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Testing Simple Indices of Habitat Proximity

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ABSTRACT: Simple measures of habitat proximity made primarily on the basis of land cover are widely used in the ecological literature to infer habitat connectivity, or the potential for animal movement among resource patches. However, such indices rarely have been tested against observations of animal movement or against more detailed biological models. We developed a priori expectations as to the types of study systems and organisms for which various habitat proximity indices would be best suited. We then used data from three study systems and four species to test which, if any, of the indices were good predictors of population-level responses. Our a priori expectations about index performance were not upheld. The indices that consider both habitat area and distance from the focal patch were highly correlated with each other, suggesting that they do index similar quantities. However, none of the indices performed well in predicting population response variables. The results suggest that the pattern of habitat cover alone may be insufficient to predict the process of animal movement.

Keywords: habitat index, proximity, isolation, patch, connectivity, landscape fragmentation.

The movement of individuals among resource patches in a landscape can be an important determinant of population persistence, population size, and genetic diversity. Thus, there is great interest among ecologists in measuring connectivity, defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). In the ecological literature, indices based primarily on habitat structure are often used as a surrogate for connectivity (reviewed in Hanski 1999; Moilanen and Hanski 2001; Bender et al. 2003). The use of such habitat proximity indices has proliferated with advances in GIS (geographical information systems) technology, which has made it easier to quantify landscape structure (Goodwin 2003), whereas collecting data on the process of animal movement remains labor intensive. Habitat proximity indices assume that ecological function (movement) can be inferred from structure (habitat cover). If this assumption were correct, proximity indices would provide a powerful way to test the importance of connectivity for numerous ecological processes.

The appropriate use of habitat proximity indices has recently been debated in the context of metapopulation biology (where the term "patch isolation index" is commonly used; Moilanen and Hanski 2001) and landscape ecology (where the term "connectivity index" is more often used; Tischendorf and Fahrig 2000*b*, 2001). One problematic issue is that despite their widespread use, simple indices based on habitat structure rarely have been tested against observations of animal movement or immigration or against models that include a greater level of ecological information (Calabrese and Fagan 2004). In the first such effort, Moilanen and Nieminen (2002) reviewed the use of three habitat proximity indices and compared their utility in explaining patch colonization by butterflies. They found that when the indices were fit to detailed biological information, the weighted sum of surrounding habitat area (see eq. [2]) performed best, and the nearest neighbor distance (see eq. [1]) performed worst. Bender et al. (2003) compared the same three indices with immigration of a

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simulated organism and found that the weighted sum and the simple proportion of habitat cover (see eq. [3]) performed best, although neither explained more than 35% of the variation.

In this article, we review the habitat proximity indices currently in use and point out some misleading indices that have appeared in the recent literature. We then compare the ability of four indices to explain animal movement in three study systems. Unlike Moilanen and Nieminen (2002), our goal is not to develop biologically realistic estimates of connectivity in these systems. Rather, we focus on systems for which we already have a detailed understanding of movement in spatially structured landscapes and test which, if any, of the simple indices are good predictors of movement. We calculate the indices using only information on land cover and a scaling constant representing organism mobility because this is the level of detail researchers generally have when they are using these indices. Specifically, we ask first, for what types of study systems and organisms is each index most suitable? Second, which indices have the most explanatory power in our study systems? Third, within each system, how concordant are the indices among themselves?

Indices Considered

In this article, we consider indices that measure habitat proximity relative to a particular focal patch or point where data were collected (location-specific indices). We do not investigate measures meant to assess the connectivity of an entire landscape without reference to a particular location (landscape-wide indices) because this is a qualitatively different question (Schumaker 1996; Wiegand et al. 1999; Tischendorf and Fahrig 2000*a*; Tischendorf 2001; Li and Wu 2004). Location-specific habitat proximity indices generally consider the area of surrounding patches of suitable habitat and their distance from the focal patch; this distance is sometimes scaled relative to the mobility of the study organism. When data are available, multiple habitat quality categories could be considered, but in this article we follow the traditional binary distinction between "suitable habitat" and "other." This assumption is consistent with situations in which researchers typically use indices; they know the distribution of suitable habitat but do not know enough to parameterize detailed models of habitat quality, occupancy of surrounding patches, and/or animal movement.

Nearest neighbor index. The least detailed index in use is the nearest neighbor index, which is simply the distance to the nearest habitat patch:

$$H_x = d_i, \tag{1}$$

where H_x is the index of habitat proximity with respect to focal patch x, and d_i is the distance to the nearest neighbor patch i. Note that this index decreases with increasing habitat proximity, whereas the others increase.

