



## Using patch isolation metrics to predict animal movement in binary landscapes

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### Abstract

Habitat isolation can affect the distribution and abundance of wildlife, but it is an ambiguous attribute to measure. Presumably, isolation is a characteristic of a habitat patch that reflects how spatially inaccessible it is to dispersing organisms. We identified four isolation metrics (nearest-neighbor distance, Voronoi polygons, proximity index, and habitat buffers) that were representative of the different families of metrics that are commonly used in the literature to measure patch isolation. Using simulated data, we evaluated the ability of each isolation metric to predict animal dispersal. We examined the simulated movement of organisms in two types of landscapes: an artificially-generated point-pattern landscapes where patch size and shape were consistent and only the arrangement of patches varied, and realistic landscapes derived from a geographic information system (GIS) of forest-vegetation maps where patch size, shape, and isolation were variable. We tested the performance of the four isolation metrics by examining the strength of the correlation between observed immigration rate in the simulations and each patch isolation metric. We also evaluated whether each isolation metric would perform consistently under varying conditions of patch size/shape, total amount of habitat in the landscape, and proximity of the patch to the landscape edge. The results indicate that a commonly-used distance-based metric, nearest-neighbor distance, did not adequately predict immigration rate when patch size and shape were variable. Area-informed isolation metrics, such as the amount of available habitat within a given radius of a patch, were most successful at predicting immigration. Overall, the use of area-informed metrics is advocated despite the limitation that these metrics require parameterization to reflect the movement capacity of the organism studied.

### Introduction

Patch isolation is a key component of patch-based approaches that seek to predict the distribution of organisms in spatially-subdivided populations. Prime examples of the patch-based approach include the theory of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Levins 1970; Hanski and Gilpin 1991). These two theories have profoundly influenced the way we think about spatially-subdivided populations or communities, and axioms like “patch size” and “patch isolation” have become embedded within the vernacular of landscape

ecology. For example, it has become almost dogma that the smallest and most isolated patches in a landscape are expected to have relatively low species richness, low abundance, and increased risk of population extinction (e.g., Diamond (1975), [p.143] figure of reserve design that appears in most college textbooks of conservation biology). This supposition is based, at least in part, on the assumption that spatially isolated patches receive few or no immigrants to colonize that patch or to offset potential population declines (MacArthur and Wilson 1967; Hanski 1998; Hanski and Ovaskainen 2000).

Patch isolation has also been a key consideration in numerous empirical studies that have examined the influence of habitat fragmentation and/or patch isolation on wildlife populations (Appendix 1), perhaps because of the influence of the theories like island biogeography and metapopulation theory. However, patch isolation is a difficult attribute to quantify in practice. Patch isolation, from a landscape ecology perspective, refers to the inaccessibility of a habitat patch for migrants moving from other patches. If one assumes that the land between patches (matrix) is homogeneous, then inaccessibility should be some function of the spatial relationships of patches (i.e., the configuration of habitat). Patch characteristics such as patch shape and size may also be a factor because larger, non-compactly shaped patches may “intercept” more immigrants than small, compact patches, particularly if there is some random component to an organism’s movement behavior.

Many metrics have been used in the literature to describe patch isolation (Appendix 1), but we are not aware of any studies that have attempted to evaluate the efficacy and reliability of different isolation metrics. Thus, the goal of this study was to determine which isolation metric provides the most reliable measure of patch isolation as it relates to dispersing organisms. We also evaluated how useful isolation is for predicting animal movement under different types of landscape scenarios, and we made the distinction between isolation (spatial configuration) effects and patch character (size and shape) effects on patch (in)accessibility.

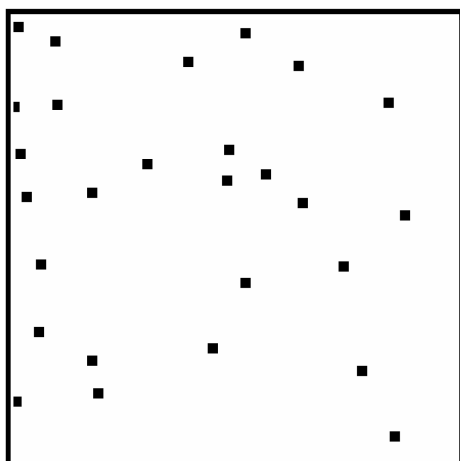
### *Types of landscapes*

Landscapes can be modeled (i.e., mapped) in at least four ways, and the different approaches affect how one employs and interprets patch isolation metrics. Figure 1 illustrates four approaches to modeling landscapes, which can be viewed as a progression of increasing complexity and realism.

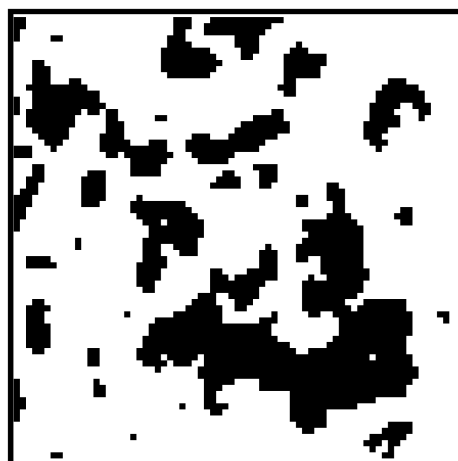
The first landscape type is the point-pattern map (Figure 1a). In this approach, patches of habitat are discrete and exist in a homogeneous matrix. The sizes and shapes of the patches are either consistent or deemed to be unimportant. The configuration of patches (i.e., spatial pattern) is of central interest. The second type of landscape is the binary landscape (Figure 1b). It is an extension of the point-pattern, except that patches have realistic, possibly irregular shapes of varying sizes. Note, however, that there are still

only two states of landscape composition, habitat and non-habitat, which identifies it as a “binary” landscape. The third type of landscape that can be considered is the mosaic landscape (Figure 1c). Unlike binary landscapes, mosaic landscapes have more than one category of land type. There is a discrete number of landscape element types expressed (e.g., different levels of habitat suitability or matrix hostility). These types of landscape models are viewed as more “realistic” because they reflect a greater degree of landscape heterogeneity that cannot be expressed in a simple binary map. The final type is the raster image approach (Figure 1d) which does not use a categorical scheme to define patches of varying landscape types. The best examples of this approach are scanned aerial photographs and unclassified satellite images. This approach uses individual points or cells in a raster grid that can be represented by a nearly continuous range of gray levels to compose a complete image or map of a landscape. Because there is no categorization of landscape type, patches are not represented as discrete spatial entities, and landscape elements can show a gradation from one type to the next (e.g., forest to shrubs to grassland). This approach is the most informative representation of the four landscape types we consider, but it is also most difficult to apply the concept of patch isolation because patches are not defined as unambiguously measurable objects.

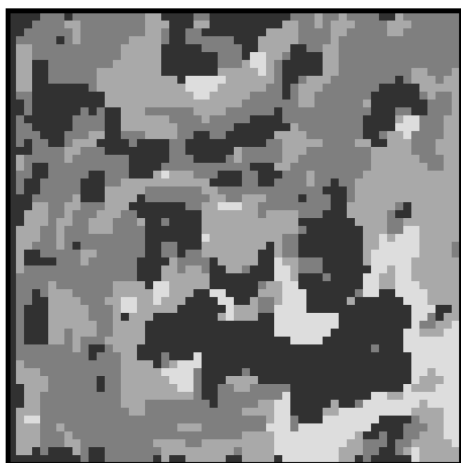
In this study, we evaluated the performance of four general types of isolation metrics in the first two types of landscapes discussed above: point patterns and binary landscapes. Point patterns serve as a type of “control” for initial evaluations of isolation metrics because these types of maps only reflect differences in the spatial configuration of habitat maps. The binary landscapes are more realistic, but introduce additional factors into the concept of patch inaccessibility because the size and shape of a patch can influence how accessible it is to dispersing organisms, independent of its isolation. Thus, we compared the ability of the different isolation metrics to predict patch inaccessibility to dispersers in both types of landscapes, and we assessed their predictive ability as the realism and complexity of the landscapes increased. In a companion paper (Tischendorf et al., this volume), we present another study that extends this work and examines isolation-dispersal relations in mosaic landscapes (Figure 1c). We did not consider analyzing raster landscapes (Figure 1d) because we are unaware of any patch isolation metrics that can be applied to non-categorical map classifications of habitat.



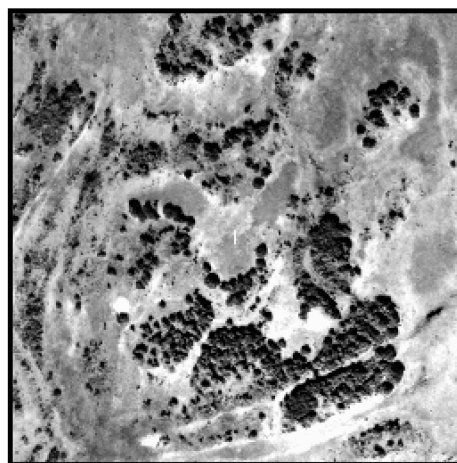
a. Point pattern



b. Realistic binary



c. Mosaic



d. Raster image

Figure 1. Four general ways that landscapes can be mapped.

### *Types of metrics*

There are many different metrics that have been used in the literature to quantify patch isolation (Hargis et al. (1998); see descriptions in Gustafson (1998)). There has also been a recent proliferation of statistical and GIS-based software packages for calculating all sorts of spatial pattern metrics, such as FRAG-STATS (McGarigal and Marks 1995), LEAP-II (Perera et al. 1997), Patch Analyst (Elkie et al. 1999), and APACK (Mladenoff and DeZonia 2000). Here we evaluate the four most common types of isolation metrics (Table 1) that can be calculated manually or

by using packages such as the ones listed above. Rather than examine each metric, we categorized each metric into one of four families, and then chose a representative metric for each to evaluate. We also wish to stress that we have not evaluated indices of landscape connectivity, which are a conceptually related set of indices that measure the arrangement of habitat at the landscape-level, rather than the patch level. A comprehensive review of landscape connectivity measures can be found in Tischendorf and Fahrig (2000) and Tischendorf (2001).

The first type of isolation metric is the simple distance-based metric, such as the nearest-neighbor dis-

Table 1. Description of the isolation metrics evaluated.

