



The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration

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ABSTRACT

Extant species in human-dominated landscapes differ in their sensitivity to habitat loss and fragmentation, although extinctions induced by environmental alteration reduce variation and result in a surviving subset of species with some degree of 'resistance'. Here, we test the degree to which variable responses to habitat alteration are (1) essentially an inherent property of a taxon subject to constraints imposed by its geographical range, as suggested by Swihart *et al.* (2003), (2) a function of the landscape in which a species occurs, or (3) a function of spatial trends occurring on large scales. We used data collected on 33 vertebrate species during 2001–04 across the upper Wabash River basin, Indiana, in 35 square 'landscapes', each 23 km² in size. Six species of forest rodent, six species of grassland rodents, seven species of bats, eight species of aquatic turtles, and six species of amphibians were sampled at 504, 212, 590, 228, and 625 patches, respectively. The fraction of patches of primary habitat (e.g. forests for tree squirrels, wetlands for aquatic turtles) occupied by a target species was used as a response variable. On a basin-wide scale, 47% of variation in proportional occupancy among species could be explained by taxon-specific variables; occupancy rates were related positively to niche breadth and negatively to the proximity of a geographical range boundary. After controlling for species effects, landscape-level occupancy rates varied significantly for 16 of 33 species, with variation partitioned among landscape variables alone (mean = 11% of variation), spatial trend variables alone (26%), and both variable sets jointly (8%). Among landscape variables, percentage forest cover positively affected occupancy rates of three bat species and a tree squirrel. Variation in occupancy rates among landscapes was consistent with large-scale spatial trends for 13 species. Our findings demonstrate the general importance of niche breadth as a predictor of species responses to habitat alteration and highlight the importance of viewing the effects of habitat loss and fragmentation at multiple spatial scales.

Keywords

Agricultural landscapes, aquatic turtles, bats, forest rodents, geographical range boundary, habitat loss and fragmentation, niche breadth, spatial location, vertebrates.

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INTRODUCTION

Differential responses of species to habitat loss and fragmentation generally are related to interspecific variation in ability to persist in local patches and to recolonize patches by moving across a landscape (Hanski, 1998; Etienne & Heesterbeek, 2001; Vos *et al.*, 2001; Goheen *et al.*, 2003a; Swihart & Verboom, 2004). Moreover, the abundance of a species tends to decline near the periphery of its geographical range boundary (Brown *et al.*,

1995), where abiotic conditions are less favourable and habitats suitable for the species niche requirements are less widespread (Enquist *et al.*, 1995; Pulliam, 2000). Using data collected on 32 vertebrate species in a single landscape, Swihart *et al.* (2003) showed that dietary and habitat components of niche breadth were correlated negatively with sensitivity to habitat alteration; i.e. patch occupancy for species with broad niches was less affected by habitat loss and fragmentation. Additionally, they found greater sensitivity to habitat alteration among species

occurring at the periphery of their geographical ranges, especially at northern or western margins where temperature and precipitation may impose physiological constraints.

The findings of Swihart *et al.* (2003) suggest that sensitivity to habitat alteration is influenced jointly by a species-specific attribute, phenotypic flexibility (plasticity) in resource use, and an historical attribute, proximity to range boundaries. Unfortunately, their study was unable to address the relative importance to patch occupancy of variation in landscape configuration or spatial juxtaposition, because it was conducted within a single landscape. Indeed, few studies have compared species responses to varying levels of alteration across multiple landscapes, although key biological processes undoubtedly are affected by variation in landscapes. For instance, a meta-analysis of 12 populations of white-tailed deer (*Odocoileus virginianus*) in North America by Long *et al.* (2005) revealed a strong negative effect of forested land cover on dispersal distances for juvenile males. Similarly, Radford and Bennett (2004) demonstrated a significant relationship between the patch occupancy of white-browed treecreepers (*Climacteris affinis*) and the proportion of woodland cover in 100-km² landscapes in Australia. Clearly, a thorough understanding of vertebrate responses to habitat alteration also must consider the role of variation in the extent of alteration among landscapes. Here, we extend the analysis of Swihart *et al.* (2003) by testing for effects on patch occupancy of niche breadth and range boundaries, landscape composition and configuration, and spatial location.