Patch-based weighted sum. Another widely used index considers all surrounding habitat patches and their areas. This index was developed in island biogeography studies done at a large scale—that of species colonizing oceanic islands (MacArthur and Wilson 1967; Diamond et al. 1976; Gilpin and Diamond 1976)—and was later used at a smaller scale for metapopulation studies (Harrison et al. 1988; Adler and Nuernberger 1994; Hanski 1994, 1999). It assumes a fragmented landscape in which discrete habitat patches can be defined. In its most basic form, this index is

$$H_x = \sum_{i \neq x} A_i e^{-d_i/D}, \tag{2}$$

where A_i is the area of patch i, d_i is the distance between the focal patch x and patch i considered over all patches in the system, and D is a mobility constant scaled to the study organism. Equation (2) assumes that population size in patch i is linearly proportional to patch area, A_i, and that per capita emigration rate is constant. (An alternative assumption is that per capita emigration rate scales with the perimeter/area ratio, so that $A^{0.5}$ is used in place of A_i in eq. [2].) Because the index can be interpreted as summing predicted immigration from the surrounding patches into the focal patch, it is often used to represent the potential for immigration or patch colonization. Moilanen and Nieminen (2002) found it to be a good predictor of butterfly colonization of habitat patches. More generally, the index provides a weighted sum of the surrounding habitat patches, where the weightings decrease with distance from the focal patch.

The next two indices we consider are suitable both for patchy landscapes and for landscapes with more continuous habitat cover where discrete habitat patches cannot be readily defined. Although both can be used as sums (i.e., by using the numerators only), we recommend the proportional forms that have the advantages of being unitless and of scaling between 0 and 1 (so that the endpoints are biologically interpretable as zero and complete habitat cover).

Simple proportion. The most commonly used proportional index is

$$H_x = \frac{A(r)}{\pi r^2}, \tag{3}$$

where $A(r)$ is the total habitat area within radius r of the focal patch. A problem with this metric is that it assumes that within radius r, all habitat affects the focal patch equally, while habitat outside of radius r has no effect. Because this index weights all habitat within the radius equally, we recommend choosing a radius similar to the movement distance of the organism under consideration. However, researchers potentially could choose very different summation radii. Lack of clear theoretical basis for choosing the radius of summation is an inherent weakness of this index.

Weighted proportion. The last index is a modified form of equation (2) adapted to use grid cells instead of habitat patches to measure habitat area and distance from the focal point (Gu et al. 2001; Luoto et al. 2001). Here we use a normalized form that provides a proportion rather than a sum:

$$H_x = \frac{\sum_{j \notin x} F_j e^{-d_j/D} A_j}{\sum_{j \notin x} e^{-d_j/D} A_j}, \tag{4}$$

where the summations are now over grid cells instead of patches and F_j is the fraction of grid cell j (where j is outside of focal patch x) that is covered by suitable habitat (Bernhardsen 1999), d_j is the distance between grid cell j and the focal point (which is generally taken to be the center of the focal patch), D is the species-specific mobility constant, and A_j is the area of a grid cell (which cancels if grid cell size is constant). Compared with the simple proportion, this index makes the assumption that the importance of surrounding habitat declines gradually with distance from the focal point.

Index data requirements. Of the four indices, the nearest neighbor (eq. [1]) has the smallest data requirements: distance to the nearest habitat patch. The simple proportion (eq. [3]) requires total habitat area within some radius relevant to study organism mobility. The patch-based weighted sum (eq. [2]) requires patch area and interpatch distance for all patches as well as an estimate of mobility. The weighted proportion (eq. [4]) requires this same information but at the greater resolution of the grid cell (assuming that grid cells are smaller than habitat patches). The land cover data required by all four indices are readily available for many parts of the world in GIS format.

Problems with Current Index Use

In the literature, some indices have been used to measure habitat proximity despite the fact that they are ill-suited for this purpose. First, equation (2) or its variants have sometimes been used in a confusing way. For example, the D term is sometimes dropped from the exponent, leaving the function as e^{-d_i} (Hanski et al. 1994; Hanski and Thomas 1994; Thies and Tscharntke 1999; Steffan-Dewenter and Tscharntke 2000). This expression is difficult to interpret because it contains units of distance in the exponent, whereas the units cancel in the original version. It could be argued that using e^{-d_i} implicitly assumes a denominator of 1 distance unit; however, failure to make this assumption explicit leads to confusion.

Another problematic modification involves adding an inappropriate denominator to equation (2), for example,

$$H_x = \frac{\sum_{i=1}^{n} A_i e^{-d_i/D}}{\sum_{i=1}^{n} e^{-d_i/D}} \tag{5}$$

(Eber and Brandl 1996; Thies and Tscharntke 1999). Equation (5) provides the weighted mean patch area for all the habitat patches in the system. This is a poor index of total habitat proximity. For example, adding habitat to a system should increase a habitat proximity index, but when equation (5) is used, adding a patch with an area smaller than the current index value ($A_j < H_x$) decreases rather than increases the value of H_x.