Name	Abbreviation	Description	Type of Metric
Nearest-neighbor distance	NDIST	Edge to edge distance to the nearest habitat patch	Simple distance-based
Voronoi polygon area	VORONOI	All area surrounding a given patch that is closer to it than any other patch	Omni-directional distance-based
Buffer area	BUFFER	Sum of all habitat cells within a buffer distance	Area-based
Proximity index	PROX	Sum of the ratio between area and inter-patch distance for all patches within a predefined buffer distance around a patch	Distance-weighted, area-based

tance. Nearest-neighbor distance is the most straightforward (and most commonly used) of all the metrics we evaluated: it is simply a measure of the distance between a patch and its closest neighbor (Figure 2a). We used patch edge-to-edge distance, but this metric could also be calculated by measuring the distance between the centers of neighboring patches. This metric is simple to use, but in theory, it could be unreliable because it does not consider the proximity of other neighboring patches beyond the closest patch.

Multiple-patch or omni-directional distance metrics are available to summarize the individual distances among a patch and its neighboring patches. We evaluated an elegant omni-directional metric called Voronoi polygons. Voronoi polygons are created by measuring the distance to all neighboring patches, dividing each distance in half, and using this information to define the “area of influence” surrounding each patch (Figure 3.2b; see also Diggle (1983)). Unlike nearest-neighbor distance, Voronoi polygons are calculated by obtaining the distance to *all* proximate patches in the landscape, and the proximity of neighboring patches is reflected in the size of a Voronoi polygon: small polygons indicate many proximate neighbors whereas large polygons indicate a greater degree of isolation. This metric was suggested as an alternative to nearest-neighbor metrics by Krebs (1989).

A third type of isolation metric is based on the amount (area) of habitat that is within a specific distance of a patch. The greater the area proximate to the patch, the less isolated the patch is said to be. Such measures are easily obtained using a GIS to “buffer” a region around the patch and then determine how much additional habitat falls within that buffer region

(Figure 2c). From a biological perspective, this approach makes a lot of sense because it provides a direct measure of how much habitat (i.e., the potential source of dispersers) is within the proximity of a patch. However, one must parameterize this metric by selecting a threshold distance that determines how proximate the buffer region will be. The optimal buffer distance should reflect the dispersal capacity of the organism (Brennan et al. 2002 (in press)), but this capacity is species-specific and often unknown, and the buffer distance must be set arbitrarily.

The fourth type of isolation metric is the distance-weighted area-based metric, which has been proposed in many different forms (see Appendix 1, especially metrics used by Hokit et al. (1999) and Hanski (1998), Hansson (1998)). Another example is the so-called proximity index (Gustafson and Parker 1994; McGarigal and Marks 1995). There are different forms of this index, but all use a distance-weighting scheme to calculate the amount of area within a threshold distance from a patch that contains habitat (Figure 2d). The proximity index sums the ratios of patch area to distance for all habitat patches that fall at least partially within some specified distance of the focal patch. This metric is also biologically realistic because it reflects the number of sources of dispersers that are proximate to a patch, as a function of their sizes and distances. However, like buffer metrics, the proximity index must be parameterized by specifying a threshold distance.

#### *Characteristics of a useful metric*

To be a useful metric of isolation, a measure must accurately and reliably reflect how spatially inaccessible

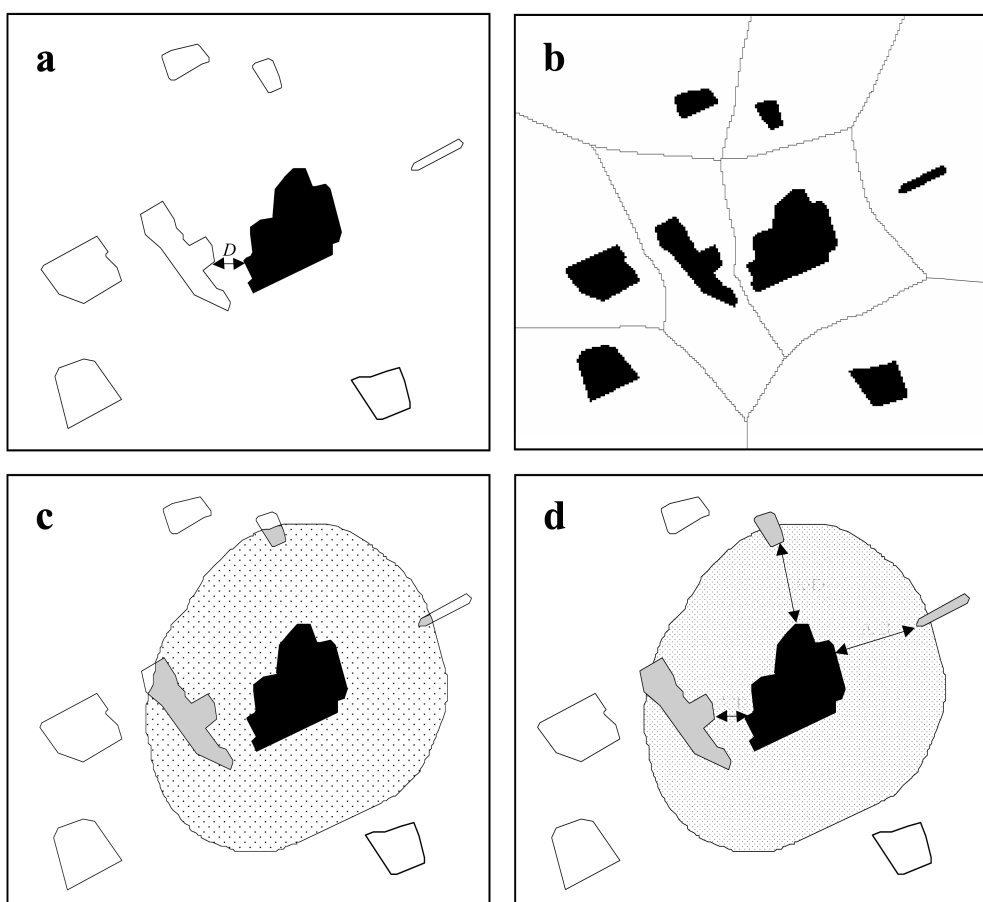


Figure 2. Illustrations of the four metrics tested in this study: a) nearest-neighbor distance ( $D$ ); b) a spatial tessellation which produces many Voronoi polygons around each; c) buffer area, which is the amount of habitat that occurs within a fixed distance of the perimeter of a patch (gray polygons); and d) the proximity index which sums the ratios of patch area/distance ( $A/D$ ) for all patches of habitat located within a fixed distance of a central patch of interest.

a patch of habitat will be to dispersers. We suggest that to satisfy this definition, a useful metric must satisfy the following conditions. First, the isolation metric should be highly correlated with immigration rates, i.e., it must be a good predictor of immigration. Second, if isolation is to be used to predict immigration, then the relationship between these two factors should be proportional (i.e., linear). If the relationship between an isolation metric and immigration is non-linear, this is less useful because one may have to parameterize and back-transform the isolation metric to obtain predicted immigration. Without movement data, however, it could be quite difficult to perform the transformation. Finally, the metric should be robust enough that it performs consistently across different landscape patterns and is not influenced by fac-

tors such as the complexity of patch shape or the total amount of habitat in a landscape.

## Methods

### General approach

It is actually quite difficult to evaluate patch isolation metrics empirically because there is an incredible paucity of movement data available in the literature (Kareiva 1990; Doak and Mills 1994), and for good reason: landscape-level animal movement, particularly lifetime dispersal events, can be difficult to obtain for many organisms (Harrison 1992; Szacki et al. 1993; Doak and Mills 1994; Sutherland et al. 2000). For landscape ecological studies, it is most often the

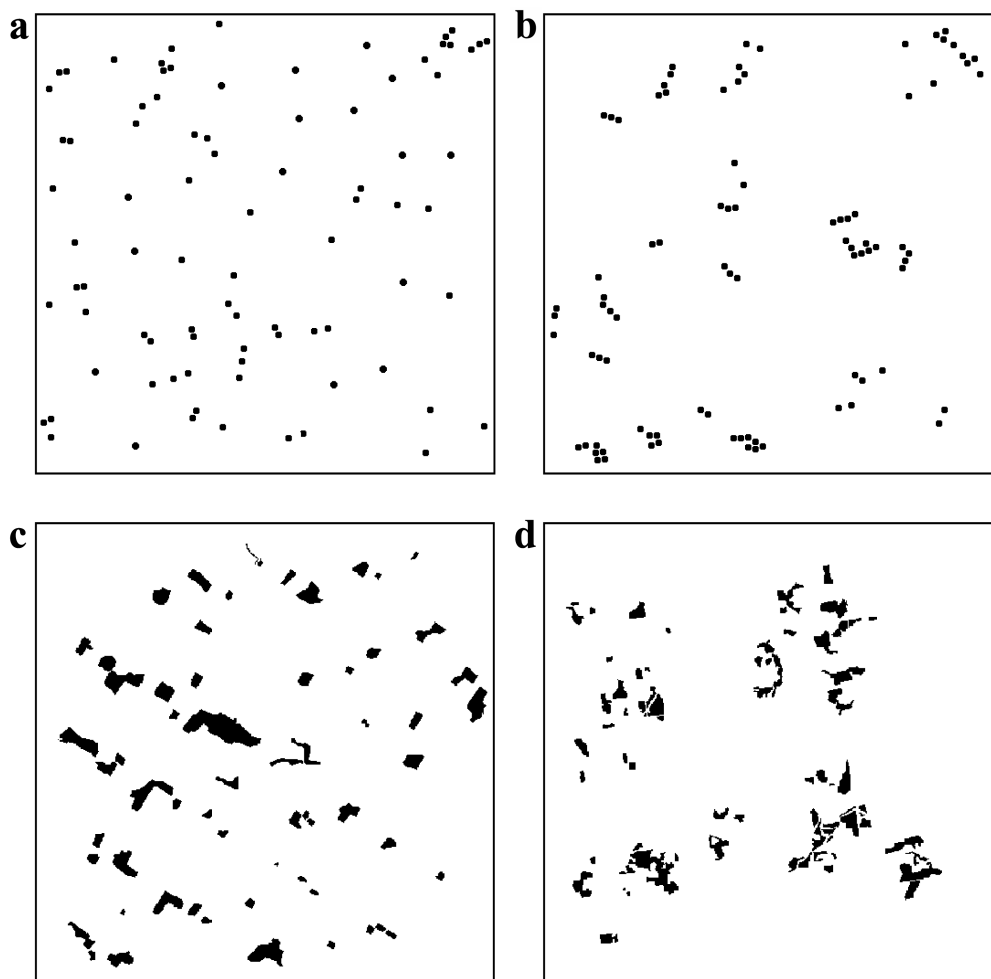


Figure 3. Sample landscapes illustrating the artificial point-pattern landscapes (a & b) and realistic binary landscapes (c & d), and spatially aggregated patches (b & d) and dispersed patches (a & c).

