

Modeling patch occupancy: Relative performance of ecologically scaled landscape indices

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Abstract In fragmented landscapes, the likelihood that a species occupies a particular habitat patch is thought to be a function of both patch area and patch isolation. Ecologically scaled landscape indices (ESLIs) combine a species' ecological profile, i.e., area requirements and dispersal ability, with indices of patch area and connectivity. Since their introduction, ESLIs for area have been modified to incorporate patch quality. ESLIs for connectivity have been modified to incorporate niche breadth, which may influence a species' ease in crossing the non-habitat matrix between patches. We evaluated the ability of 4 ESLIs, the original and modified indices of area and connectivity, to explain patterns in patch occupancy of 5 forest rodents. Occupancy of eastern gray squirrels (*Sciurus carolinensis*), North American red squirrels (*Tamiasciurus hudsonicus*),

fox squirrels (*Sciurus niger*), white-footed mice (*Peromyscus leucopus*), and eastern chipmunks (*Tamias striatus*) was modeled at 471 sites in 35 landscapes sampled from the upper Wabash River basin in Indiana. Models containing ESLIs received support for gray squirrels, red squirrels, and chipmunks. Modified ESLIs were important in models for red squirrels. However, none of the models demonstrated high predictive ability. Incorporating habitat quality and using surrogate measures of dispersal can have important effects on model results. Additionally, different responses of species to area, isolation, and habitat quality suggest that generalizing patterns of metapopulation dynamics was not justified, even across closely related species.

Keywords Connectivity · Forest rodent · Metapopulation · Niche breadth · Patch area

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Introduction

Habitat fragmentation is the breaking apart of habitat patches, resulting in increased isolation and almost certainly habitat loss (Fahrig 1997, 2003). Lindenmayer and Fischer (2007) stressed the importance of separating these two processes; the effects of habitat loss and habitat isolation are distinct. By identifying which process better explains a species' distribution pattern, mitigation could be accomplished more effectively. Additionally, one should determine

whether non-spatial factors should be considered, such as habitat quality or interspecific interactions. Several studies have suggested that habitat patch quality may be as important as area and isolation for metapopulation dynamics (Thomas et al. 2001; Franken and Hik 2004). The influence of habitat quality on metapopulation dynamics could overshadow any patterns associated with area or isolation.

Vos et al. (2001) introduced ecologically scaled landscape indices (ESLIs) to link the ecological profile of a species to quantitative measures of landscape pattern. Their two original indices incorporate characteristics that presumably are important to species' metapopulation dynamics: a "patch carrying capacity" index accounts for individual area requirements and reflects extinction risk; and a "patch connectivity" index reflects colonization by incorporating empirical estimates of dispersal distance. ESLIs have proven useful in explaining patterns of patch occupancy (Vos et al. 2001; Swihart and Verboom 2004). To incorporate habitat quality into ESLIs, Swihart et al. (2003a) modified the ESLI for carrying capacity with a correction factor to account for habitat needs of the focal species. The ESLI was multiplied by a variable scaled from 0 to 1 representing quality of the patch. Additionally, since dispersal distance is unknown for many species, Swihart et al. (2003a) modified the second ESLI of Vos et al. (2001) to incorporate the expected dispersal distance based on an allometric relationship between home range size and dispersal distances known for 44 species of mammals. However, expected dispersal distances may differ from "effective dispersal distance" in fragmented landscapes, and these differences may depend on whether species are considered habitat generalists or specialists. Adjusting ESLIs further to account for niche breadth might better reflect the landscape permeability for a species than an estimate of dispersal calculated in a homogeneous landscape. Thus, Swihart et al. (2003a) also modified the ESLI for connectivity with an index of niche breadth for different species. These modified ESLIs demonstrated reasonable fit when applied to patch occupancy patterns of 137 North American mammals (Swihart et al. 2003a).

Swihart et al. (2003a) demonstrated that "ESLIs are superior in some instances to traditional landscape indices when the objective is predicting species occupancy." However, the modified ESLIs were not constructed from empirical data on dispersal distance

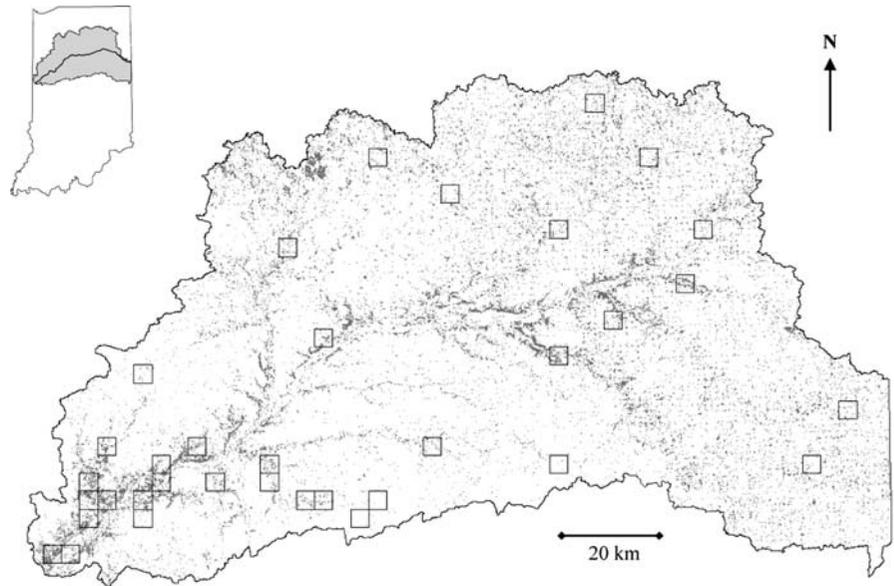
or habitat quality (surrogates were used), and usefulness of such indices as surrogates for directly measured variables (e.g., describing habitat quality) is unknown in terms of their ability to predict species occurrence. Here we evaluate the relative performance of ESLIs and modified ESLIs in modeling forest patch and landscape occupancy of 5 granivorous rodent species (eastern gray squirrel, North American red squirrel, fox squirrel, white-footed mouse, and eastern chipmunk) in 35 landscapes within Indiana. We compared results based on ESLIs with those of Moore and Swihart (2005), who modeled patch occupancy of these species in the same study area without ESLIs. Instead, they used a variety of directly measured habitat variables at each study site along with traditional patch- and landscape-level metrics. We maintain their modeling framework, which also addressed species non-detection error, to determine whether ecological scaling indices describe patterns of patch occupancy similarly to more data-intensive methods that measure ecological variables directly. With respect to the two different types of ESLIs, we expected that adjusting the carrying capacity index according to habitat quality should better represent patch occupancy patterns than the original ESLI for area in landscapes where patches differ appreciably in levels of food or cover. Similarly, we expected using niche breadth to estimate the ESLI for connectivity might better account for variation in species' abilities to disperse through a heterogeneous landscape than the original connectivity index, even though the latter was based on empirical dispersal estimates. Thus, our analysis addresses the utility of modeling occupancy using surrogate measures of dispersal.