Another index in use (Sullivan and Shaffer 1975; Whitcomb et al. 1981; Siegfried et al. 1998) is

$$H_x = \sum_{i=1}^{n} \frac{A_i}{d_i^2}. \tag{6}$$

This index has the advantages of being dimensionless and simple to calculate. However, it cannot be scaled to the study organism, and unlike indices (1)–(4), it does not converge as the area for which data are available increases. Indices (5) and (6) are not considered further here.

General Properties of the Indices

Due to their basic properties, the indices differ in their suitability for types of study systems and organisms. The patch-based indices (eqq. [1], [2]) are well suited for systems that are highly fragmented relative to the mobility of the study organism (Moilanen and Hanski 2001; Moilanen and Nieminen 2002). These indices assume that the distance between two patches can be represented by a single value, which is most precise when habitat patches are clearly definable and are widely separated relative to organism mobility. The nearest neighbor index is most suitable for extremely fragmented landscapes because it assumes that populations will be affected by only the closest habitat patch.

In contrast, the grid-based or proportional indices (eqq. [3], [4]) are well suited for cases in which habitat patches are difficult to define, oddly shaped, or close together relative to the mobility of the study organism. These indices, in effect, average patch area over all of the intercell distances found within the landscape.

None of the indices fully accounts for directed movement—that is, for the organism preferentially moving toward or settling in suitable habitat. The nearest neighbor index is the most compatible with directed movement because the nearest neighboring patch could be the most important when movement is directed. Table 1 summarizes the ecological circumstances for which each index is most appropriate.

Empirical Studies

We tested the ability of all four indices to predict distribution and movement in three study systems that span a broad range of situations in which researchers lacking detailed information might choose to use proximity indices. On the basis of the properties of the indices, our expectations were as follows. First, in general, the nearest neighbor index would perform less well than the others because it does not include information about the two-dimensional surrounding habitat cover or organism mobility; however, we thought it might perform well for the butterflies (see "Study Systems"), which have slightly directed movement and inhabit a highly fragmented system (Schultz and Crone 2001, forthcoming). Second, the grid-based weighted proportion would perform best because it represents the existing habitat cover most precisely. Third, the patch-based weighted sum would perform as well as the grid-based index only in the most fragmented system, where habitat patches are so small and widely separated that there is no reason to use a grid. Fourth, the simple proportion would perform less well than the weighted indices because it only weakly accounts for the distance of each surrounding habitat patch from the focal plot.

Study Systems

Fender's blue butterfly. The Fender's blue butterfly (*Icaricia icarioides fenderi*) is an endangered species that inhabits patches of upland prairie in the Willamette Valley, Oregon. The butterfly is found only in patches containing its larval host plants, Kincaid's lupine (*Lupinus sulphureus* spp. *kincaidii)* and spur lupine (*Lupinus arbustus*), so that suitable habitat is clearly defined. The study system consisted of a set of 19 habitat patches, most of which are highly isolated (fig. 1*A*). Two of us have studied the Fender's blue extensively (Schultz 1998; Schultz and Crone 1998, 2001, forthcoming). In many ways, the Fender's blue typifies the kinds of animals for which proximity indices are used. Habitat is highly fragmented, movement is only slightly directed (Schultz and Crone 2001), and larger patches, if occupied, support larger populations (Schultz and Hammond 2003).

We reasoned that in this system, biologists would be interested in using habitat proximity indices as a surrogate for immigration. For example, conservation biologists and land managers are interested in determining whether restored patches would be naturally colonized or whether reintroductions are necessary to initiate restored populations. We therefore chose immigration as the most relevant measure of movement in this system. We compared index predictions to immigration results from Schultz and Crone's (2001) biased, correlated random walk model for this species, which is based on field observations of 447 female butterfly flight moves. We used the model to simulate the lifetime movement of one generation of butterflies, starting with empirical population sizes in each patch and repeating the simulation 150 times. We measured immigration as the total number of individuals arriving in each patch. For additional details on the mechanics of these simulations, see the article by Schultz and Crone (forthcoming). In the index calculations, we used 1,000 m for the scaling parameter, D; this number is an estimate of the lifetime displacement of an individual butterfly from its birth location (Schultz 1998). The GIS land cover data used to calculated index values were developed during Schultz's previous research on this system. GIS data from the Oregon Natural Heritage Program were modified using topographic maps, street maps, aerial photos, and researcher knowledge of the sites to delimit patches of host plants with a line accuracy of 10–30 m.