case that movement is inferred from landscape pattern, not measured directly, which usually leads us back to some immigration-isolation relation that may not have been empirically established. Given that we have a small body of empirical movement data with sufficiently large sample size of individuals in a large number of landscapes with varying patch attributes (e.g., size, shape, isolation), we pursued a simulation approach where a large sample size and replication are easily obtainable and do not constrain analysis and interpretation. The other advantage of a simulation approach is that we were able to experimentally control for possibly confounding factors that influence immigration rate. Often, such confounding factors are uncontrollable and immeasurable in empirical studies. A good example of a confounding factor that influences immigration rate but does not contribute to

landscape pattern (i.e., is not a component of spatial isolation) is dispersal-related mortality. Note that many such factors could be a *consequence* of landscape pattern, and therefore, may be related to patch isolation. However, our goal was not to evaluate how all the factors related to patch isolation can affect successful dispersal; we were interested in determining only how spatial isolation *alone* affects movement and how this relation can be appropriately measured. This is a very important distinction. It is of particular importance to patch-based models in ecology, like island biogeography or metapopulation theory, because movement is the key element of the model that links community/population dynamics to the spatial pattern of the landscape.

Another reason for using simulated data from a computer model of animal movement is that it al-

lowed us to incorporate two very important aspects of dispersal: (1) we used a rule-based movement algorithm that ensured simulated animals were “aware” of the structure of the landscape (see below), so they did not just move in a purely random pattern, and (2) we used actual GIS landscapes in the simulation model so that realistic patch structures could be incorporated, including variation in patch number, shape, and size. Although it is possible to use closed-form analytical models to investigate some aspects of the relationship between spatial structure and dispersal (e.g., models of random movement using diffusion equations; see Okubo (1980) and Turchin (1998)), rule-based movement and realistic patch structures would have been difficult or impossible to incorporate in an analytical model. The limits of using closed-form analytical models with complex, realistic spatial patterns has already been explored and discussed by With and King (1999).

### *Model implementation*

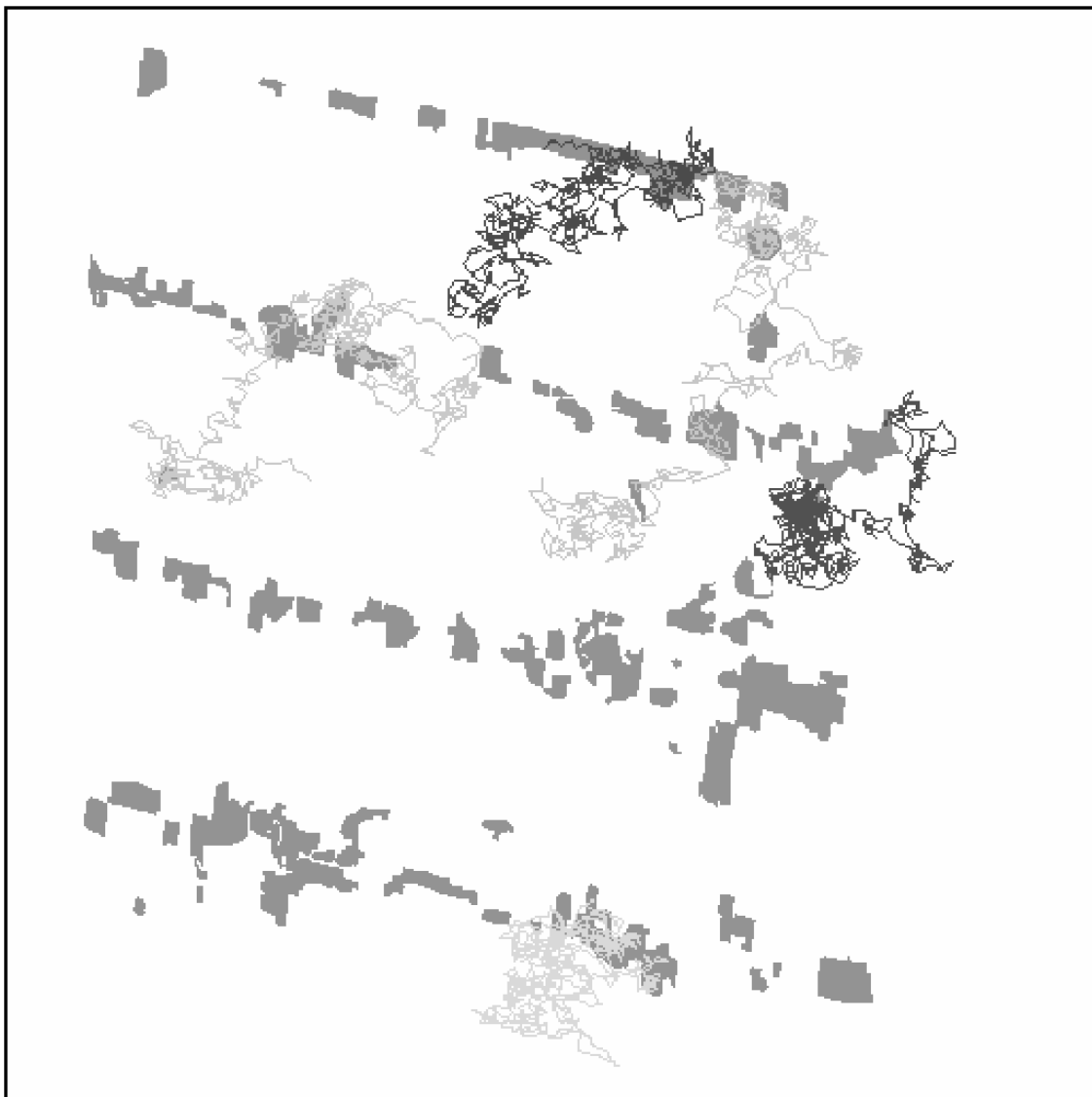
To determine how the various patch isolation metrics reflect immigration rate, the movement of “generic” animals was modeled in 100 artificially-generated point-pattern landscapes and 95 realistic binary landscapes (details below). The model was constructed to simulate the movement of organisms across different landscapes and recorded the number of successful immigrations for each patch in the landscapes. Because we were only concerned with inter-patch dispersal events, straightforward demographic parameters were used so that births equaled deaths, and the number of emigrants out of the landscape equaled new immigrants into the landscape, which greatly simplified the modeling and interpretation of results. Although this approach may seem over-simplistic, it was desirable to use consistent demographics because it functions as a strict experimental control allowing only movement-related processes to be measured. We relax this assumption in Tischendorf et. al (this issue) and explore the influence matrix mortality as a factor affecting dispersal success, but the general outcome and conclusions regarding the relative performance of spatial isolation metrics is not greatly affected.

For each run of the model, the population size began with 250 animals placed randomly within habitat patches and the population size remained constant. Any animal that moved beyond the boundaries of the landscape was replaced by a new animal that appeared at a randomly selected location along the land-

scape boundary. Sex of the organism was not considered and every animal was potentially reproductive. Each run of the model simulated stochastic, rule-based movement of animals across the landscape (see details below). The goal was to track the movement of each individual and record all new immigration events occurring at each habitat patch. A patch immigration event occurred when an animal moved out of its patch of origin and encountered unoccupied habitat in another patch. Following immigration, each animal reproduced exactly one new individual and then died. New individuals were then free to move within or outside of this patch, and matrix mortality was not included. Each simulation run was performed for 1000 time steps, and 500 replications of each simulation were performed on every landscape. The total number of immigrants to move into each habitat patch was recorded for every landscape, and the mean (across replicate runs) total number for each patch within each landscape was used as the dependent variable to describe patch accessibility in subsequent statistical analyses.

At each time step, an animal could move up to 5 cells (pixels) in distance in any (360°) randomly chosen direction. The animal would move that full 5 cells distance if the landscape composition along the route was homogeneous. However, if a boundary was encountered, then the animal would stop at that boundary and have to make a “decision” about whether to continue on its current path. The remainder of its maximum per-step movement distance could be used to continue moving in its current direction or in a new direction, depending on the outcome of the “decision”. This basic algorithm was implemented recursively until the animal moved the full five pixels (path length, not displacement) in each time step, or until it found unoccupied habitat. The maximum “lifetime” distance an animal dispersed was not limited in the model, but operationally, it was determined by how quickly it found habitat, which is a function of how aggregated patches are and how much habitat is in the landscape.

A semi-permeable patch boundary was incorporated to simulate the preference that animals may have for remaining within habitat rather than entering matrix. In this model, a semi-permeable patch boundary was defined as a boundary that could only be crossed by animals (arbitrarily) 50% of the time when leaving a patch. There was no restriction enforced when an animal entered a patch, however. A graphic



*Figure 4.* An example of the movement paths (light and dark lines) simulated by the model in the GIS landscapes. Note that the simple movement rules ensure that the animals spend more time searching for available habitat within patches (gray polygons) than in the non-habitat matrix (white area), which is observable from the shorter movement steps and frequent changes in direction within habitat patches. To maintain a simple graphic that is easily visualized, a run of only 500 time steps is shown, and the distinction between the route of a parent and its progeny that replaces it is not depicted. Thus, each path represents one lineage of an organism (in this case, from about 25 to 150 generations per line), not the lifetime movement of a single organism (see text for details).

depicting the movement of five animals during one simulation run is shown in Figure 4.