Methods

Field sampling

Study areas were located in the upper Wabash River basin in north-central Indiana (Fig. 1). The basin includes about 2 million hectares, or 21% of the state, and encompasses 8 watersheds associated with the Wabash River, the longest free-flowing river in the United States east of the Mississippi River (Swihart and Slade 2004). Approximately 88% of the area is under agricultural use, primarily for corn and soybeans, and approximately 8% is forested.

Fig. 1 Map of the upper Wabash River basin in Indiana, showing the distribution of forest and locations of 35 23-km² study landscapes



Vertebrate sampling was conducted in 35 randomly selected 23-km² (4.8 × 4.8 km) landscapes throughout the basin from May to August 2001–2003. Because sampling was conducted under 2 concurrent projects, the majority of landscapes occurred in the southwest region of the basin (Swihart and Slade 2004); however, the stratified selection algorithms for both projects were based on capturing the range of variation in landcover. Across the 35 landscapes, the proportion of forest cover ranged from 1.1% to 38.3%. Each 23-km² landscape plus a surrounding 1.6 km buffer was digitized with 1-m resolution using 1998 digital aerial ortho quads. The buffer allowed for accurate estimation of indices for patches near the edge of a landscape.

Sampling methodology is described in Moore and Swihart (2005). In brief, 471 sites across the 35 landscapes were randomly sampled for both small mammals and vegetation characteristics. At each site, a grid of Fitch live traps (2001), Sherman live traps (2003) or both (2002), were placed according to forest patch size, 3 × 3 up to 7 × 7, with trap spacing of 15 m. Tomahawk squirrel traps were placed at every other Sherman or Fitch trap. Sherman and Fitch traps were baited with sunflower seed and Tomahawk traps with black walnuts. Traps were pre-baited for 3 days, followed by a 5-day trap session during which traps were checked twice daily. Each site was trapped for a single session. Vegetation was characterized in a rapid assessment at the center of

each sample site. These measures included basal area of nut-trees (MAST), an index of down woody debris (DWD), a count of understory trees <5 cm dbh (STEM), and an index of understory density (DENS). MAST was measured from a single variable-radius plot using a 10 basal-area-factor prism for *Quercus*, *Carya*, and *Juglans* species. DWD was calculated as the volume of all log sections >5 cm in diameter within a 10-m radius. STEMS included all woody stems within a 5-m radius. Finally, DENS was calculated from 4 sub-samples, 5 m in each cardinal direction from the plot center. For each sub-sample, a vertical board (3 m tall and 0.3 m wide) divided into a checkerboard pattern was raised, and the number of checkerboard squares at least half obstructed visually by vegetation was counted.

ESLI formulation

We calculated two sets of ESLIs. First, following Vos et al. (2001), we constructed two ESLIs as indicators of a species' expected response to patch area and isolation. The first index uses the individual area requirement of a species to modify patch size to a measure of carrying capacity for a patch:

$$\text{AREA}_{si} = A_i / \text{IAR}_{si}$$

where AREA_{si} is an estimate of the number of individuals of species s that can occupy patch i , A_i is the area of patch i , and IAR_{si} is the individual area

requirement for a single reproductive unit of species s in patch i . Individual area requirements for the tree squirrels were taken from Goheen et al. (2003) and for mice and chipmunks from Swihart and Verboom (2004) (Table 1).

The other index of Vos et al. (2001) measures connectivity of specific patches for each species:

$$\text{CONN}_{si} = \sum_{j \neq i}^n A_j \exp(-\alpha_s D_{ij})$$

where CONN_{si} is the connectivity of species s in patch i , which is the sum of all contributions of neighboring patches j , calculated as the product of their area (A_j) and a function of their distance to focal patch i (D_{ij}). The connectivity between patches i and j declines exponentially with distance at a rate specified by α_s , where $1/\alpha_s$ represents the mean dispersal distance of species s . We estimated dispersal distance as the 50th percentile of a negative exponential distribution of distances fit to data collected in experimental studies of mobility (Goheen et al. 2003; Rizkalla and Swihart 2007). In these studies, radio-collared forest rodents were translocated into corridors and agricultural fields at increasingly greater distances from a forest patch until they failed to reach the forest. The distance distribution was constructed from data on individuals that reached the forest or that had not reached the forest within 1 week but had moved from the release site. This included 22 gray squirrels, 15 fox squirrels, 23 red squirrels, 39 white-footed mice, and 58 chipmunks. Predated animals were not included. The negative

exponential distribution can be used to conservatively predict dispersal distance for a variety of species (Sutherland et al. 2000). Because the mobility studies did not test distances greater than 1 km, our estimate of mean dispersal may be an underestimate. Therefore, we also constructed ESLIs using the 75th and 95th percentile of the estimated distance distribution. If models performed better using these higher dispersal estimates, we would infer these as more appropriate scales of response by the study species.

