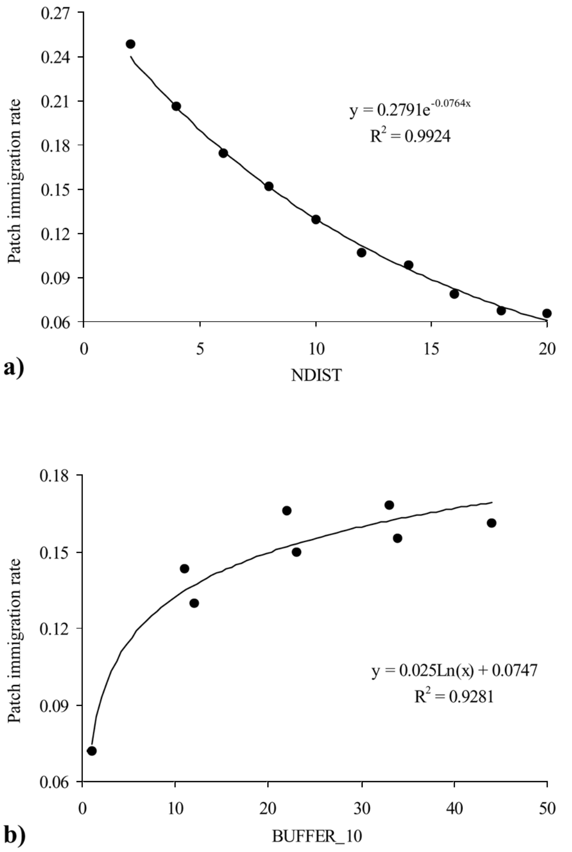

Figure 3. Nonlinear relationships between patch isolation metrics and patch immigration: a) exponential decline of patch immigration with increasing distance to nearest neighbour patch (NDIST see Table 3); b) logarithmic increase of patch immigration with increasing habitat amount in a 10 cell wide buffer surrounding the focal patch (BUFFER see Table 3).

and slope values varied greatly with changes in habitat amount. Generally, the predictive potential (slopes of relationship lines) of patch isolation metrics declined with increasing habitat amount; high correlation coefficients only coincided with higher slope values at low amounts of habitat.

Discussion

All patch isolation metrics were correlated with patch immigration. Correlation coefficients were generally higher for area-based isolation metrics than distance-based metrics. Our results suggest that the buffer metrics have the highest potential correlation with patch immigration, but the correlation depends on size of the buffer area used. Proximity metrics have lower overall correlations, but are robust to increases in the buffer area. Proximity metrics predict patch immigration more consistently than buffer metrics because they include effects of patches whose area lies mostly outside of the buffer zone of the focal patch. An increase in the buffer distance will only result in a dif-

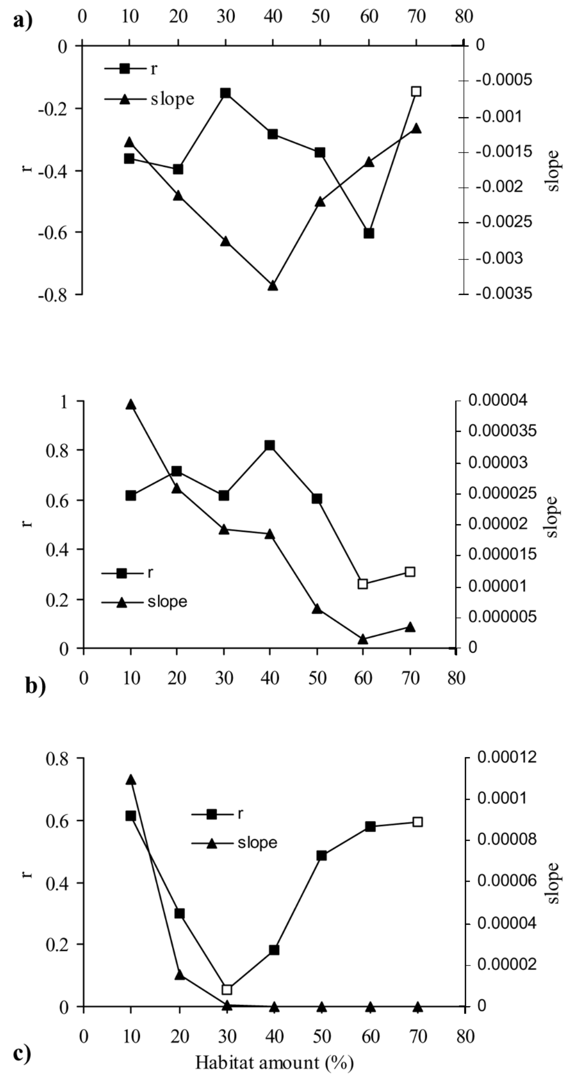

Figure 4. Correlation coefficients and slope values of the relationships between patch isolation – (a) NDIST; (b) BUFFER_30; (c) PROX_30 – and patch immigration for different habitat amounts in the model landscapes. Black squares indicate significant ($p < 0.01$) and white squares indicate non-significant correlations. Correlation and slope values for BUFFER_30 and PROX_30 declined with increasing habitat amount. This results from the nonlinear relationships between these patch isolation metrics and patch immigration (see Figure 3). Note that PROX_30 produces high correlation coefficients at high habitat amount despite very low slope values. These correlation coefficients are therefore not reliable.

ferent proximity value if a new patch is included in the calculation. In contrast, the value of a buffer metric increases steadily with increasing buffer distance. The most reliable buffer metric is obtained when the buffer distance matches the dispersal distance of the organism (Bender et al. 2002).