STUDY AREA

Occupancy data were collected within the Wabash River basin in north-central Indiana. The Wabash River drains > 20,000 km², representing > 20% of the state's land area (Swihart & Slade, 2004). Colonization by European settlers has transformed the landscape within the river basin. Currently, 88% of the basin is in cultivation, primarily corn and soybean, and only 8% is forested. Approximately 2.5% of the area was classified as wetland, representing 23.5% of the total wetland area in Indiana. Statewide, presettlement cover of forest and wetland was estimated at 87% and 24% (Smith *et al.*, 1994), but currently these levels are only 19% and 3.5%, respectively. The remaining forest cover, predominantly oak–hickory–maple, is highly fragmented and patchily distributed throughout the basin, whereas wetlands include lakes, impoundments, forested pools, and rivers. Despite the general predominance of agriculture in the study area, considerable spatial variation in land cover and land use exists. For instance, median forest cover within 800 23-km² cells that fall entirely within the basin was 7%, but forest cover ranged from 0.25% to 56% (Moore & Swihart, 2005).

MATERIALS AND METHODS

Field sampling

To capture the range of landscape variation when selecting our study areas, we characterized each grid cell according to several

Geographical Information System (GIS) layers, including a classified land-use layer for the percentages of forest, farmland, water, urban, and grassland cover. We selected for biological sampling 35 square cells (hereafter, landscapes), each 23 km², representing all eight major watersheds in the basin (Fig. 1). Nearly two-thirds of the landscapes were located in the two south-west-most watersheds (Fig. 1) to accommodate a concurrent tristate comparison; in addition to this constraint, the selection algorithm was based on assigning landscapes into multiple strata based on GIS classification and selecting landscapes to span the range of variation observed across the basin. Within each landscape, sample plots were randomly assigned in a stratified manner according to the relative proportion of each land-use type occurring in the landscape (Appendix).

We included species from four taxa in our analysis: aquatic turtles, amphibians, rodents, and bats. Individual species within these taxonomic groups were selected to represent a broad range of life-history traits and habitat types. Sampling was conducted from mid-May to early August in 2001–03. Occupancy rate was calculated for each species as the proportion of sites in which the focal species was detected during surveys in its primary habitat. Ideally, patch-specific demographic data would be used (e.g.; Pulliam, 2000). Unfortunately, these data seldom are feasible to collect when extensive sampling is conducted, nor are they meaningful for species that incorporate > 1 patch into individual home ranges. We assessed occurrence during and shortly after the breeding season to limit masking the effects of population growth and dispersal on local extinction events. Although it is possible that sink patches or the matrix could be used during this period, we are reasonably confident that occupancy was not an artefact of density-dependent habitat selection. Occupancy data should thus serve as a useful surrogate of a population's viability and tolerance to fragmentation (Hanski, 1994; Laurance, 1995; Vos *et al.*, 2001).

We sampled 228 sites at 159 wetlands for aquatic turtles using hoop nets and mark–recapture methods. Samples were collected over a 5-day interval, with sampling effort stratified by wetland size. Two hoop nets were placed in wetlands less than 0.08 ha. Wetlands between 0.08 and 0.28 ha had four nets, and at least eight nets were placed at wetlands greater than 0.28 ha. Hoop nets were baited with sardines and creamed corn.

Larval amphibians were sampled with funnel traps at 89 wetlands, each for 4 days. At least two traps were placed in each wetland. These larval captures were supplemented with dip netting on day 3 or 4 at each site. Dip-netting effort was proportional to the size and complexity of the wetland. Adult amphibians were sampled with visual encounter surveys on 700 transects (forest = 342, wetland = 159, grassland = 115, cropland = 75, and urban = 9) at 536 patches. Transects ranged from 75 m to 630 m (mean = 107 m), depending on patch shape and size, and each landscape had 2 to 52 transects (mean = 20). We used visual-encounter data from transects in all habitat types. All cover objects within 1 m of a transect were moved to search for amphibians. All animals detected beyond 1 m were recorded using perpendicular distance. We excluded from analysis species with early spring breeding periods not covered well by our sampling frame.