The second set of ESLIs was modified as in Swihart et al. (2003a) to incorporate habitat quality and dispersal distance based on niche breadth. In the modified index of area effects, the carrying capacity of a patch:

$$\text{AREA}_{si}^* = h_{si} A_i / \text{IAR}_{si}$$

is modified to include a term h_{si} to represent the quality of the patch in terms of meeting the habitat needs of the species. In the absence of empirical data on habitat quality in each patch, patches might be ranked according to expert opinion, or some other semi-quantitative approach might be used. In our case, since habitat had been previously sampled, we calculated h_{si} from the habitat variables included in the species-specific occupancy models of Moore and Swihart (2005). Where they found a positive linear relationship between occupancy and a single habitat variable, the site-specific estimates of that variable's values were scaled between 0 and 1 to provide a positive value of h_{si} . Where a negative linear relationship existed, the site-specific values were

Table 1 Ecological characteristics used in calculating ecologically scaled landscape indices (ESLI) for forest rodents in Indiana and average ESLIs

	IAR (ha)	$1/\alpha_s$ (km)	$1/\alpha_s^{75}$ (km)	$1/\alpha_s^{95}$ (km)	Niche breadth Z-score	$1/\alpha_s^*$ (km)	AVG AREA (log _e)	AVG CONN (log _e)	AVG AREA* (log _e)	AVG CONN* (log _e)
Gray squirrel	0.8	0.32	0.64	1.38	-0.62	0.01	3.68	13.10	2.34	3.39
Red squirrel	0.24	0.33	0.66	1.41	0.96	1.11	4.88	13.16	3.96	14.72
Fox squirrel	1.0	0.45	0.90	1.94	-0.62	0.52	3.46	13.67	3.39	13.88
White-footed mouse	0.05	0.20	0.39	0.85	2.52	2.35	6.45	12.09	3.80	15.29
Eastern chipmunk	0.1	0.30	0.60	1.29	-0.29	0.005	5.76	12.98	3.93	-2.85

IAR = individual area requirement (taken from the literature); $1/\alpha_s$ = mean dispersal distance (calculated from mobility studies); $1/\alpha_s^{75}$ and $1/\alpha_s^{95}$ = 75th and 95th percentile dispersal distance (calculated from mobility studies); $1/\alpha_s^*$ = expected mean dispersal distance is calculated from niche breadth or home range size (see text); AREA = ESLI for carrying capacity; CONN = ESLI for connectivity based on mean dispersal distance; AREA* = ESLI for carrying capacity modified for habitat quality; CONN* = ESLI for connectivity based on expected mean dispersal distance

reverse-scaled between 0 and 1, such that higher values of h_{si} reflected the preference for lower values of the habitat variable. Thus, values of h_{si} closer to 1 always reflected higher-quality habitat. Where two habitat variables were included in the models of Moore and Swihart (2005), the scaled variables were weighted by the standardized coefficient estimates of the occupancy model to provide a single value of h_{si} between 0 and 1. Although their habitat coefficient estimates were not independent of other variables included in their occupancy models (e.g., patch and landscape metrics), we believed our method sufficiently captured the relative variation in species-specific habitat quality across patches. Habitat quality for gray squirrels was based on a positive relationship with MAST. For red squirrels, there was a positive relationship with DENS and a negative relationship with MAST. Fox squirrels showed a negative relationship with DENS. There was a positive relationship between DWD and mice occupancy. For chipmunks, habitat quality was based on a positive relationship with STEM and DENS.

The index for connectivity was modified via the dispersal parameter:

$$\text{CONN}_{si}^* = \sum_{j \neq i}^n A_j \exp(-\alpha_s^* D_{ij})$$

where the mean dispersal distance ($1/\alpha_s^*$) was estimated from the niche breadth of the species. As in Swihart et al. (2003a), each species was assigned a dietary breadth rating on a scale of 1–5 (specialist to generalist), and a habitat breadth score on a scale of 1–15 representing the variety of habitats used. A single niche-breadth variable with a mean of 0 and a standard deviation of 1 was derived as

$$\text{NB}_Z = \frac{Z_H + Z_D}{s_{(Z_H + Z_D)}}$$

where Z_H and Z_D are standardized variables for the habitat and dietary breadth scores, respectively, and the denominator is the standard deviation of the sum of these variables. Swihart et al. (2003a) developed a predictive allometric model for maximum dispersal distance from home range size and niche breadth based on 44 terrestrial mammalian species:

$$d_{\max}^* = 20.86\text{HR}^{0.31} + (8.48\text{NB}_z - 1.27)$$

We applied this model to determine d_{\max}^* for the 5 rodent species. Home range sizes were taken from Swihart et al. (2003a). The model yielded a negative value for gray squirrels and chipmunks, so for these species, we used 1 home-range diameter as the d_{\max}^* value. The maximum dispersal distance was considered the 99th percentile of a negative exponential distribution, from which $(1/\alpha_s^*)$ was estimated using the 50th percentile. We did not use the 75th and 95th percentiles here to maintain consistency with the original formulation of Swihart et al. (2003a).

Statistical analysis

Although logistic regression is commonly used to model species occupancy, it assumes that during sampling a species is detected at all sites it occupies (i.e., detectability = 1). Failure to detect a species during sampling can result in serious errors in subsequent logistic regression models (Gu and Swihart 2004). To address the issue of nondetection error, we modeled occupancy and detectability using program MARK. This software implements estimation of site-occupancy rates (ψ) and species detectability (p) when $p < 1$ according to the model developed by MacKenzie et al. (2002). The model uses a likelihood approach to estimate the probabilities of detection and occupancy, based on encounter histories. Detectability may be a function of site variables or environmental conditions, which vary on each trapping occasion. We used the same variables as in Moore and Swihart (2005) to model detectability. These variables were: trap occasion as a linear (OCC) and quadratic function (OCC²) because the first and last trap occasions were half days, trapping year (YR), number of days of rain recorded during a trapping session at a site (RAIN), trap effort calculated from the number of traps multiplied by the number of trap occasions minus the number of traps disturbed (EFF), and timing of the trapping session during the year (SEAS). Trap success was greatest in the middle of the season, so this term also was modeled as a quadratic function (SEAS²).