Results of a related study (Bender et al. 2002) indicate a much lower predictive potential of the proximity indices when applied in landscape patterns obtained from GIS landcover maps. These lower correlations result from the co-occurrence of very large and very small patches in realistic landscapes, in contrast to the occurrence of similar patch sizes in artificially generated landscapes. For instance, if a very large habitat patch overlaps with the buffer zone surrounding a small focal habitat patch, then the area of the very large patch will significantly increase the value of the proximity index. However, this is unlikely to be reflected in a similar increase in patch immigration. This potential for disproportional changes in a predictor variable (proximity index) relative to the response variable (patch immigration) may weaken statistical relationships.

Our results indicate a generally lower predictive potential of patch isolation metrics for the specialist disperser type than the generalist disperser type. This seems counter-intuitive at first. We expect specialists to be sensitive to patch isolation because habitat loss in a landscape and patch isolation are directly related (Fahrig 1997). However, our study indicates that the relationship between spatial isolation of a habitat patch and patch immigration is weaker for specialists than generalists. This can be explained by the fact that the specialist has a more pronounced (negative) response to the matrix (nonhabitat) cover types of the landscape. Therefore, the specialist's immigration rate into habitat patches is more strongly affected by matrix structure than is the generalist's. This reduces the strength of the relationship between patch isolation metrics and patch immigration for the specialist, because matrix structure is not incorporated in the calculation of the patch isolation metrics. The dispersal behaviour of an organism therefore affects the reliability of patch isolation metrics.

None of the patch isolation metrics suggested to date considers the structure of the non-habitat or matrix portion of the landscape. We found that matrix composition (i.e., the proportion of hospitable and inhospitable matrix types) and matrix fragmentation affected the relationships between some patch isolation metrics and patch immigration. This suggests that omission of matrix structure from isolation metrics can compromise these metrics. This effect was strongest for the patch isolation metric D_PROX.

What are the implications of these findings and how important are they for future work related to patch isolation? Bender et al. (2002) showed that some isolation metrics are better than others, but that variation in patch size and shape and the spatial extent (scale) over which the metric is calculated strongly influence the reliability of these metrics. From the current study we predict that matrix structure and dispersal behaviour in response to landscape structure can also compromise the reliability of isolation metrics. In aggregate, the results are therefore not encouraging regarding the generic application of patch isolation metrics. However, they should help in interpretation of results of future studies and facilitate comparisons of these with existing patch isolation studies. Such interpretations will be made easier if the conditions associated with a study are reported. These include information about patch sizes and shapes, the scale of dispersal relative to the isolation metric (e.g., ratio between dispersal distance and buffer width), the structure of the landscape (including the matrix), and the dispersal behaviour of the organism in response to the various landscape elements. While detailed information is unlikely to be available on all of these, some information, such as whether the species is considered a specialist or generalist, can help with the assessment.

Our results also suggest that there are problems in the application of patch isolation metrics in metapopulation models to empirical systems, where these metrics are assumed to be correlated with immigration (or colonization) rates (e.g., Verboom et al. (1991) and Adler and Nuernberger (1994), Hanski (1994), Hanski and Thomas (1994), Lindenmayer and Lacy (1995), Moilanen and Hanski (1995), Hess (1996), Lindenmayer and Possingham (1996)). Patch isolation metrics are also the 'virtual' link of metapopulation simulators to real landscapes (e.g., RAMAS, VORTEX or ALEX (Lindenmayer et al. 1995; Lindenmayer and Lacy 1995; Boyce 1996; Lindenmayer and Possingham 1996; Swart and Lawes 1996). Projections of the survival probability of metapopulations made by these models depend on values of patch isolation metrics derived from landcover maps. However, our results suggest that these values do not necessarily predict the immigration rates into patches. An overestimation of patch immigration might result in too optimistic projections of metapopulation persistence. Individual parameterization or calibration, rather than generic application of patch isolation metrics in metapopulation models is necessary to avoid misleading conclusions (Haig et al. 1998).

In conclusion, our results generally confirm the finding of a related study (Bender et al. 2002) that area-based isolation metrics are more reliable predictors of immigration than distance-based metrics. However, our results suggest that the reliability of these metrics can depend on the structure of the whole landscape and, in particular, how sensitive the dispersal behaviour (including dispersal mortality) of the organism in question is to the structure of the nonhabitat or matrix portions of the landscape. We suggest that patch isolation metrics are least reliable for specialist species, which are expected to show the highest sensitivity to matrix structure.

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