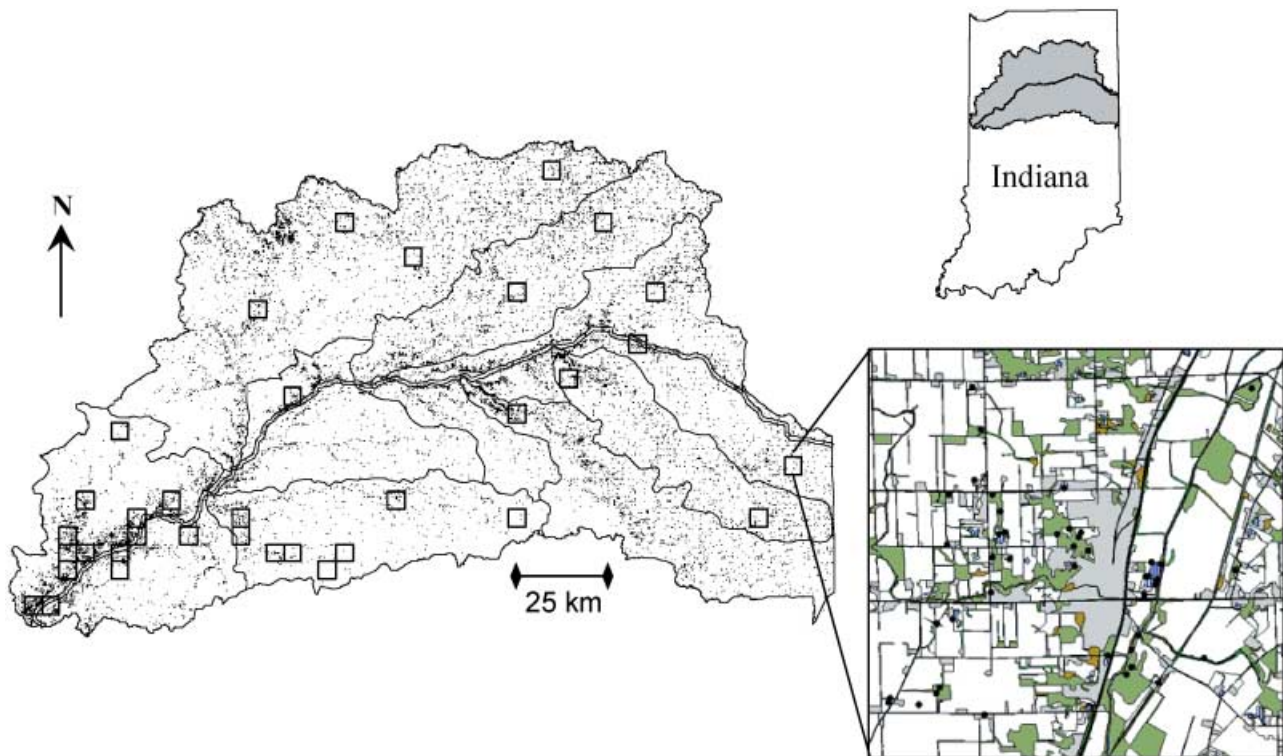


Figure 1 Map of upper Wabash River basin, Indiana, USA. Inset shows position of the basin in the state of Indiana. The left enlargement shows distribution of forest cover (dark shaded areas), Wabash River (double line), boundaries of the basin's 8 major watersheds, and locations of 35 23-km² study landscapes. The right enlargement illustrates an example of sample sites (dots) within one landscape, in which forest cover still represented by shaded areas.

Small rodents were sampled in 504 forest patches and 212 grassland patches. At each site, we placed a grid of soda-can Fitch live traps (2001), Sherman live traps (2003), or a mixture of the two (2002), with traps spaced at 15-m intervals. Tomahawk squirrel traps were placed with every other Sherman or Fitch trap (30-m spacing). We also placed larger Tomahawk traps at the corner of each grid to help reduce disturbance by opossums and raccoons. Following a 3-day prebaiting period, we trapped for five consecutive days with four morning and four afternoon checks.

Bats were sampled at 590 forest patches across 29 landscapes. Echolocation calls of bats were recorded using ANABAT II detectors and ZCAIMs (Tittle Electronics, NSW, Australia) recording to digital media. We placed two detectors at each survey site and set them to record for one night. Bat-call sequences were identified to species using a discriminant function model (Britzke *et al.*, 1999). Measured parameters from a known call library were used to construct quadratic discriminant functions using R (version 1.8, 2004). A call sequence was identified by taking the mode of the species assignments for calls within that sequence. Call sequences were deemed unidentified if the mode of identified calls either was < 4 or < 60% of all calls in the sequence.