The discovery of unoccupied habitat within a patch was modeled as a probabilistic encounter rate. Once an animal reached a patch, it “searched” for habitat within the patch once per time-step. A “search” was successful if a randomly-drawn number between zero and one was greater than the proportion

of unoccupied territories in the patch. The number of unoccupied territories in each landscape was fixed so that the maximum number of territories in each point-pattern landscape was equal to the average number of maximum territories in the realistic binary landscapes, which was approximately 500 territories per landscape. This maximum was set arbitrarily so that immigration would only be partially limited by habi-



Table 2. Patch characteristics in point-pattern landscapes (simulated) vs. realistic binary landscapes (real forest patterns). The unit of measure for patch area and nearest neighbor distance is number of raster cells.

Patch Characteristic	Point-pattern Landscapes	Realistic binary Landscapes
Mean number of patches per landscape	90	89.5
Minimum patch area	45	1
Maximum patch area	45	6878
Mean patch area (+ SD)	45 (0)	47.1 (208)
Mean nearest neighbor distance (+ SD)	3.4 (10.6)	7.3 (9.5)

tat availability (i.e., there would usually be empty habitat in a patch, all else being equal, if an animal were to search for it).

Two types of landscapes were used in the simulations (see examples in Figure 3). The first type were simple, artificially generated maps, each containing 90 equal-sized circular patches. These landscapes are essentially point-pattern maps. Hereafter, we refer to these as the point-pattern landscapes. A clumping algorithm was used to vary the arrangement of patches in each point-pattern landscape. The clumping algorithm had two parameters: first, a random number (3–12) of clusters of patches was selected, and a “seed” location was picked for each cluster using randomly selected coordinates. Second, the degree of clumping was set by choosing a random number to be the maximum distance a patch could occur from its associated seed location. Each landscape was generated by distributing the 90 habitat patches among the seed locations, and the locations of the patches were determined by choosing random coordinates about each “seed” location that satisfied the maximum distance criterion. This method ensured that the only difference among the 100 simple landscapes was the configuration of patches, which served as a control to isolate the effect of patch accessibility from the effect other patch characteristics (patch size and shape) that could affect immigration rates.

The second type of landscape that we used was the realistic binary landscapes in which the sizes and shapes of patches were not consistent. These 95 landscapes were obtained from a GIS database of 10 km × 10 km forest vegetation maps from agricultural regions in southern Ontario, Canada (described in Trzcinski et al. (1999)). Hereafter, we refer to these maps as the realistic landscapes.

All point-pattern and realistic binary landscapes were 512 × 512 cells in size, providing considerable resolution for small and complex patch features (Figure 3). The properties of the point-pattern landscapes

were also intended to be reasonably similar to the mean properties of the realistic landscapes. Details comparing the number of patches and variation in patch area for point-pattern vs. realistic landscapes appear in Table 2.

#### *Analysis of model output*

A list of the patch isolation metrics that were evaluated is in Table 1. To determine which metrics were the best descriptors of isolation, squared Pearson product-moment correlations ( $r^2$ ), were calculated between each metric in Table 1 and immigration rates obtained from the simulations. Each patch was described by the mean number of total immigrants to colonize it across the 500 simulation runs. To minimize the lack of statistical independence among patches within a single landscape, a nested design was used to calculate  $r^2$  for patch indices by nesting mean patch immigration rates within each unique landscape. This method does not completely correct for lack of independence, but it does make it fair to compare individual patch-level responses in a relative fashion, which was our sole purpose here. Although it is standard practice to linearize data (e.g., log-transform) prior to correlation and regression analysis, this was not done in our analysis because one of our evaluation criteria (above) was to find a linear predictor of immigration rate. Note that for the purposes of reporting, we rely solely on the  $r^2$  values and we do not present their associated significance probabilities. Given our very large sample size, all relations are statistically significant from a random (null) relation, so we focus the reader’s attention on the effect sizes themselves, which are given directly by the  $r^2$  values.

There were some factors that could have confounded our results when analyzing the realistic landscapes. Immigration success may be related to characteristics of a patch that are independent of patch isolation (e.g., patch area, shape, length of perimeter),

and it also may be influenced by the total amount of habitat in each landscape. We investigated how large an effect patch characteristics should have on immigration by performing stepwise linear regressions on the following patch characteristics: patch area, perimeter length, perimeter/area ratio, patch shape index (Patton (1975), as implemented by McGarigal and Marks (1995)), and the double-log fractal dimension of the patch. The former two indices reflect the size of the patch, and the latter three indices are different metrics that measure the complexity of the shape of a patch. If it appeared that any of these patch characteristics influenced immigration rate, these confounding effects were eliminated with residual analysis to statistically correct for their effects prior to subsequent analyses of the isolation metrics. To be comprehensive, we report the strength of the relations between immigration rate and each isolation metric using both raw immigration rates and immigration rates statistically corrected to remove the confounding influence of patch size and shape.

The total amount of habitat in a landscape might also influence our results because, all else being equal, it is to be expected that there will be higher immigration rates in landscapes that have more habitat (but only given our limited range of habitat amounts). This effect can occur simply because organisms spend less time searching in non-habitat areas. If immigration rates are much higher in some landscapes than others, there will be more extremely high immigration rate values in some patches, and therefore, there will be a greater possible range of observed values. Because it is easier to detect statistical relationships when there is a greater range of values to regress, the statistical relationship between isolation and immigration will be more apparent (see Opdam (1991) and Hill et al. (1996)). This situation is not an issue if all isolation metrics perform consistently, but is a concern if a particular metric is sensitive to a bias introduced by variability in habitat amount. To investigate this effect, the unexplained (residual) error was examined to see if it was related to the amount of habitat in a landscape.

One other factor that could have a confounding effect in both the point-pattern and realistic landscapes was the proximity of a habitat patch to the edge of the landscape. In our simulations, new individuals were allowed to enter the landscape at the boundary to exactly replace the animals that left the landscape. This introduces a potential discrepancy between immigration and patch accessibility/isolation

because the isolation metrics do not consider a patch's proximity to the landscape boundary, which is an artificial source of potential immigrants. This issue is also relevant to field studies that do not consider patches which fall outside the arbitrary landscape boundary when one measures isolation. This boundary proximity effect was assessed by examining the statistical relationships between a patch's distance to the boundary and the predictive ability of each isolation metric.

## Results

Figure 5 summarizes the correlations obtained from the independent relationships between mean immigration rate and each patch isolation metric for the point-pattern landscapes. Immigration rate was best predicted by the two area-informed metrics, buffer area and proximity index, as indicated by their high mean  $r^2$  values. Contrary to prediction, the omnidirectional distance metric, Voronoi polygon area, had the lowest mean  $r^2$  value. Note that the direction of these relationships cannot be obtained from squared correlation coefficients. However, in all of our analyses in both types of landscapes, the relationship between each isolation metric and immigration rate was in the predicted direction: immigration rate increased as nearest-neighbor distance and Voronoi polygon area decreased, and immigration rate increased as buffer area and proximity scores increased.

In the realistic landscapes, patch size and shape characteristics accounted for approximately one half of the variability in patch immigration rate (Table 3), and as expected, there was considerable correlation among characteristics (Table 4) indicating that the inclusion of some variables may have been redundant. Figure 6 summarizes the correlation scores between immigration rate and patch isolation for each metric using both the raw and statistically corrected immigration rates. Generally, squared correlation coefficients were much lower in the GIS landscapes in comparison to the point-pattern landscapes, presumably because things other than patch configuration also influenced immigration rates (e.g., patch size and shape). Patch characteristics and patch isolation can also be entered into a multiple regression/correlation model as simultaneous predictors to determine, overall, how predictable immigration rates are in realistic landscapes (Figure 7). Taken together, patch size, shape and isolation do explain a large proportion of

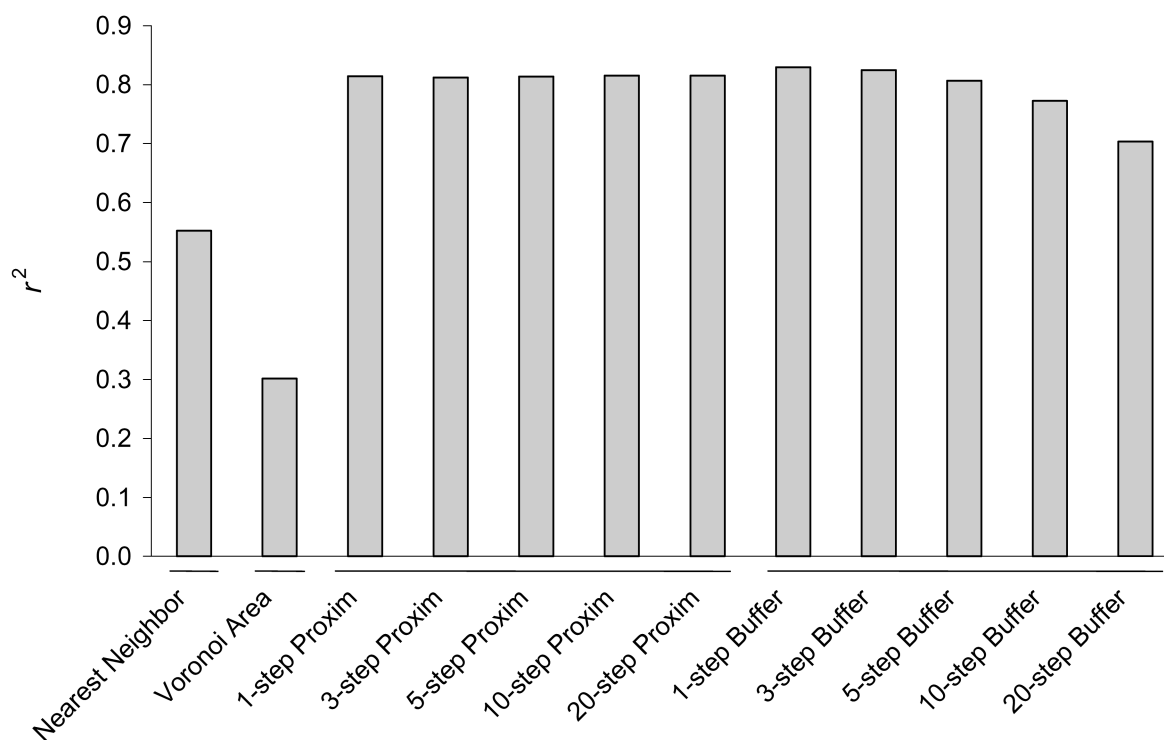


Figure 5. Summary of correlations between each isolation metric and observed mean immigration rate for the point-pattern landscapes. The height of each bar is a direct measure of how well a metric was able to predict mean immigration rate into a given patch. There are multiple bars for the buffer and proximity indices because these indices must be parameterized by defining a threshold distance from the patch perimeter. These distances were set in terms of the maximum distance an organism could move during each time step of the simulation. Thus, a 5-step buffer area defines all the available habitat within a distance from the focal patch that is equal to the maximum distance an organism could move in five time steps.

the variability in immigration rate (up to ca. 85%), and the  $R^2$  values from these multivariate analyses are actually quite comparable in magnitude to the  $r^2$  values obtained for the point-pattern landscapes where patch characteristics are consistent (Figure 5). (Note that hereafter, we use the notation  $R^2$  to indicate the squared multiple correlation coefficient, and  $r^2$  to indicate a squared Pearson product-moment correlation coefficient or squared partial correlation coefficient, following the notation of Steel and Torrie (1980).)