Tvärminne field voles. Our second study system consisted of 72 islands in the Tvärminne archipelago of Finland (fig. 1*B*), which are inhabited by field voles (*Microtus agrestis*). This population has been the subject of intensive

Table 1: A priori expectations for suitability of the habitat proximity indices for different ecological circumstances

	Habitat patches widely separated and easily definable	Habitat patches close together or difficult to define
Study species with directed dispersal	Nearest neighbor (eq. [1])	None of the indices considered here
Study species with nondirected dispersal	Nearest neighbor (eq. [1]) Weighted patch sum (eq. [2]) Simple proportion (eq.[3]) Weighted proportion (eq. [4])	Simple proportion (eq. [3]) Weighted proportion (eq. [4])

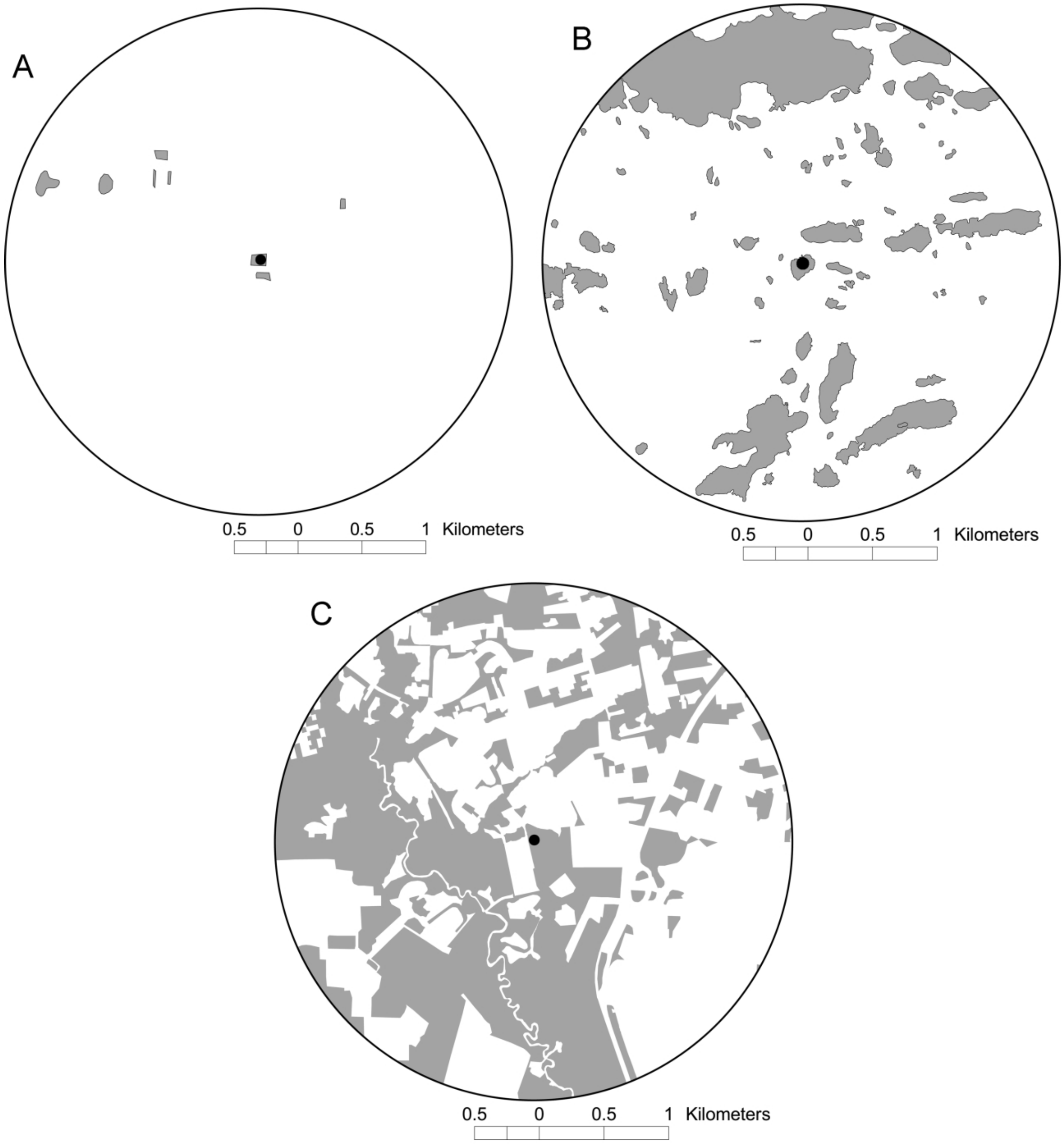

Figure 1: Habitat cover surrounding a typical focal patch in each of the three study systems. *A*, Lupine patches suitable for Fender's blue butterfly in Oregon, United States. *B*, Islands inhabited by field voles in the Tvärminne Peninsula, Finland. *C*, Pine-oak-ericaceous heath habitat used by two species of bees in New Jersey, United States. Black dots show the centroid of the focal patch (butterflies) or island (voles) or location where data were collected (bees). The study systems ranged from highly fragmented for the butterflies (mean of 0.6% ± 0.1% SE suitable habitat cover at a radius of 2*D* around each focal patch, where *D* is the typical movement distance of the study organism) to moderately fragmented for the voles (17% ± 1% habitat cover at radius 2*D*) to relatively unfragmented for the bees (63% ± 8% habitat cover at radius 2*D*).