Predictor variables

Predictor variables (Table 1) were grouped into one of three explanatory sets describing (1) characteristics of species or

populations, (2) the spatial arrangement of the survey sites, and (3) attributes of the landscapes in which survey sites were embedded. Species variables were obtained from published reports and described ecological context or taxonomic affiliation of each species. Based on prior work (Swihart *et al.*, 2003), we included taxon, niche breadth, and range-edge boundary. Taxon was coded using three indicator variables to represent the four taxonomic groups. We felt that it was important to include this variable as a means of accounting for variation in sampling methods and intensity among the various species groups. Niche breadth was a composite variable based on published information regarding food habits and habitat requirements; specific details on computation of the niche breadth components are provided in Swihart *et al.* (2003). The composite niche breadth variable was standardized to a *z* score within each taxon (Table 2). Range-edge boundary included information on the proximity of the species population to their range boundary and information on whether the range boundary was likely to be biologically (range edge at southern or eastern margins) or abiotically (northern and western margins) induced (Swihart *et al.*, 2003) (Table 2). A species was classified as near the edge of its range if the study area occurred in the outer 10% of the range as determined by visual inspection of range maps (Hall, 1981; Conant & Collins, 1998). The 10% cut-off was arbitrary and intended to identify populations for which stressors could influence occupancy. Range-edge boundary was represented in the models by

Table 1 Definitions of variables and variable sets used to model patch occupancy in the upper Wabash River basin in central Indiana, USA

Variable set	Variable	Definition
Species attributes	Taxon	Dummy-coded identifier for taxa included in model*
	Rodent	Coded 1 for rodents, else 0
	Bat	Coded 1 for bats, else 0
	Reptile	Coded 1 for reptiles, else 0
	Niche breadth	Composite of food habits and habitat requirements
	Range-edge boundary 1 and 2	Two indicator variables indicating: 00 = not in proximity to range edge, 01 = in proximity to a biotically induced edge, 10 = in proximity to an abiotically induced edge
Spatial	<i>x</i> UTM	Geographical (E–W) coordinate of site
	<i>y</i> UTM	Geographical (N–S) coordinate of site
Landscape	Shannon diversity	Measure of land cover diversity
	Clumpiness	Degree of clumping of the species primary habitat (%)
	Cover (%)	Percentage of cover of each habitat type

*Taxa included small rodents, bats, aquatic turtles, and amphibians. Amphibians were represented in the model with zeros for all taxa identifiers.

two indicator variables with three possible combinations: 00 indicates no proximity to a range edge, 01 indicates proximity to a biotically induced range edge, and 10 indicates proximity to an abiotically induced range edge.

We defined the spatial trend variables as the UTM coordinates of the centre of each landscape. The spatial trend variables (*x*, *y*, *xy*) were selected because of a general east–west gradient in precipitation and land use across the basin and because the Wabash river runs roughly from north-east to south-west in the upper basin (Fig. 1).

For each landscape and 1.6-km buffer, we digitized major (e.g. forest, grassland/pasture, water, urban, and agriculture) and secondary (e.g. roads, streams, corridor elements) land-cover types as vector data from USGS digital orthophotos with 1-m resolution. These vector data subsequently were converted into raster data with 3-m grid resolution and were transferred into FRAGSTATS 3.3 (McGarigal & Marks, 1995) to calculate landscape metrics. Based on our prior experience and other work on these or similar species (Walsh & Harris, 1996; Gehrt & Chelstvig, 2004; Moore & Swihart, 2005; C.E. Rizkalla, unpublished data), we selected as landscape predictors the Shannon diversity of cover types (landcover diversity), as well as the percentage cover and the degree of clumpiness (%) of each species' primary habitat type within the landscape. A species' primary habitat type was determined from the literature (references in Table 2).

We conducted the analysis in two phases to assess (1) the general importance of species attributes and (2) the contributions of attributes measured at the extent of our landscapes. In the first phase, we regressed basin-wide occupancy rates on species life-history characteristics using least-squares regression. Regressions were carried out in SYSTAT version 11 (SYSTAT Software, Inc., Point Richmond, CA, USA), and significance was determined using a permutation test with 9999 permutations (Legendre, 2002). Basin-wide occupancy rate for species X was calculated as the number of patches of primary habitat in which X was detected divided by the total number of patches of primary habitat that were sampled for X. The regression equation was

then used to estimate an expected occupancy rate for each species, which we used in the next phase of the analysis.

In phase two, we calculated a residual occupancy rate for each species by landscape combination. To do this, we subtracted the expected occupancy rate for each species, calculated from the phase-one regression, from the observed occupancy rate of each species in each of the landscapes in which it occurred. The results represented residual variation in occupancy rate after removing the effects of niche breadth, proximity to range boundary, and taxon for each species.