The amount of habitat in a landscape had a very small or negligible association with the predictive ability of the isolation metrics evaluated (Table 5). However, we only evaluated a fairly narrow range of habitat amount (approximately 5 to 35% habitat cover), so it is difficult to extrapolate to landscapes that contain more habitat. Yet, it may be that measuring isolation is not an issue above this amount because at higher levels of habitat amount, it is improbable that a highly isolated patch will occur (e.g., Gustafson and Parker (1992) and Andrén (1994)).

There did appear to be small effects associated with measuring isolation for patches located near the edges of the landscapes. Figure 8 shows plots of the residual errors from the isolation-immigration rate regressions in the point-pattern landscapes. If a metric is unaffected by how far a patch lies from the landscape boundary, then one would expect to see an even distribution of residuals across a gradient of distance. However, Figure 8 shows that for each metric, there is a preponderance of negative residuals for patches that are close (ca. < 30 cells) to the edge of the landscape. This result indicates that immigration rates tend to be overestimated by patch isolation for patches very close to the landscape boundary. Voronoi polygons appear to be affected the most because the delineation of a polygon is dependent on the position of the landscape boundary for peripheral patches. Beyond the 30 cell threshold, all metrics seemed to perform fairly consistently. Figure 9 shows similar plots for the realistic landscapes. It appears that boundary effects have little influence in the realistic landscapes;

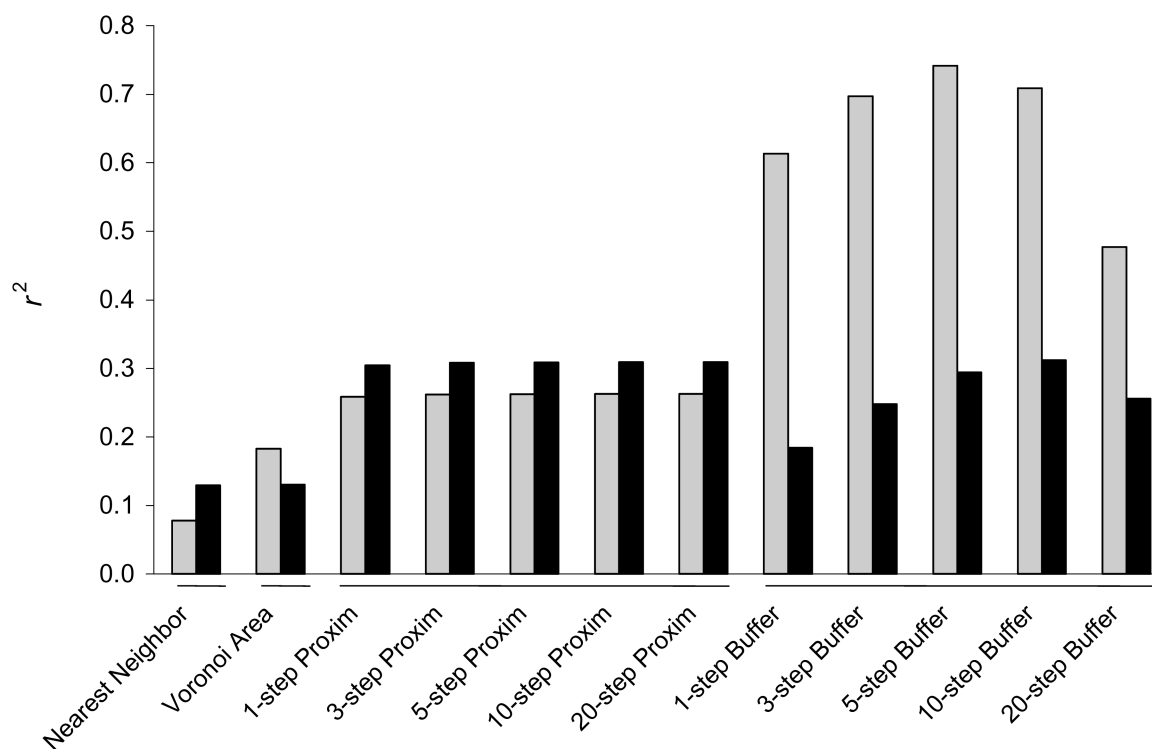


Figure 6. Summary of correlations between each isolation metric and observed mean immigration rate for the realistic (GIS) landscapes. The gray bars indicate the squared correlation coefficients ( $r^2$ ) obtained when patch shape and size characteristics are not accounted for. The black bars indicate the squared correlation coefficients obtained after statistically removing the effects of the patch characteristics (shown in Table 3).

the spread of residuals seems fairly consistent along the gradient of distance from edge.

## Discussion

The area-informed metrics, buffer area and proximity index, clearly out-performed the distance-based isolation metrics, nearest-neighbor and Voronoi polygon area, in both types of landscapes (Figure 4 and Figure 5). This result is not particularly surprising because nearest-neighbor distance and Voronoi polygons are calculated using only the distance to neighboring patches, and they do not account for the *amount* of habitat that occurs within the neighborhood. In our simulations, the presence of suitable habitat represents a potential source of migrants, so there should be a link between the amount of nearby habitat and the amount of immigration. The problem with distance-based metrics is that they cannot account for the amount of proximate habitat, which must influence the number of migrants in the neighborhood, so

they are poor predictors of immigration. For the point-pattern landscapes, the amount of proximate habitat is only a function of the number of patches within the neighborhood, because all patches were of equal size. Distance metrics might fail to predict immigration rate if they cannot reflect this function. The nearest-neighbor metric is an extreme example of this because it does not look beyond one neighboring patch. For the realistic landscapes, patch shape and size are irregular so the amount of proximate habitat is not necessarily reflected by number of patches or the distance to them, which explains why the area-informed metrics perform so much better in these landscapes. Because the area-informed metrics performed very well in both types of landscapes, we conclude that these metrics are the most robust and reliable metrics across various landscape spatial patterns.

A surprising result was seen in the point-pattern landscapes, where the simple nearest-neighbor distance was a better predictor of immigration than the Voronoi polygons. Nearest-neighbor distance should characterize patch isolation well if patches are fairly

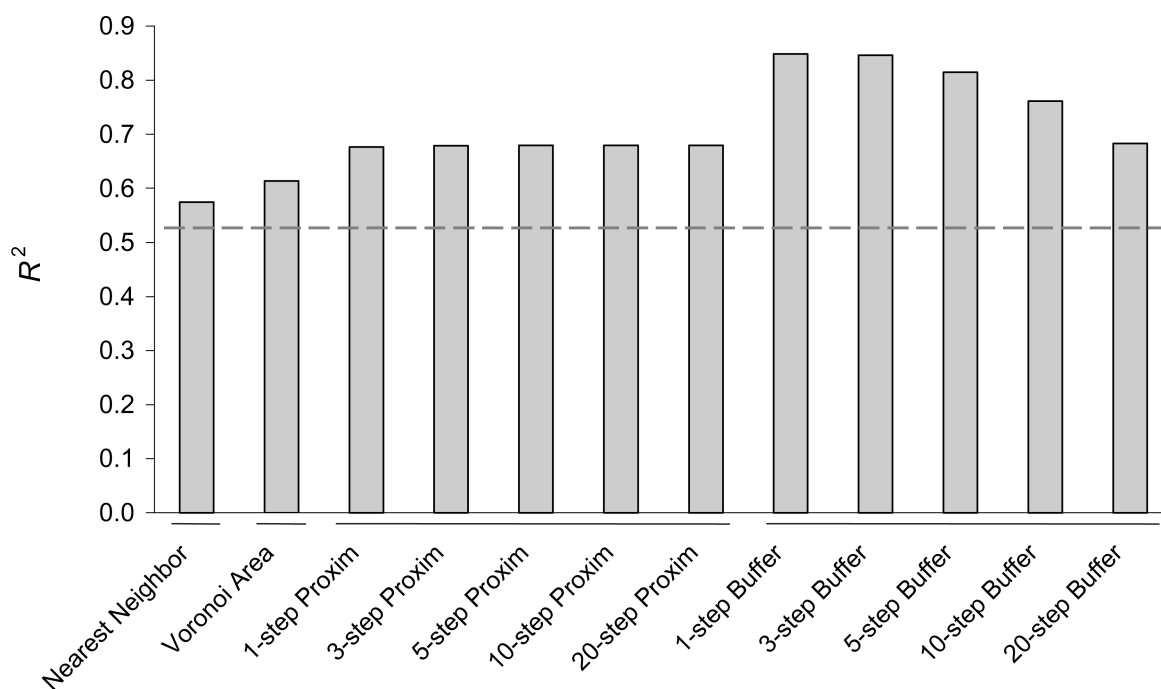


Figure 7. The proportion of variation in mean immigration rate (expressed as the multiple correlation coefficient,  $R^2$ ) that can be explained by patch characteristics and each isolation metric combined. In each case, patch characteristics account for the first 52% of variation in immigration rate (horizontal dashed line), and the remaining explained variation in each vertical bar is attributable to the isolation metric.

Table 3. Statistical summary of stepwise multiple regression illustrating the relative influence of the different patch characteristics on immigration rate ( $R^2 = 0.5251$ ,  $n = 6761$ ,  $p < 0.001$ ).