previous analysis (Pokki 1981; Crone et al. 2001). On the basis of these studies, we know that the Tvärminne vole metapopulation experiences frequent extinctions and colonizations of island subpopulations. Larger islands are likely to be occupied by voles and support large vole populations that exist for ~10 generations. Smaller islands are less likely to be occupied, support smaller populations when occupied, and persist for ~1 vole generation.

Given frequent local extinctions and colonizations, we chose the colonization rate for each island as the most relevant measure of movement. For each island, we calculated the fraction of all possible unoccupied → occupied transitions that occurred during the 6-year study period. To calculate indices for the voles, we used 180 m for D; this is a typical interisland movement distance, determined on the basis of movements of individual voles (Pokki 1981). The GIS data were obtained from the National Land Survey of Finland, which has a scale accuracy of about 5 m. Since the analysis includes only two categories, land and water, and was done on the basis of high-resolution data, the classification accuracy will be very high.

New Jersey bees. Our third study system consisted of 20 locations in the New Jersey Pinelands Biosphere Reserve where we studied two wild bee species, *Augochlorella aurata* and *Lasioglossum (Dialictus) oblongus* (R. Winfree and C. Kremen, unpublished data). Bees of all species were collected by standard methods (hand-netting and pan trapping) from late spring to fall 2002, and we used the total number of bees collected at each site as our measure of abundance. The two species with the largest sample sizes ($N = 44$ and 125 individuals, respectively) were used in the analysis. Unlike the butterfly and vole systems, where habitat is highly fragmented and interpatch movement is infrequent, natural habitat is relatively continuous in this system, and movement is dominated by daily foraging of these central-place foragers. In other words, local abundance primarily reflects daily movement among habitat areas, as opposed to population dynamics over time within a discrete patch. We therefore chose abundance as our population response variable for both solitary bee species. Because it is difficult to define discrete habitat patches in this system (fig. 1*C*), we did not attempt to measure patch-level abundance of bees but instead defined a 110-m transect where bees were collected, and we calculated index values around the center of the transect. We defined suitable habitat as pine-oak-ericaceous heath, which is the natural habitat in this system; although the bees are not known to be limited to this habitat type, further studies have shown both species to be strongly associated with it (R. Winfree, unpublished data). Because suitable habitat is not as clearly defined, and movement was indirectly measured, the bee system provides a weaker test of the indices than do the butterfly and vole systems.

The estimate of D for each bee species was made on the basis of intertegular length, a body size measurement that explains 78% of the variation in daily foraging distances for bees (Greenleaf et al. 2005). Mean intertegular lengths of 1.45 ± 0.02 (SE) mm for *A. aurata* resulted in an estimated typical foraging distance of 151 ± 8 m, and lengths of 1.13 ± 0.02 (SE) mm for *L. (Dialictus) oblongus* resulted in an estimated typical foraging distance of 65 ± 4 m. We therefore used $D = 151$ m for *A. aurata* and $D = 65$ m for *L. oblongus*. The GIS land cover data were obtained from the state of New Jersey and were based on aerial photos taken at a 1-m resolution. Photos were subsequently classified to 53 land cover types at a resolution of at most 0.4 ha; in practice, land cover polygons in the data set are as small as 0.004 ha. Because of the high resolution of the original data, and because we combined multiple natural land cover types for this analysis, the classification accuracy will be very high.

Methods

We used GIS land cover data and software (ArcGIS 9.0 and Arcview 3.3; Environmental Systems Research Institute) to calculate index values for all three systems. The simple proportion of habitat cover at a radius of $1D$ and $2D$ around the focal patch was calculated using buffers in Arcview. (See discussion of summation radius under "Indices Considered"; eq. [3].) We calculated nearest-neighbor and patch-based weighted sums by defining continuous habitat to be a "patch" and using the centroids of each patch and the closest points on the patch perimeters to calculate interpatch distances, using the Arcview software extension "Distance by ID" (Jenness Enterprises). As discussed above ("Indices Considered"; eq. [2]), we calculated patch-based weighted sums using both A and $A^{0.5}$, to represent area-proportional and perimeter/area-proportional emigration, respectively. We calculated grid-based indices by overlaying a 60×60-m grid on the land cover data for each landscape, and calculating the proportion of habitat cover within each grid cell (Bernhardsen 1999) and the distances between the focal plot and grid cell j. The grid-based index had a higher resolution than the patch-based index, both because grid cells were smaller than patches (the average-sized patch contained four to seven grid cells) and because we used proportional habitat cover within each grid cell rather than binary values. The indices that use a weighting function (eqq. [2], [4]) were calculated out to a radius of $4D$; habitat patches beyond this radius had a minimal effect on index values (R. Winfree, unpublished data). In calculating the weighted indices, we used the most commonly used distance function, the negative exponential. Other distance functions could be used (Tufto et al. 1997; Turchin 1998; Clark et al. 1999),