For each species, we evaluated 11 models. We first evaluated connectivity calculated from the 50th, 75th, and 95th percentile of dispersal distances (CONN). We used AIC with a bias-correction term (AIC_c) and

AIC_c weights (w) for model selection (Akaike 1973; Burnham and Anderson 2002). The index with the lowest AIC value was then used in the remaining model comparisons, including a null model and all possible combinations of the four ESLIs. The modified dispersal distance (CONN*) for chipmunks was so low (Table 1) that all patches received the same connectivity value. Thus, only 8 different models were evaluated for chipmunks. When competing models had $\Delta\text{AIC}_c < 2$, we performed model averaging to estimate parameters (Burnham and Anderson 2002). Model accuracy was assessed using receiver operating characteristic (ROC) curves. Area under the curve (AUC) provides a measure of accuracy where 0.5 indicates no difference between classification of true- and false-positives, and 1.0 indicates a perfect fit to the data (Fielding and Bell 1997). A value of 0.5 indicates the model is no better than a null model. AUC values greater than 0.7 generally indicate acceptable accuracy.

Goodness-of-fit tests are not available in MARK for models with individual covariates. We evaluated goodness-of-fit for each species by bootstrapping the most parameterized model that did not include individual covariates [$p(\text{OCC}) \psi(\cdot)$]. Model fit will only be greater for a more general model (Moore and Swihart 2005). One hundred bootstrap simulations yielded an expected mean deviance to which we compared the observed deviance of the model (Cooch and White 2004). For all species, we found that \hat{c} , the ratio of observed and expected mean deviance, was $0.95 < \hat{c} < 1.1$ indicating adequate fit of the models.

In addition to the MARK analysis of species occupancy at the patch scale, we also modeled occupancy of each species at the landscape scale using generalized linear models. The proportion of patches occupied within each landscape ($n = 35$) was calculated and for each of the ESLIs for each landscape an average value was computed. We evaluated the same combination of models as above, using the best CONN index as identified in the patch-scale models, again using AIC with a bias-correction term (AIC_c) and AIC_c weights (w) (Akaike 1973; Burnham and Anderson 2002). When competing models had $\Delta\text{AIC}_c < 2$, we performed model averaging to estimate parameters (Burnham and Anderson 2002). We assessed model accuracy using R^2 from a linear regression of the predicted values against observed. Analysis was conducted in R 2.1.1.

Results

Of the 471 sites included in this analysis, gray squirrels were detected at 64 sites (14%), red squirrels at 154 sites (33%), fox squirrels at 201 sites (43%), white-footed mice at 374 sites (79%), and eastern chipmunks at 350 sites (74%). Compared to the ESLIs of Vos et al. (2001), the patch values for the modified area index (AREA*) were lower than the original index (AREA) because the modified index was defined such that it only equals the original index when habitat was considered optimal ($h_{si} = 1$) (Table 1). Modifying the connectivity index for dispersal distance estimates based on niche breadth (CONN*) increased connectivity for red squirrels, fox squirrels, and white-footed mice (relative to CONN), but decreased average patch connectivity values compared to the original CONN for gray squirrels and eastern chipmunks since the maximum dispersal distance was taken as the home range diameter for these latter two species (see above).

For gray squirrels, two patch-level models received support (Table 2), both containing the unmodified ESLI for connectivity (CONN) using the 95th percentile and one containing the modified ESLI for area. Patch occupancy increased as connectivity increased (Table 3). Area under the ROC curve was 0.74 indicating marginally acceptable predictive ability. The best model for red squirrels contained both modified ESLIs. Patch occupancy increased as connectivity decreased and area/habitat suitability increased. Area under the ROC curve was 0.69 indicating somewhat poor accuracy. Two models received support for eastern chipmunks, both driven principally by the original AREA index; occupancy increased as area decreased. The chipmunk model performed poorly, however; area under the ROC was 0.53. For fox squirrels, the null model received the greatest support, although all single-variable models were within 2 AIC units from the null (Table 2). For white-footed mice no model received substantially greater weight than another (all $\Delta\text{AIC} < 2$). These results suggest that ESLIs provided no explanatory power for these latter two species, and thus model averaging was not performed.

In comparison to the models of Moore and Swihart (2005), the ESLI models revealed many (but not all) of the same general patterns for most species, but with lower accuracy. Our gray squirrel model included

Table 2 Model selection results for MARK occupancy (Ψ) models

Ψ model	Gray squirrel ^a		Red squirrel ^b		Fox squirrel ^c		White-footed mouse ^d		Eastern chipmunk ^b	
	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
NULL	37.99	0.00	46.21	0.00	0.00	0.21	1.29	0.07	5.58	0.04
CONN50	15.20	0.00	21.85	0.00	1.83 ^x	0.09	1.14 ^x	0.08	7.53	0.01
CONN75	0.69	0.28	24.19	0.00	1.87	0.08	2.15	0.05	6.35 ^x	0.03
CONN95	0.00 ^x	0.40	21.70 ^x	0.00	1.89	0.08	2.16	0.05	6.49	0.02
CONN*	37.48	0.00	3.24	0.13	1.81	0.09	1.12	0.08		
AREA	29.22	0.00	41.44	0.00	0.74	0.15	0.18	0.13	0.00	0.61
AREA*	30.45	0.00	45.63	0.00	1.23	0.11	0.13	0.13	5.23	0.04
CONN + AREA	2.03	0.15	23.67	0.00	2.80	0.05	0.00	0.14	1.96	0.23
CONN* + AREA	30.32	0.00	2.62	0.18	2.78	0.05	0.13	0.13		
CONN + AREA*	1.78	0.17	23.30	0.00	3.28	0.04	1.86	0.06	6.93	0.02
CONN* + AREA*	31.37	0.00	0.00	0.68	3.29	0.04	1.43	0.07		