Patch Characteristic	Standardized Regression Coefficient	Student's $T$
Area	0.312	7.223
Perimeter	-0.169	-2.573
P/A Ratio	-0.185	-21.133
Shape Index	0.763	13.349
Fractal Dimension	-0.237	-6.684

consistently spaced apart (Diggle 1983). However, if a clumpy distribution of patches occurs then the distribution of clumps themselves (particularly clumps composed of few patches) may determine the degree of isolation. Simple nearest-neighbor distance does not reflect the distribution of clumps of patches. It only reflects the distance from one patch to its closest neighbor, perhaps limiting its usefulness. Voronoi polygon area should be a better measure for assessing isolation because this metric is calculated by measuring the distance to all proximate neighboring patches, and therefore, should better reflect how “clumpy” a distribution of patches is in a landscape.

Yet, this was not supported in our results. Voronoi polygons were the worst predictor of immigration in point-pattern landscapes, with only about one-half the predictive power of the nearest-neighbor metric. In the realistic landscapes, they were about tied with the nearest-neighbor metric as the worst predictor of immigration. One problem is that Voronoi polygons are “unclosed” at the edge of the landscape for patches that lie adjacent to the boundary (see Figure 2b). Our residual analysis that examined the influence of this boundary effect demonstrates that Voronoi polygons near the landscape edge tended to underestimate polygon area, and therefore, overestimate immigration rate in the point-pattern landscapes (Figure 8). A similar effect was not observed for the realistic forest landscapes (Figure 9) but may have been masked by confounding patch characteristics that increase the variability of immigration rate and reduce the ability to detect a boundary effect.

An interesting result of the simulations on realistic landscapes was that patch isolation alone did not explain most of the variation in immigration rate. Rather, patch size and shape, which are unrelated to patch location, explained approximately one-half of the variation in immigration rate (Table 3). Thus, the

Table 4. Intercorrelations among patch characteristics and correlations between patch characteristics and isolation metrics. Values are Pearson product-moment correlation coefficients. Abbreviations are from Table 1.

	Area	Perimeter	P/A Ratio	Shape Index	Fractal Dimension
Perimeter	0.9548				
P/A Ratio	-0.2082	-0.2547			
Shape Index	0.6579	0.8020	-0.2695		
Fractal Dimension	0.4071	0.5363	-0.2180	0.9042	
NDIST	-0.0831	-0.0983	-0.0511	-0.1449	-0.1490
VORONOI	0.7025	0.7250	-0.2867	0.6048	0.4277
BUFFER05	1.0000	0.9552	-0.2086	0.6593	0.4085
BUFFER15	0.9969	0.9568	-0.2144	0.6711	0.4216
BUFFER25	0.9847	0.9513	-0.2236	0.6805	0.4347
BUFFER50	0.8953	0.8797	-0.2402	0.6656	0.4451
BUFFER100	0.6120	0.6205	-0.2225	0.5162	0.3701
PROXIM05	0.1179	0.1314	-0.0093	0.1316	0.0938
PROXIM15	0.1189	0.1326	-0.0097	0.1328	0.0948
PROXIM25	0.1190	0.1327	-0.0098	0.1330	0.0949
PROXIM50	0.1190	0.1327	-0.0099	0.1331	0.0950
PROXIM100	0.1190	0.1327	-0.0099	0.1331	0.0950

Table 5. Summary of relationships between amount of habitat area in a landscape and the residual error associated with each patch for each isolation metric. A weak relationship indicates that an isolation metric is not sensitive to changes in habitat amount if used as a predictor or immigration rate. Most *P*-values are statistically significant, but it is more important to note that the absolute magnitudes of the effect (illustrated by Pearson product-moment coefficients and standardized regression coefficients) are practically negligible in all cases.

Isolation Metric	$r^2$	Standardized Regression Coefficient
NDIST	0.0013	-0.0359
VORONOI	0.0028	-0.0528
PROXIM05	0.0072	-0.2279
PROXIM15	0.0068	-0.0823
PROXIM25	0.0067	-0.0817
PROXIM50	0.0066	-0.0811
PROXIM100	0.0065	-0.0807
BUFFER05	0.0019	-0.0433
BUFFER15	0.0001	-0.0097
BUFFER25	0.0003	0.0168
BUFFER50	0.0010	0.0311
BUFFER100	0.0003	0.0163

accessibility of a patch can be strongly influenced by factors other than a patch's position in the landscape. It should be stressed that there are two components of accessibility that need to be considered: patch location (isolation) and patch size/shape. Obviously, the

relative importance of these two components will depend on the context of the landscape, and for highly isolated patches, the influence of patch size/shape may be slight. However, we demonstrate that immigration into the "average" patch was significantly determined by patch size and shape, and for very proximate patches, this component largely determines immigration success. It may not be necessary to consider all of the five patch shape/size characteristics that we used to characterize the patch shape/size component, especially since many of them are highly correlated (see Table 4). Our results suggest that a reasonable surrogate would be to use either perimeter or the patch shape index because it was found that by themselves, each of these metrics explained most of the variation attributable to the overall patch size/shape component ( $R^2 = 0.43$  and  $0.44$ , respectively). If two metrics are used, the patch shape index and patch area combined explain nearly the same amount of variation in immigration rate ( $R^2 = 0.49$  for shape index and patch area vs.  $R^2 = 0.52$  for all five patch characteristics combined).

One may also question whether the influence of patch size/shape on immigration would have been so great if we had modeled a more sophisticated or sentient form of movement. We believe that the amount of variation explained by patch size/shape, relative to the amount of variation explained by patch isolation, would actually decline as animal movement becomes

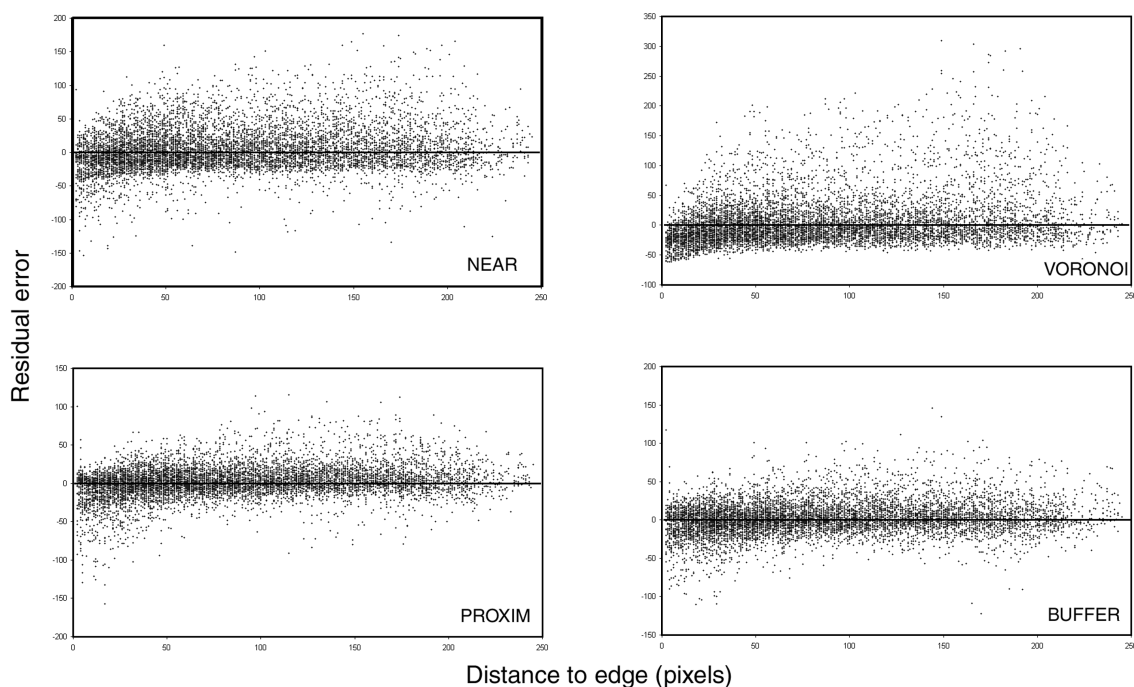


Figure 8. Plots of the residuals from the immigration rate-isolation regressions against distance to edge for the point-pattern landscapes (see text).

more intelligent or aware of its environment. Our movement algorithm was based on random chance and some simple movement rules, such as the random selection of direction outside of patches. Under such a scenario, animals tend to randomly encounter new habitat patches. The frequency of encounters will be higher for patches with a large and/or convoluted perimeter than small, compact patches that have much less exposure to dispersers. If movement direction was to be more intelligent and directed towards neighboring patches, the importance of patch size/shape should become less important, because the probability of encountering a new patch is dependent upon the ability of an animal to detect and move to that patch. This prediction was supported in a different application of the movement model where different types of movement behavior were simulated (Bender 2000), and we examine the affect of movement capability more fully in our companion article to this paper (Tischendorf et al., this issue). We contend that the explanatory power of patch size/shape is probably at its realistic maximum in this study, making it a baseline for relative comparison. If animals move in a more random fashion (e.g., many insects), then one can expect that up to two-thirds of the variation in movement can be predicted by patch size and

shape alone. However, this proportion should decline as movement becomes more directed (e.g., a sentient vertebrate), and patch isolation should become a more important determinant of immigration rate. Finally, the relative performance of each isolation metric to predict immigration should not necessarily vary as movement types change. This prediction is tested and confirmed in Tischendorf et al. (this issue).

Regardless of the source of explained variation, we were able to statistically explain up to 85% of the variation in immigration rate when both patch size/shape and patch isolation components were taken into account (Figure 2), and up to 35% by isolation alone (Figures 6 and 7). This result represents a very high degree of predictability when one considers that the organisms simulated in this model were moving between patches in a fashion that was based on a substantial amount of random chance. We expected that for more sentient organisms that move in a less random and less unpredictable manner, one should be able to predict movement and immigration to an even higher degree from patch isolation.