Table 2: Explanatory value of indices

			Bee abundance	
	Butterfly, immigration	Vole colonization	*Augochlorella aurata*	*Lasioglossum (Dialictus) oblongus*
NN, centroid	.075	1.32	NA	NA
NN, edge	.079	−.08	NA	NA
PBWS, centroid, A	.009	1.43	NA	NA
PBWS, centroid, $A^{.5}$	.021	.99	NA	NA
PBWS, edge, A	.001	1.70	NA	NA
PBWS, edge, $A^{.5}$	.011	1.54	NA	NA
SP	.002	.69	.11	.14
WP	.008	1.06	.12	.17*

Note: NN = nearest neighbor (eq. [1]); PBWS = patch-based weighted sum (eq. [2]); SP = simple proportion (eq. [3]) calculated at a $2D$ radius; WP = weighted proportion (eq. [4]). Interpatch distances were measured either between patch centroids ("centroid") or as the shortest distance between patch perimeters ("edge"). For the butterfly data, we report the squared partial correlation coefficient for each index, from multiple regressions with focal patch area included as a covariate. For the vole data, we report the Wald's Z for each index, from logistic regressions in which focal patch area was included as a covariate. For the bee data, we report the adjusted R^2 from bivariate regression; the focal patch is not considered separately, and patch-based indices are not calculated because discrete patches are not definable in this system.

* $P < .05$.

but more information about the actual distribution of dispersal distances would be required to choose among them, and our objective was to compare the performance of indices in the absence of more detailed biological information. We used our empirical typical movement distances as D in the index equations (see appendix in the online edition of the *American Naturalist*). For the butterfly system, we had occupancy data for all of the patches in the system, and we were thus able to calculate the indices a second way, by including only occupied patches in the index summation (e.g., Moilanen and Nieminen 2002).

To assess the predictive value of the indices we regressed each population response variable against each index. To separate the effects of focal patch area and the surrounding habitat proximity, we calculated index values without the focal patch and included focal patch area as a covariate in the regressions. We report the squared partial correlation coefficient (Johnson and Wichern 1988) and the P value for each index; P values were calculated using robust standard errors to minimize the effect of any heteroskedasticity in the data (White 1980). Analyses were done in JMP, version 5.0.1 (SAS Institute), and Stata 8.2 (StataCorp). We analyzed vole colonization using logistic regression of the number of colonization events relative to the number of years in which each island was unoccupied (R statistical package, version 1.7.0) and report Wald's Z for each index (Sokal and Rohlf 1995).

In the New Jersey bees system (fig. 1*C*) habitat cover is relatively continuous, and discrete habitat patches are difficult to define. In this system, we did not calculate the patch-based indices (eqq. [1], [2]), and we did not attempt to separate the focal patch from the surrounding habitat cover because many such distinctions would be arbitrary. Instead, we regressed the population response variables against the two indices that do not require the use of discrete patches (eqq. [3], [4]) and compared the resulting R^2 values between indices.

To ask whether the different indices ranked the focal patches in the same way within a system, we used nonparametric correlation to make all pairwise comparisons among indices (JMP 5.0.1).

Results

Overall, proximity indices were poor predictors of movement (table 2). None of the indices predicted simulation results for butterfly immigration into focal patches (all partial $R^2 \leq 0.08$, $P > .10$) or island colonization for the Tvärminne voles (Wald's $Z \leq 1.70$, $P > .09$). For the bees, the simple proportion index was not significantly related to abundance of either species (both $R^2 \leq 0.14$, $P > .06$). The weighted proportion index was weakly related to *L. (Dialictus) oblongus* abundance ($R^2 = 0.17$, $P > .04$) but not to *A. aurata* abundance ($R^2 \leq 0.12$, $P > .08$). Focal patch area was not significantly related to any population response variable. Different forms of the patch-based weighted sum (A vs. $A^{0.5}$ and centroid-to-centroid vs. edge-to-edge distances) differed little in explanatory ability. Similarly, measuring distance using centroids versus closest edges made little difference in the functioning of the nearest neighbor index. For the simple proportion index, we tried two different radii ($1D$ and $2D$), but neither was explanatory; the results we report are for the more explanatory 2*D* radius. Using only occupied patches in the index summation, which we were able to do for the butterfly system, improved index performance somewhat, but still only one index was a significant predictor of immigration (the patch-based weighted sum using $A^{0.5}$ and centroid-to-centroid measurements, $P = .02$; other P values $\geq .07$).