^a $p(\text{OCC} - \text{OCC}^2 - \text{RAIN})$

^b $p(\text{YR} + \text{OCC} - \text{OCC}^2 + \text{SEAS} - \text{SEAS}^2 + \text{EFF})$

^c $p(\text{YR} + \text{OCC} - \text{OCC}^2 + \text{EFF})$

^d $p(\text{YR} - \text{OCC} + \text{SEAS} - \text{RAIN} + \text{EFF})$

CONN50 = ecologically scaled landscape index (ESLI) for connectivity based on mean dispersal distance; CONN75 and CONN95 = ESLI for connectivity based on 75th and 95th percentile of negative exponential distribution of dispersal distances; CONN* = ESLI for connectivity based on mean dispersal distance modified by niche breadth (not evaluated for eastern chipmunks, see text for explanation); AREA = ESLI for carrying capacity; AREA* = ESLI for carrying capacity modified for habitat quality. X superscript indicates CONN dispersal percentile used in additive models. Footnotes indicate variables used to model the detection function

Table 3 Parameter estimates for final MARK occupancy models

Covariate	Gray squirrel		Red squirrel		Eastern chipmunk	
	β	SE	β	SE	β	SE
ρ						
Year			-0.002	0.28	-0.001	0.00
OCC	0.070	0.15	1.158	0.27	2.045	0.20
OCC ²	-0.029	0.03	-0.172	0.04	-0.380	0.03
RAIN	-0.437	0.17				
SEAS			1.072	0.31	1.023	0.21
SEAS ²			-0.182	0.05	-0.178	0.03
EFF			0.012	0.01	0.006	0.00
Ψ						
INTERCEPT	335.806	9.90	-577.902	4.91	-79.604	27.07
CONN	0.754	0.03			0.012	0.04
CONN*			-1.083	0.01		
AREA					-0.282	0.08
AREA*	0.023	0.14	0.369	0.02		

Estimates are model-averaged for gray squirrels and eastern chipmunks

No model was selected for fox squirrel or white-footed mouse

CONN and AREA* (AUC = 0.74); their model similarly included the distance to the nearest patch, patch area, and a habitat proxy variable for food abundance (AUC = 0.92). Our model for red squirrels included both CONN* and AREA* (AUC = 0.69); theirs included the traditional “proximity” index (a measure of patch isolation) and a proxy of food abundance but not patch area (AUC = 0.81). Our chipmunk model included AREA (AUC = 0.53); their model also included patch area plus a habitat measure of understory density (AUC = 0.74). Neither our models nor theirs identified important patch area or isolation effects for white-footed mice. For fox squirrels, our model did not include any patch metrics, whereas they found higher fox squirrel occurrence rates in patches with greater distance to the nearest patch. Note that while our indices may be analogous to the patch-level metrics of Moore and Swihart (2005), their models also accounted for spatial autocorrelation and included principal components for landscape-level variables (e.g., total amount of forest in a 23-km² area).

ESLI models at the landscape scale generally revealed similar patterns as those at the patch scale, but with some exceptions (Table 4). Explanatory power of these models was generally low. For gray squirrels, the two landscape models that received support were driven by the unmodified ESLI for connectivity (CONN), with proportional occupancy increasing as average connectivity increased

($R^2 = 0.26$), but we did not identify a strong landscape level AREA or AREA* effect (Table 5), which contrasts with the patch-level models and also with findings of Moore and Swihart (2005), whose model included a variable (distance from Wabash River) that they interpreted as a landscape-level forest cover effect. For red squirrels, the strongest models included the modified ESLI for connectivity (CONN*) ($R^2 = 0.18$), with occupancy increasing as connectivity decreased, but unlike the patch-level models and consistent with the red squirrel model of Moore and Swihart (2005), there was no strong support for a forest area effect at the landscape level. For chipmunks, proportional occupancy decreased with average AREA ($R^2 = 0.09$). This was consistent with our patch-level models and with the chipmunk model of Moore and Swihart (2005). Again, there was no particularly strong support for any landscape-level area or connectivity effects for fox squirrels and white-footed mice.

Discussion

Our analysis represents an attempt to improve on existing landscape metrics by incorporating additional ecological realism (e.g., habitat quality) into traditional ESLIs and using surrogate information (e.g., niche breadth) to estimate landscape indices in the absence of empirical data for certain parameters

Table 4 Model selection results for landscape occupancy (Ψ) models

Ψ model	Gray squirrel		Red squirrel		Fox squirrel		White-footed mouse		Eastern chipmunk	
	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
NULL	9.59	0.00	4.42	0.04	0.00	0.29	0.00	0.26	0.87	0.25
CONN	0.69	0.35	1.95	0.14	2.07	0.10	2.09	0.09	2.36	0.12
CONN*	11.13	0.00	0.00	0.36	2.05	0.10	1.83	0.10		
AREA	8.88	0.01	3.19	0.07	2.18	0.10	0.51	0.20	0.00	0.38
AREA*	10.75	0.00	4.95	0.03	0.76	0.20	1.93	0.10	3.12	0.08
CONN + AREA	2.58	0.14	4.04	0.05	4.46	0.03	1.98	0.10	2.20	0.13
CONN* + AREA	11.10	0.00	2.39	0.11	4.44	0.03	2.56	0.07		
CONN + AREA*	0.00	0.50	4.34	0.04	2.78	0.07	4.27	0.03	4.41	0.04
CONN* + AREA*	12.84	0.00	1.67	0.16	2.71	0.07	3.41	0.05		

CONN = ecologically scaled landscape index (ESLI) for connectivity based on dispersal distance selected in patch models; CONN* = ESLI for connectivity based on mean dispersal distance modified by niche breadth (was not evaluated for eastern chipmunks, see text for explanation); AREA = ESLI for carrying capacity; AREA* = ESLI for carrying capacity modified for habitat quality