One other interesting result (shown in Figure 6) was that by using buffer areas as the metric, one can still explain most (ca. 75%) of the variation in immigration rate without having to consider patch size/

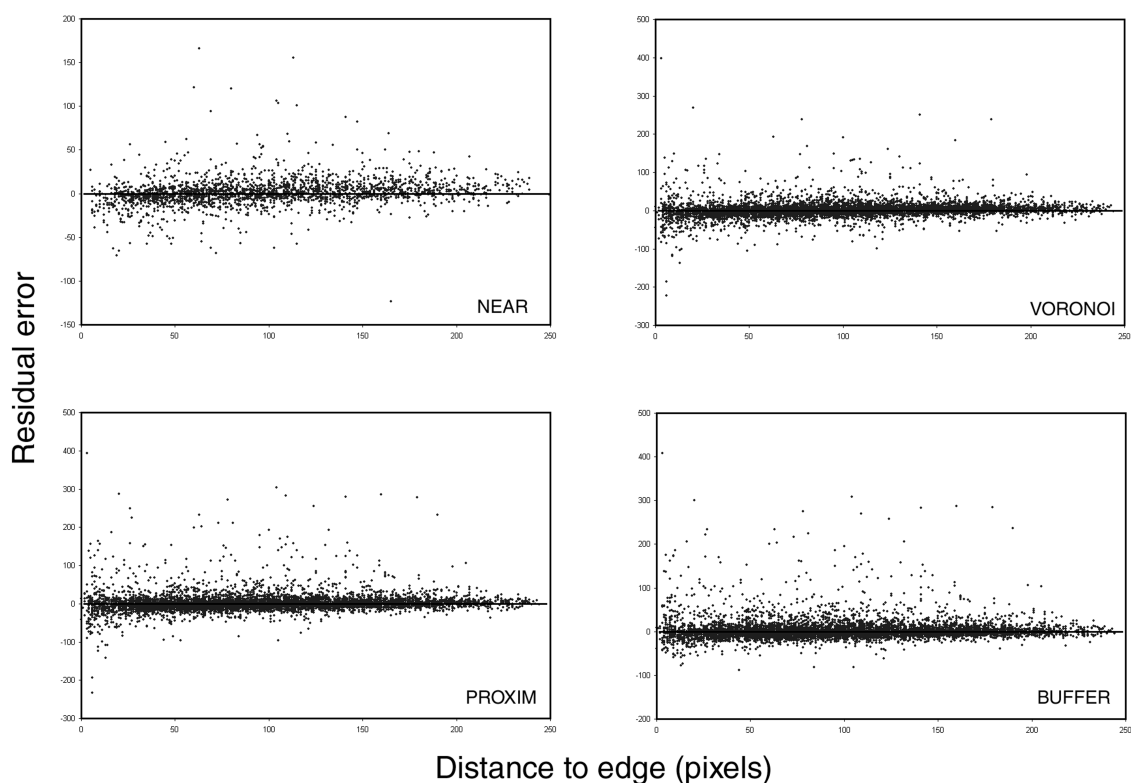


Figure 9. Plots of the residuals from the immigration rate-isolation regressions against distance to edge for the realistic binary landscapes (see text).

shape at all, provided that an optimal buffer distance is used (in this case, it was equal to the maximum distance that an organism could travel in five time steps of the simulation). This result demonstrates that buffer areas can be a powerful and robust metric if they can be parameterized correctly. The difficulty, of course, lies in obtaining appropriate measures of maximum dispersal distance because empirical studies of dispersal capabilities are rare in the literature, although other methods for inferring dispersal capability may be possible from allometric relations (Sutherland et al. 2000, Bowman et al. in press).

In conclusion, our results demonstrate that area-informed metrics such as buffer areas, and distance-weighted area-based metrics such as the habitat proximity index, are superior predictors of immigration over commonly used distance-based indices such as the nearest-neighbor distance. The buffer and proximity metrics were both consistent and adequate predictors of immigration, and appeared to be relatively insensitive to variation in patch size/shape, distance to the landscape boundary, and the total amount of habitat within a landscape. In our evaluation, buffer area

was the most predictive metric, but only if the buffer radius was correctly parameterized. Presumably, the optimal buffer radius is one that reflects the average dispersal distance of a migrating organism. However, average dispersal distances are rarely known and this may limit the actual usefulness of this metric unless one experiments with a variety of distances as we have done. Another option is to simply use the proximity metric, which appears to be relatively insensitive to correct parameterization. In this study, we simply chose a range of reasonable proximity distances for the metric (based on knowledge of the dispersal characteristics of our organism) and all the scores obtained were quite similar, suggesting that the proximity index will perform optimally if the distance parameter is close to matching the dispersal ability of an organism. In either case, the area-informed metrics are advocated for their predictive ability, reliability, and ease of calculation. The buffer-area operation is a fundamental operation of any geographic information system, and can be performed unambiguously. The proximity metric requires a little more work to calculate manually, but there is a wealth of readily



available and free software that can be used to automate the process. These metrics are not as simple as measuring a nearest-neighbor distance, but we predict that as the popularity and wide use of GIS and software-based map analysis continues, area-informed isolation metrics could replace the more commonly used distance-based metrics.

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## Appendix 1

Table A1. Overview of recent patch isolation studies, applied patch isolation measures and results. Studies are assembled in descending chronological order.

Study	Patch isolation metric(s)	Response variable (s)	Species	Results
Johannessen et al. (2000)	Distance to nearest patch	Degree of reproductive synchrony	Root vole ( <i>Microtus oeconomus</i> )	Patch isolation favours within-patch reproductive synchrony
Delin and Andrén (1999)	Distance to the nearest habitat patch (> 30 ha)	Density	Eurasian red squirrel ( <i>Sciurus vulgaris</i> )	No effect of patch isolation on density
Hokit et al. (1999)	$S_i = \sum e^{(-d_{i,j}/A_j)}$  $S_i$ : isolation of focal patch i (sum over all occupied patches) $d_{i,j}$ : distance between patch i and patch j $A_j$ : area of patch j	Occupancy	Florida shrub lizard ( <i>Sceloporus woodi</i> ), Racerunner ( <i>Chenidophorus sexlineatus</i> )	Negative effect of patch isolation on <i>Sceloporus woodi</i> , but no effect on <i>Chenidophorus sexlineatus</i>
Marsh et al. (1999)	Distance from experimental ponds to natural breeding ponds	Occupancy and nest density	Tungara frog ( <i>Physalaemus pustulosus</i> )	Negative effect of pond isolation on frequency of use and nest density
Hanski (1998)	$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_j^\alpha$  $S_i$ : connectivity (inverse of isolation) of focal patch i $d_{i,j}$ : distance between patch i and patch j $N_j$ : population size of patch j $\alpha$ : constant reflecting inverse of species-specific migration range	Patch occupancy	Review of incidence function models applied to various taxa; see Hanski (1998)	Patch colonization rate is dependent on patch connectivity/isolation
Hansson (1998)	$S_i = \sum_{j=1}^n A_j e^{-\alpha d_{i,j}}$  $S_i$ : isolation of focal patch i (sum over all occupied patches) $d_{i,j}$ : distance between patch i and patch j $A_j$ : area of patch j $\alpha$ : constant	Colonization rate of various plant species	See Hansson (1998)	Higher colonization rates into less isolated patches, effect of patch isolation depends on dispersal media of the species

Table A1. Continued.

Study	Patch isolation metric(s)	Response variable(s)	Species	Results
Vos and Jardon (1998)	Distance to nearest (occupied) pond, area of a) occupied ponds, b) moorland, and c) weighted road-length within buffers of various width (250 m–2000 m) surrounding focal patch	Presence/absence and density	Moor frog ( <i>Rana arvalis</i> )	Area of moorland within 250 m buffer best predictor, increasing buffer width did not result in higher correlation
Bolger et al. (1997)	Distance to the nearest source canyon (> 100 ha)	Species diversity	Shrub inhabiting rodents, (e.g. California mouse, cactus mouse, pocket mouse, desert woodrat)	No effect of patch isolation on species diversity
Cappuccino and Martin (1997)	Distance to the nearest shore, distance to the nearest point of land (island or shore), sum of distances to nearest land	Density	Birch tube-maker ( <i>Acrobasis betulella</i> )	Positive effect of patch isolation on larval density
Fitzgibbon (1997)	Distance to nearest wood patch, area of wood within 1 km buffer surrounding focal patch, length of hedge within 400 m buffer	Density	Wood mice ( <i>Apodemus sylvaticus</i> ), bank vole ( <i>Clethrionomys glareolus</i> )	Higher population increase in more isolated wood patches, more hedges support higher densities of both species
Grashof-Bokdam (1997)	Forest and length of wooded banks within buffers of 100 m, 500 m, 1000 m widths surrounding focal patch	Occurrence of plant species	See Grashof-Bokdam (1997)	Higher probability of occurrence in less isolated patches
Luiselli and Capicci (1997)	Number of fencerows radiating from forest patch, distance to closest habitat patch, area of nearest patch, habitat area within 1 km buffer surrounding focal patch	Presence and abundance of species	Various snakes	Number of fencerows and distance to nearest patch affected presence of most species, generalist species less affected by patch isolation
de Vries et al. (1996)	Amount of heath within buffers of 500 m, 1000 m and 2000 m surrounding focal patch	Presence/absence	Various ground beetle species	No effects of patch isolation variations on presence/absence
Hill et al. (1996)	Distance to nearest neighbor patch	Probability of colonization	Silver-spotted skipper butterfly ( <i>Hesperia comma</i> )	Higher colonization probability into less isolated patches
Hjermann and Ims (1996)	$S_i = \sum_{j \neq i} c_{ij} A_j$	Occupancy	Wart-biter ( <i>Decticus verrucivorus</i> )	Probability of occupancy increased with decreasing isolation

$S_i$ : isolation of focal patch  $i$  (sum over all occupied patches)

$c_{ij}$ : distance based index (see ref.)

$A_j$ : area of patch  $j$

Table A1. Continued.