Within a given study system, most indices were highly concordant (table 3). The weighted indices (all variants of the patch-based weighted sum and the weighted proportion) were highly correlated with each other (Spearman's $\rho \geq 0.61$, $P \leq .002$). The simple proportion was highly correlated with all of the weighted indices (Spearman's $\rho \geq 0.71$, $P \leq .001$) except in the butterfly system, where it was not significantly correlated with one version of the patch-based weighted sum. The nearest neighbor index was in some cases significantly correlated with the area-based indices, and in other cases it was not.

Discussion

We were struck by the overall poor fit of the simple indices to patterns in well-studied systems. Although neither the butterfly nor the vole systems conformed perfectly to the assumptions of index models, both met the key assumptions of discrete habitat/nonhabitat distinctions, larger populations in larger occupied habitat patches, and local dispersal. We speculate that none of the indices adequately predicted population response variables because simple static relationships with patch size and location do not adequately capture the dynamics in these systems. In the vole system, an important factor may be that emigration appears to be tightly tied to stochastic fluctuations in food availability and population size (Crone et al. 2001); per capita emigration is much higher from small islands than from large islands because of larger fluctuations in food availability (Pokki 1981). In the Fender's blue system, we know that in addition to patch size, habitat quality (which is rapidly changing due to presence or absence of invasive

Table 3: Values of Spearman's ρ showing the rank correlation among indices

	NN, edge	PBWS, centroid, *A*	PBWS, centroid, $A^{.5}$	PBWS, edge, *A*	PBWS, edge, $A^{.5}$	SP	WP
NN, centroid:							
Butterfly	.90***	−.41	−.73***	−.37	−.69***	−.01	−.42
Vole	.51***	−.19	−.43***	.03	−.07	−.15	−.13
NN, edge:							
Butterfly		−.54*	−.66**	−.49*	−.67**	−.18	−.52*
Vole		−.05	−.22	−.06	−.24*	−.11	.01
PBWS, centroid, *A*:							
Butterfly			.77***	.98***	.84***	.74***	.98***
Vole			.83***	.90***	.82***	.88***	.94***
PBWS, centroid, $A^{.5}$:							
Butterfly				.69***	.98***	.31	.75***
Vole				.61***	.69***	.77***	.77***
PBWS, edge, *A*:							
Butterfly					.76***	.76***	.99***
Vole					.92***	.76***	.84***
PBWS, edge, $A^{.5}$:							
Butterfly						.39	.81***
Vole						.71***	.75***
SP:							
Butterfly							.72***
Vole							.84***
Bee							.97***

Note: Expected sign of relationship is negative for comparisons involving the nearest neighbor index and positive for all others. NN = nearest neighbor (eq. [1]); PBWS = patch-based weighted sum (eq. [2]); SP = simple proportion (eq. [3]) calculated at a 2*D* radius; WP = weighted proportion (eq. [4]). Interpatch distances were measured either between patch centroids ("centroid") or as the shortest distance between patch perimeters ("edge").

* $P < .05$

** $P < .01$.

*** $P < .001$.

species and of habitat management) has a significant influence on abundance (Schultz and Dlugosch 1999; Schultz et al. 2003). In addition, successful emigration by Fender's blues scales with area more slowly than $A^{0.5}$ (Schultz and Crone, forthcoming). A related point is that butterflies will have longer residence times in larger patches, so that individuals from large patches have less time to reach other patches before the end of their 2–3-week life spans (Crone and Schultz 2003). The indices cannot capture this complexity but rather assume that all emigrants disperse in the same way. In the butterfly system, we tested whether a mismatch between habitat area and occupancy prevented the indices from being predictive by calculating the indices using occupied patches only. One index then became a significant predictor of immigration, although it was not significant after correcting for multiple comparisons. In sum, we conclude that the indices were poor predictors of animal movement in the two fragmented systems.

The simple-proportion and weighted-proportion indices were also tested in the bee system, where habitat cover is more continuous. These are the only two indices suitable for landscapes where discrete habitat patches are not readily defined. The indices performed similarly and neither was strongly predictive, although one index (the weighted proportion) was a significant predictor for one bee species. These indices performed better in the bee system, however, than in the butterfly or vole systems. It is possible that daily foraging movements are better reflected by the proximity indices than are rare movement events among butterfly habitat patches or vole dispersal among islands. Consistent with this explanation, the simple proportion index has explained abundance for central place foragers in other studies (e.g., Kremen et al. 2004). Alternatively, we cannot rule out the possibility that higher apparent predictive power reflects spurious correlation because none of the relationships would be significant after accounting for multiple comparisons.