Table 5 Parameter estimates for final landscape occupancy models

Covariate	Gray squirrel		Red squirrel		Eastern chipmunk	
	β	SE	β	SE	β	SE
INTERCEPT	3.96	1.16	-4.75	2.16	-0.55	1.42
CONN	0.15	0.05	-0.02	0.04		
CONN*			-0.10	0.07		
AREA					-0.04	0.04
AREA*	-0.04	0.05	0.01	0.03		

Estimates are model-averaged for all species

No model was selected for fox squirrel or white-footed mouse

(e.g., dispersal distance). We found that the relative performance of our modified ESLIs compared to conventional indices (Vos et al. 2001) was mixed. Modifications of ESLIs to account for both niche breadth and habitat quality substantially improved patch occupancy models for the red squirrel. For gray squirrels, the conventional connectivity metric was a better predictor of occurrence than CONN*, but AREA* performed slightly better than the conventional AREA metric. For eastern chipmunks, the conventional AREA metric was the best predictor of occurrence, rather than our modified AREA* metric. For fox squirrels and white-footed mice, neither set of metrics served as good predictors of species occurrence. Results were similarly mixed for landscape-level models (Table 4).

There were some pitfalls associated with our modified ESLIs that may have limited their performance. With respect to the index for patch area, multiplying the original AREA metric by a value between 0 and 1 (h_{si}) forced our modified index, AREA*, to always be \leq AREA. Thus, only for habitat patches of “maximum quality” ($h_{si} = 1$) would the carrying capacity estimate for AREA* match the value of AREA, which ideally would have been calculated using empirical estimates of “average home range size” in an “average-quality patch.” This is of little practical consequence, since both AREA and AREA* are merely indices—larger values of either metric are hypothesized to predict higher patch occupancy rates. However, our formulation of the metric does preclude its direct interpretation as patch carrying capacity, since, for example, we would expect “high-quality” patches to have a considerably higher carrying capacity than what

would be calculated using the original AREA metric. Of greater practical importance, our estimates of h_{si} did not account for the relative importance of habitat vs. patch variables in the Moore and Swihart (2005) models. Thus, in our analysis a large patch (which would have a large AREA value) would have a small AREA* value if it had a small value for a significant habitat variable in the Moore and Swihart (2005) model, even if patch area was a stronger predictor of occurrence than the habitat variable in their model. This likely explained the lower AUC values in our models relative to those of Moore and Swihart (2005).

Additionally, by including habitat and patch area effects in a single index, it can be difficult to interpret which of these elements is driving the relationship. This could explain, for example, why our best red squirrel patch model included AREA* whereas the model of Moore and Swihart (2005) included a habitat variable but not a patch-area variable: it was likely that habitat, not area, drove the significance of AREA* in our model. Further modification of the carrying capacity ESLI to address patch quality may benefit from a different form of scaling that better captures the relative importance of habitat and patch area in the index and also maintains its direct interpretation of patch carrying capacity. Or, it may be more prudent to simply include separate terms for describing patch area (e.g., $ESLI_K$) and habitat quality in predicting species occupancy.

With respect to the index for connectivity, the ability of CONN* to accurately characterize species' dispersal abilities through a fragmented landscape depends on the quality of information informing the surrogate metrics that Swihart et al. (2003a) related to the “maximum dispersal distance.” Unfortunately, the application of interspecific allometric equations for individual species rarely will provide estimates that are as reliable as field-derived values. Our estimates of dispersal distance based on niche breadth and home range size for gray squirrels and chipmunks were negative, and the expected mean dispersal distances we used (based on home-range diameters) were still 30 and 60 times less for gray squirrels and chipmunks, respectively, than those observed in field studies (Goheen et al. 2003; Rizkalla and Swihart 2007). Small mammals likely travel greater distances in heavily fragmented landscapes than would be predicted from their home-range size (Kozakiewicz

1993). Niche breadth is an important determinant of species' response to human habitat alteration including fragmentation (Swihart et al. 2003b; Julliard et al. 2006; Devictor et al. 2007), but these examples point to the limitation of this approach from an empirical perspective.

On the other hand, the mean dispersal distance for red squirrels estimated from the allometric equation using home range and niche breadth was more than triple that empirically estimated by Goheen et al. (2003), and in this case, we believe our estimate may more accurately reflect the ability of the species. The red squirrel is a relatively recent colonist of Indiana (Mumford and Whitaker 1982), where it has expanded concurrent with declining gray squirrel populations (Goheen et al. 2003; Swihart et al. 2007). Similarly, our estimate of mean dispersal distance for white-footed mice was an order of magnitude higher than that empirically estimated by Rizkalla and Swihart (2007), but the latter study did not estimate the potential of naturally dispersing individuals, and circumstantial evidence suggests that white-footed mice may be very capable dispersers (e.g., Merriam and Lanoue 1990; Cummings and Vessey 1994; Mossman and Waser 2001).

The red squirrel and white-footed mouse examples, along with the fact that the 75th and 95th percentile empirical estimates of dispersal distance were better predictors of chipmunk and gray squirrel occupancy than were mean dispersal distance estimates, suggest that field measures of mean dispersal distance may often be gross underestimates. They may also suggest that maximum dispersal estimates are more sensible than mean dispersal estimates for use in certain types of landscape occupancy models. However, our estimate of mean dispersal distance for fox squirrels, based on the niche-breadth approach, was similar to that estimated by Goheen et al. (2003, Table 1). Thus, there may be cases where our approach can provide a reasonable proxy of dispersal for purposes of estimating an ESLI for connectivity in the absence of direct dispersal estimates.

Pellet et al. (2007) found that area and connectivity were not good predictors of extinction and colonization probabilities. They did not evaluate habitat quality but acknowledged that it was probably important, especially for mobile species. In our analysis, incorporating habitat quality was important for red squirrels, with higher occurrence rates in

patches with fewer mast bearing trees (reflected in higher AREA* values). Moore and Swihart (2005) hypothesized that suboptimal sites (lower basal area of mast trees and higher understory density) were not probably preferred by red squirrels but that they represented sites where gray squirrels—a likely competitor—did not occur. Additionally, red squirrels likely chose patches containing conifers (Nupp 1997; Goheen and Swihart 2005), although this factor was not included in our measure of habitat quality.