Study	Patch isolation metric(s)	Response variable(s)	Species	Results
Kinnunen et al. (1996)	Three isolation groups of patches (dependent on distance to nearest farmland patch)	Presence/absence and abundance	Farmland carabids	Fewer individuals and species were caught in more isolated patches
Matter (1996)	Sum of the distances from a focal patch to all other patches	Movement rates and distances, occupancy	Red milkweed beetle ( <i>Tetraopes tetraophtalmus</i> )	Unoccupied patches were more isolated
Paillet and Butet (1996)	Total length of hedges in a 0.5 km radius around sampling plot	Abundance	Bank vole ( <i>Clethrionomys glareolus</i> )	Patch isolation measure was best predictor of vole abundance
Dunning et al. (1995)	Distance to potential source patches	Density	Bachman's Sparrow ( <i>Aimophila aestivalis</i> )	Isolated habitat patches were less likely to be colonized than nonisolated patches
Vos and Stumpel (1995)	Distance to nearest pond, various measures based on number of ponds, area of high herbs and area of shrubs within buffers of 100 m and 2000 m width	Presence/absence	Tree frog ( <i>Hyla arborea</i> )	Buffer measures gave better predictions of isolation than distance measures
Fitzgibbon (1993)	Area of wood within 1 km buffer surrounding focal patch, distance to nearest wood, length of hedgerow within 400 m buffer surrounding focal patch	Drey density	Grey squirrel ( <i>Sciurus carolinensis</i> )	Only distance to the nearest wood (> 0.5 ha) influenced drey density
van Apeldoorn et al. (1992)	Area of nearest neighbor woodlot, distance to nearest wood area (> 25 ha)	Presence/absence, abundance	Bank vole ( <i>Clethrionomys glareolus</i> )	Area of nearest woodlot affects numbers of voles
Laan and Verboom (1990)	Number of pools within 0.5 km radius from centre of a pool, several distances to nearest field, wood, shelter, pasture	Presence/absence	Various amphibian species	Distance to nearest wood (> 0.1 ha) + distance to nearest old pool + distance to nearest field (> 0.5 ha) explained up to 28% of the number of species
Verboom and van Appledorn (1990)	Distance to nearest woodlot (> 5 ha), distance to nearest woodlot (> 30 ha), amount of wood in buffer rings of (i) 200–400 m, (ii) 400–600 m, and (iii) 200–600 m widths surrounding focal patch	Presence/absence	Red squirrel ( <i>Sciurus vulgaris</i> )	Distance to nearest woodlot (> 30 ha) significantly affected squirrel presence
van Dorp and Opdam (1987)	Distance to nearest wood (> 20 ha), various buffer measures	Abundance	Forest bird communities	Isolation variables explained small but significant parts of the residual variances in species number

Table A1. Continued.

Study	Patch isolation metric(s)	Response variable (s)	Species	Results
Kozakiewicz (1985)	Distance of 400 m to nearest compact forest area	Reproduction, trappability, spatial organization	Bank vole ( <i>Clethrionomys glareolus</i> )	Habitat isolation decreased reproduction, increased trappability and influenced spatial organization
Opdam et al. (1985)	Distance to large forest area, distance to nearest mature deciduous wood (> 20 ha), area of wood within buffer of 3 km width surrounding focal patch	Spatial distribution	Forest bird communities	No correlation between number of breeding bird species and isolation variables

## References

- Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* 71: 355–366.
- Bender D.J. 2000. Wildlife Movement in Fragmented Habitats: The Influence of Landscape Complexity. PhD Dissertation, Carleton University, Ottawa, Ontario, Canada.
- Bolger B.M., Alberts A.C., Sauvajot R.M., Potenza P., McCalvin C., Tran D. et al. 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7: 552–563.
- Bowman J., Jaeger J.A. and Fahrig L. Dispersal distance of mammals is proportional to home range size. *Ecology* (in press).
- Brennan J.M., Bender D.J., Contreras T.A. and Fahrig L. 2002. Experimental design for management at a landscape scale. In: Lui J. and Taylor W.A. (eds), *Integrating Landscape Ecology into Natural Resource Management*. Cambridge University Press, Cambridge, UK (in press).
- Cappuccino N. and Martin M. 1997. The birch tube-maker *Acrobasis betulella* in a fragmented habitat: the importance of patch isolation and edges. *Oecologia* 110: 69–76.
- de Vries H.H., den Boer P.J. and van Dijk T.S. 1996. Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia* 107: 332–342.
- Delin A.E. and Andrén H. 1999. Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forest landscape. *Landscape Ecology* 14: 67–71.
- Diamond J.M. 1975. The island dilemma: Lessons from modern biogeographic studies for the design natural reserves. *Biological Conservation* 7: 129–146.
- Diggle P.J. 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, London, UK.
- Doak D.E. and Mills L.S. 1994. A useful role for theory in conservation. *Ecology* 75: 615–626.
- Dunning J.B., Borgella R., Clements K. and Meffe G.K. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9: 542–550.
- Elkie P.C., Rempel R.S. and Carr A.P. 1999. *Patch Analyst User's Manual: A Tool for Quantifying Landscape Structure*. Ontario Ministry of Natural Resources. Technical Manual TM-002 TM-002. Northwest Science & Technology, Thunder Bay, Ontario, Canada.
- Fitzgibbon C.D. 1993. The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. *Journal of Applied Ecology* 30: 736–742.
- Fitzgibbon C.D. 1997. Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology* 34: 530–539.
- Grashof-Bokdam C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *Journal of Vegetation Science* 8: 21–28.
- Gustafson E.J. 1998. Quantifying spatial pattern: What is state of the art? *Ecosystems* 1: 143–156.
- Gustafson E.J. and Parker G.R. 1992. Relationships between land-cover proportion and indices of landscape spatial pattern. *Landscape Ecology* 7: 101–110.
- Gustafson E.J. and Parker G.R. 1994. Using an index of habitat patch proximity for landscape design. *Landscape and Urban Planning* 29: 117–130.
- Hanski I. 1998. Metapopulation dynamics. *Nature* 396: 41–49.
- Hanski I. and Gilpin M. 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society* 42: 3–16.
- Hanski I. and Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755–758.
- Hansson L. 1998. Local hot spots and their edge effects: small mammals in oak-hazel woodland. *Oikos* 81: 55–62.
- Hargis C., Bissonette J. and David J. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* 13.
- Harrison R.L. 1992. Toward a theory of inter-refuge corridor design. *Conservation Biology* 6: 293–295.
- Hill J.K., Thomas C.D. and Lewis O.T. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *Journal of Animal Ecology* 65: 725–735.
- Hjermann D.O. and Ims R.A. 1996. Landscape ecology of the wart-biter *Decticus verrucivorus* in a patchy landscape. *Journal of Animal Ecology* 65: 768–780.
- Hokit D.G., Stith B.M. and Branch L.C. 1999. Effects of landscape structure in Florida scrub: a population perspective. *Ecological Applications* 9: 124–134.
- Johannesen E., Andreassen H.P. and Ims R.A. 2000. The effect of patch isolation on reproductive synchrony in the root vole. *Oikos* 89: 37–40.
- Kareiva P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London, Series B* 330: 175–190.
- Kinnunen H., Järveläinen K., Pakkala T. and Tiainen J. 1996. The effect of isolation on the occurrence of farmland carabids in a fragmented landscape. *Annual Zoological Fennici* 33: 165–171.
- Kozakiewicz M. 1985. The role of habitat isolation in formation of structure and dynamics of the bank vole population. *Acta Theriologica* 30: 193–209.
- Krebs C.J. 1989. *Ecological Methodology*. Harper, New York, New York, USA.
- Laan R. and Verboom B. 1990. Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54: 251–262.
- Levins R. 1970. Extinction. In: Gerstenhaber M. (ed.), *Some Mathematical Questions in Biology*. The American Mathematical Society, Providence, Rhode Island, USA, pp. 77–107.
- Luiselli L. and Capicci D. 1997. Influences of area, isolation and habitat features on distribution of snakes in mediterranean fragmented woodland. *Biodiversity and Conservation* 6: 1339–1351.
- MacArthur R.H. and Wilson E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Marsh D.M., Fegraus E.H. and Harrison S. 1999. Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the tungara frog, *Physalaemus pustulosus*. *Journal of Animal Ecology* 68: 804–814.
- Matter S.F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: Individual responses to patch size and isolation. *Oecologia* 105: 447–453.

- McGarigal K. and Marks B. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Mladenoff D.J. and DeZonia B. 2000. APACK 2.14 Analysis Software: User's Guide (Draft Version: 2-18-00). Forest Landscape Ecology Laboratory, Dept. of Forest Ecology and Management, University of Wisconsin – Madison, Madison, Wisconsin, USA.
- Okubo A. 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, New York, New York, USA.
- Opdam P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology* 5: 93–106.
- Opdam P., Rijdsdijk G. and Hustings F. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* 34: 333–352.
- Paillat G. and Butet A. 1996. Spatial dynamics of the bank vole (*Clethrionomys glareolus*) in a fragmented landscape. *Acta Oecologica* 17: 553–559.
- Patton D.R. 1975. A diversity index for quantifying habitat “edge”. *Wildlife Society Bulletin* 3: 171–173.
- Perera A.H., Baldwin D.J.B. and Schnekenburger F. 1997. LEAP II: A Landscape Ecological Analysis Package for Land Use Planners and Managers. Forest Research Report no. 146. Ontario Forest Research Institute, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario, Canada.
- Steel R.D.G. and Torrie J.H. 1980. Principles and Procedures of Statistics. A Biometrical Approach. McGraw-Hill Book Company, New York, New York, USA.
- Sutherland G.D., Harestad A.S., Price K. and Lertzman K.P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4: 16.
- Szacki J., Babinska-Werka J. and Liro A. 1993. The influence of landscape spatial structure on small mammal movements. *Acta Theriologica* 38: 113–123.
- Tischendorf L. 2001. Can landscape indices predict ecological processes consistently? *Landscape Ecology* 16: 235–254.
- Tischendorf L., Bender D.J. and Fahrig L. 2002. Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* (this issue).
- Tischendorf L. and Fahrig L. 2000. How should we measure landscape connectivity? *Landscape Ecology* 15: 633–641.
- Trzcinski M.K., Fahrig L. and Merriam G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications* 9: 586–593.
- Turchin P. 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer, Sunderland, Massachusetts, UK.
- van Apeldoorn R.C., Oostenbrink W.T., van Winden A. and van der Zee F.F. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. *Oikos* 65: 265–274.
- van Dorp D. and Opdam P. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* 1: 59–73.
- Verboom B. and van Appledorn A. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris*. *Landscape Ecology* 4: 171–176.
- Vos C.C. and Jardon J.P. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* 35: 44–56.
- Vos C.C. and Stumpel H.P. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution parameters in the tree frog (*Hyla arborea*). *Landscape Ecology* 11: 203–214.
- With K.A. and King A.W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314–326.