Moilanen and Nieminen (2002) tested variations of equations (1)–(3) against data on patch colonization by butterflies in a highly fragmented landscape. Their data sets included far more biological detail than those we used to calculate indices here; for example, they included additional scaling parameters that related patch area to emigration and immigration, and indices were calculated using the area of occupied patches only. Our goals differ fundamentally from theirs in that they asked what level of detail is required for indices to predict colonization, whereas we asked whether simple indices, if used in the absence of biological knowledge, would have power to predict movement. In their study, the nearest neighbor performed the worst and the weighted sum index performed the best. In contrast, we found that none of the indices consistently worked well. Comparison of the two studies suggests that in order to make simple indices predictive, more detailed biological information must be used in conjunction with land cover.

Although indices designed to measure the connectivity of an entire landscape without reference to a focal patch (landscape-wide indices) are qualitatively different from the indices investigated in this article, it is worth noting that recent studies have questioned their ability to predict animal movement as well (Schumaker 1996; Wiegand et al. 1999; Tischendorf and Fahrig 2000*a*; Tischendorf 2001; Li and Wu 2004). Perhaps both landscape-wide and location-specific indices fail to predict connectivity successfully because animal movement can vary with factors such as habitat type, habitat heterogeneity, edge-crossing behavior, perceptual ability, and density (see Goodwin 2003), none of which are captured by indices, which are based on habitat structure alone and assume undirected movement. For example, Bender and Fahrig (2005) observed that patch size and connectivity were poor predictors of animal movement when the matrix consisted of many habitat types, which probably have different effects on the study organism.

Overall, our results also suggest that simple indices function better as measures of habitat structure than as measures of habitat connectivity from the organism's point of view. In all three systems, the area-based indices (eqq. [2]–[4]) were highly correlated with each other, suggesting that they were measuring the same qualitative property. However, no index performed well in the tests against animal movement. Indices based on land cover alone might be best used to ask whether surrounding land cover has an effect on some response variable of interest (Ricketts et al. 2001; Pearman 2002; Kremen et al. 2004), rather than assuming that these indices represent animal movement or habitat connectivity. The choice of which simple index to use may be less important than the decision to use a simple index at all, as opposed to a more biologically detailed model.

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Appendix from R. Winfree et al., "Testing Simple Indices of Habitat Proximity"

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Weighting Functions and Distance Distributions

In order to use the weighted indices (eqq. [2], [4]), researchers need to incorporate their empirical measure of study organism mobility into the distance weighting function, $\exp(-d/D)$, where d is the distance from the focal point to a given habitat patch or grid cell, and D is a mobility constant scaled to the study organism. The purpose of this appendix is to clarify the relationship between empirical measures of organism mobility and the index parameter D.

It is often implicitly (and incorrectly) assumed that an exponential weighting function of points on the landscape corresponds to an exponential distribution of distance traveled. In a two-dimensional landscape, if the relative probability of arriving at any point is $\exp(-d/D)$, where d is the distance of the point from the focal point, then the relative probability of traveling a distance d is $d\exp(-d/D)$. This is because the length of the arc at distance d from the focal point has length $2\pi d$.

Thus, a function that treats the weight of a point as $\exp(-d/D)$ corresponds to a movement kernel that is proportional to $d\exp(-d/D)$. We make this kernel into a distribution by normalizing it:

$$g(d) = \frac{d\,\exp(-d/D)}{\int x\,\exp(-x/D)dx} = \frac{d\,\exp(-d/D)}{D^2}.$$

The mean distance is given by

$$\int dg(d)dd = 2D.$$

The modal distance is given by

$$0 = dg(d)/dd = \left(1 - \frac{d}{D}\right)\frac{\exp(-d/D)}{D^2}.$$

Thus, the mode is D. The median distance satisfies

$$\int_0^m g(d)dd = \frac{1}{2}.$$

This can be scaled to remove D and solved numerically to find that $m \approx 1.68D$.

If researchers using the indices know whether their empirical estimates represent means, modes, or medians, they can relate them to D as above. The more likely situation, however, is that researchers using simple indices will not have complete distributions of movement distances and therefore will not know whether their empirical estimate of typical movement distance represents a mean, mode, or median. This situation suggests the importance of doing sensitivity analysis around the empirical estimate.

By contrast, an exponential distance distribution $\exp(-d/D)/D$), which would correspond to the singular weighting function $\exp(-d/D)/d$), has mean D, mode 0, and median $\approx 0.69D$. We do not consider this distribution in our analysis.