The unmodified ESLI for connectivity proved to be the best predictor of gray squirrel occupancy; less isolated patches were more likely to contain gray squirrels. Gray squirrel occurrence thus appears to be constrained by colonization ability. Gray squirrels generally are unwilling to disperse across non-forested habitat (Goheen et al. 2003) and were only detected in large patches with high mast tree basal area (Moore and Swihart 2005). The requirement for mature mast trees in large patches, combined with an inability to cross large gaps, appears to have limited the distribution of gray squirrels in this intensively agricultural basin.

The unmodified ESLI for area was important in the chipmunk model, although predictive ability was poor. Occupancy tended to be positively related to connectivity and negatively related to area. Moore and Swihart (2005) concluded from the presence of chipmunks in small patches and their overall high occupancy rate, that there was no negative effect of fragmentation. Given the support for connectivity in the models, there may be a threshold of patch isolation beyond which chipmunks cannot colonize, or the composition of the matrix and the presence of corridors may influence successful dispersal (Rizkalla and Swihart 2007).

The lack of a relationship between connectivity and patch occupancy was expected for fox squirrels and white-footed mice. Fox squirrels are able and willing to disperse through agricultural fields (Goheen et al. 2003). They evolved at the interface of central hardwoods and tallgrass prairie (Koprowski 1994), so edge habitat may be a better predictor of fox squirrel occurrence. White-footed mice are considered habitat generalists with a tolerance for fragmented landscapes (Henein et al. 1998; Moore and Swihart 2005). Mice readily use treelines and fencerows within the matrix, and also reside in those with structural complexity (Bennett et al. 1994;

Merriam and Lanoue 1990). Given their ability to use a variety of habitats, area and isolation do not appear useful as predictors of white-footed mice occupancy.

More complicated metrics do not necessarily produce better results (Matter et al. 2005). Moilanen and Hanski (1998) found that area and isolation were sufficient for modeling a butterfly metapopulation; habitat quality did not improve predictive power. But habitat characteristics, in addition to spatial variables, have been important elsewhere in a variety of taxa (Parris 2004; Schmid-Holmes and Drickamer 2001). Vanreusel et al. (2007) advocate the use of models composed solely of functional variables, those related to ecological functions. Although useful for predicting species occurrence, they cannot describe metapopulation dynamics on a larger scale. ESLIs are useful in metapopulation models, and more informative than simple area and isolation metrics (Swihart et al. 2003a; Vos et al. 2001). However, neither type of ESLI model in our analysis performed as well as the fuller and more data-intensive approach of Moore and Swihart (2005), who built multi-scale models (site, patch, and landscape) that included habitat variables measured in situ for each site and also autocorrelates to control for spatial dependency in response data. Area under the ROC in their models were 15%, 22%, and 32% higher for red squirrels, gray squirrels, and chipmunks, respectively, over the best ESLI models in the current study. They also obtained fairly good predictive models (AUC = 0.81 and 0.85) for fox squirrels and white-footed mice using other variables than patch area or isolation measures. Others have similarly shown that indices do not perform as well as more complex modeling efforts (Schumaker et al. 2004); although in some instances, greater complexity did not significantly change model results (Nelson et al. 2008). Indices may be most useful when computational feasibility is a consideration, such as when dealing with multiple species assessments and large landscapes. When not confronted with such limitations, and if species-specific habitat covariates are available, they should be incorporated into the model explicitly rather than used in surrogates.

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References

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second international symposium on information theory. Akademiai Kiado, Budapest
- Bennett AF, Henein K, Merriam G (1994) Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. *Biol Conserv* 68:155–165. doi:10.1016/0006-3207(94)90347-6
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference. Springer-Verlag, New York
- Cooch E, White G (2004) Program MARK: a gentle introduction. Available from <http://www.phidot.org/software/mark/docs/book/>
- Cummings JR, Vessey SH (1994) Agricultural influences on movement patterns of white-footed mice (*Peromyscus leucopus*). *Am Midl Nat* 132:209–218. doi:10.2307/2426575
- Devictor V, Julliard R, Couvet D et al (2007) Functional homogenization effect of urbanization on bird communities. *Conserv Biol* 21:741–751. doi:10.1111/j.1523-1739.2007.00671.x
- Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *J Wildl Manage* 61:603–610. doi:10.2307/3802168
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515. doi:10.1146/annurev.ecolsys.34.011802.132419
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49. doi:10.1017/S0376892997000088
- Franken RJ, Hik DS (2004) Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *J Anim Ecol* 73:889–896. doi:10.1111/j.0021-8790.2004.00865.x
- Goheen JR, Swihart RK (2005) Resource selection and predation of North American red squirrels in deciduous forest fragments. *J Mammal* 86:22–28. doi:10.1644/1545-1542(2005)086<0022:RSAPON>2.0.CO;2
- Goheen JR, Swihart RK, Gehring TM et al (2003) Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions

- of forest connectivity and carrying capacity. *Oikos* 102:95–103. doi:[10.1034/j.1600-0706.2003.12336.x](https://doi.org/10.1034/j.1600-0706.2003.12336.x)
- Gu W, Swihart RK (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biol Conserv* 116:195–203. doi:[10.1016/S0006-3207\(03\)00190-3](https://doi.org/10.1016/S0006-3207(03)00190-3)
- Henein K, Wegner J, Merriam G (1998) Population effects of landscape model manipulation on two behaviourally different woodland small mammals. *Oikos* 81:168–186. doi:[10.2307/3546479](https://doi.org/10.2307/3546479)
- Julliard R, Clavel J, Devictor V et al (2006) Spatial segregation of specialists and generalists in bird communities. *Ecol Lett* 9:1237–1244. doi:[10.1111/j.1461-0248.2006.00977.x](https://doi.org/10.1111/j.1461-0248.2006.00977.x)
- Koprowski JL (1994) *Sciurus niger*. *Mamm Species* 479:1–9
- Kozakiewicz M (1993) Habitat isolation and ecological barriers—the effect on small mammal populations and communities. *Acta Theriol (Warsz)* 38:1–30
- Lindenmayer DB, Fischer J (2007) Tackling the habitat fragmentation panchreston. *Trends Ecol Evol* 22:127–132. doi:[10.1016/j.tree.2006.11.006](https://doi.org/10.1016/j.tree.2006.11.006)
- MacKenzie DI, Nichols JD, Lachman GB et al (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- Matter SF, Roslin T, Roland J (2005) Predicting immigration of two species in contrasting landscapes: effects of scale, patch size and isolation. *Oikos* 111:359–367. doi:[10.1111/j.0030-1299.2005.14127.x](https://doi.org/10.1111/j.0030-1299.2005.14127.x)
- Merriam G, Lanoue A (1990) Corridor use by small mammals: field measurement for three experimental types of *Peromyscus leucopus*. *Landsc Ecol* 4:123–131. doi:[10.1007/BF00132856](https://doi.org/10.1007/BF00132856)
- Moilanen A, Hanski I (1998) Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503–2515
- Moore JE, Swihart RK (2005) Modeling patch occupancy by forest rodents: incorporating detectability and spatial autocorrelation with hierarchically structured data. *J Wildl Manage* 69:933–949. doi:[10.2193/0022-541X\(2005\)069\[0933:MPOBFR\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069[0933:MPOBFR]2.0.CO;2)
- Mossman CA, Waser PM (2001) Effects of habitat fragmentation on population genetic structure in the white-footed mouse (*Peromyscus leucopus*). *Can J Zool* 79:285–295. doi:[10.1139/cjz-79-2-285](https://doi.org/10.1139/cjz-79-2-285)
- Mumford RE, Whitaker JO Jr (1982) *Mammals of Indiana*. Indiana University Press, Bloomington
- Nelson E, Polasky S, Lewis DJ et al (2008) Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proc Natl Acad Sci USA* 105:9471–9476. doi:[10.1073/pnas.0706178105](https://doi.org/10.1073/pnas.0706178105)
- Nupp TE (1997) Population dynamics and community structure of granivorous forest rodents in a fragmented landscape. Dissertation, Purdue University
- Parris KM (2004) Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. *Ecography* 27:392–400. doi:[10.1111/j.0906-7590.2004.03711.x](https://doi.org/10.1111/j.0906-7590.2004.03711.x)
- Pellet J, Fleishman E, Dobkin DS et al (2007) An empirical evaluation of the area and isolation paradigm of meta-population dynamics. *Biol Conserv* 136:483–495. doi:[10.1016/j.biocon.2006.12.020](https://doi.org/10.1016/j.biocon.2006.12.020)
- Rizkalla CE, Swihart RK (2007) Explaining movement decisions of forest rodents in fragmented landscapes. *Biol Conserv* 140:339–348. doi:[10.1016/j.biocon.2007.08.019](https://doi.org/10.1016/j.biocon.2007.08.019)
- Schmid-Holmes S, Drickamer LC (2001) Impact of forest patch characteristics on small mammal communities: a multivariate approach. *Biol Conserv* 99:293–305. doi:[10.1016/S0006-3207\(00\)00195-6](https://doi.org/10.1016/S0006-3207(00)00195-6)
- Schumaker NH, Ernst T, White D et al (2004) Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. *Ecol Appl* 14:381–400. doi:[10.1890/02-5010](https://doi.org/10.1890/02-5010)
- Sutherland GD, Harestad AS, Price K et al (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv Ecol* 4(1):16. <http://www.consecol.org/vol4/iss1/art16/> (online)
- Swihart RK, Slade NA (2004) Modeling interactions of private ownership and biological diversity: an architecture for landscapes with sharp edges. In: Swihart RK, Moore JE (eds) *Conserving biodiversity in agricultural landscapes: model-based planning tools*. Purdue University Press, West Lafayette
- Swihart RK, Verboom J (2004) Using ecologically scaled landscape indices to assess biodiversity consequences of land use-decisions. In: Swihart RK, Moore JE (eds) *Conserving biodiversity in agricultural landscapes: model-based planning tools*. Purdue University Press, West Lafayette
- Swihart RK, Atwood TC, Goheen JR et al (2003a) Patch occupancy of North American mammals: is patchiness in the eye of the beholder? *J Biogeogr* 30:1259–1279. doi:[10.1046/j.1365-2699.2003.00925.x](https://doi.org/10.1046/j.1365-2699.2003.00925.x)
- Swihart RK, Gehring TM, Kolozsvary MB et al (2003b) Responses of “resistant” vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Divers Distrib* 9:1–18. doi:[10.1046/j.1472-4642.2003.00158.x](https://doi.org/10.1046/j.1472-4642.2003.00158.x)
- Swihart RK, Goheen JR, Schnelker SA et al (2007) Testing the generality of patch and landscape-level predictors of tree squirrel occurrence at a regional scale. *J Mammal* 88:564–572. doi:[10.1644/06-MAMM-A-275R.1](https://doi.org/10.1644/06-MAMM-A-275R.1)
- Thomas JA, Bourn NAD, Clarke RT et al (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc R Soc Lond B Biol Sci* 268:1791–1796. doi:[10.1098/rspb.2001.1693](https://doi.org/10.1098/rspb.2001.1693)
- Vanreusel W, Maes D, Van Dyck H (2007) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conserv Biol* 21:201–212. doi:[10.1111/j.1523-1739.2006.00577.x](https://doi.org/10.1111/j.1523-1739.2006.00577.x)
- Vos CC, Verboom J, Opdam PFM et al (2001) Toward ecologically scaled landscape indices. *Am Nat* 157:24–41. doi:[10.1086/317004](https://doi.org/10.1086/317004)