We used the residual occupancy rate as the response variable in a partial regression analysis to partition the variation between the spatial- and landscape-variable sets. Partial regression allows the estimation of how much of the variation in a response variable is attributable to one variable set while controlling for the effects of another variable set (Legendre & Legendre, 1998: 528). In this case, we were interested in the variation accounted for by the landscape variable set [a] after accounting for variation jointly with spatial trends [b] or solely by spatial trends [c].

We regressed residual occupancy rate against combined landscape and spatial trend variable sets to obtain the total proportion of variation ($a + b + c = R^2$) explained by the predictors. Next, we regressed residual occupancy rate against the landscape variable set alone, thereby obtaining the component of R^2 attributed to the pure and joint effects of these variables (i.e. $a + b$). Finally, we regressed residual occupancy rate against the spatial trend variable set to obtain their joint and pure effects (i.e. $b + c$). Partitioning of the individual components of variation was accomplished by subtraction. Note that with this procedure it is possible to obtain negative components of variation. Negative fractions indicate that the two variable sets explained more variation in residual occupancy rate together than the sum of their individual effects (Legendre & Legendre, 1998: 533). This could occur when one of the pair of variable sets has effects opposite in sign to the other variable set, resulting in lower total covariance of the variable sets with residual occupancy. Alternatively,

Table 2 Attributes of the 33 species in this analysis occurring in the upper Wabash River basin of Indiana, USA. Standardized niche breadth scores and proximity to range boundaries were computed based on published studies* and range maps. Means and standard errors for proportional occupancy of patches in landscapes also are provided. Definitions of variables are given in Table 1

Species	Taxa			z niche	Range edge boundary†	Mean occupancy‡	SE
	Rodent	Bat	Reptile				
<i>Glaucomys volans</i>	1	0	0	-1.36	00	0.011	0.005
<i>Sciurus niger</i>	1	0	0	0.20	00	0.035	0.038
<i>Sciurus carolinensis</i>	1	0	0	-0.81	00	0.172	0.041
<i>Spermophilus tridecemlineatus</i>	1	0	0	-0.54	01	0.109	0.040
<i>Tamias striatus</i>	1	0	0	0.26	00	0.763	0.035
<i>Tamiasciurus hudsonicus</i>	1	0	0	0.18	01	0.306	0.048
<i>Microtus ochrogaster</i>	1	0	0	-1.02	00	0.404	0.059
<i>Microtus pennsylvanicus</i>	1	0	0	-0.70	01	0.408	0.051
<i>Peromyscus leucopus</i>	1	0	0	1.53	00	0.844	0.028
<i>Peromyscus maniculatus</i>	1	0	0	1.72	00	0.172	0.032
<i>Reithrodontomys megalotis</i>	1	0	0	0.11	01	0.0001	0.000
<i>Zapus hudsonius</i>	1	0	0	0.43	00	0.144	0.022
<i>Eptesicus fuscus</i>	0	1	0	0.65	00	0.368	0.035
<i>Lasiurus borealis</i>	0	1	0	1.31	00	0.273	0.028
<i>Lasiurus cinereus</i>	0	1	0	-1.31	00	0.052	0.011
<i>Myotis lucifugus</i>	0	1	0	0.65	00	0.140	0.025
<i>Myotis septentrionalis</i>	0	1	0	0.00	00	0.188	0.031
<i>Myotis sodalis</i>	0	1	0	-1.311	00	0.192	0.028
<i>Pipistrellus subflavus</i>	0	1	0	0.00	10	0.084	0.017
<i>Chelydra serpentina</i>	0	0	1	1.98	00	0.482	0.082
<i>Sternotherus odoratus</i>	0	0	1	-0.70	10	0.008	0.008
<i>Graptemys geographica</i>	0	0	1	-1.29	10	0.078	0.043
<i>Graptemys pseudogeographica</i>	0	0	1	-0.79	10	0.026	0.019
<i>Trachemys scripta</i>	0	0	1	0.30	10	0.133	0.071
<i>Chrysemys picta</i>	0	0	1	0.30	00	0.278	0.046
<i>Emydoidea blandingii</i>	0	0	1	-0.11	01	0.023	0.013
<i>Apalone spinifera</i>	0	0	1	0.30	00	0.171	0.052
<i>Plethodon cinereus</i>	0	0	0	-1.28	10	0.019	0.006
<i>Eurycea cirrigera</i>	0	0	0	-0.38	10	0.016	0.009
<i>Rana catesbeiana</i>	0	0	0	-0.61	00	0.076	0.015
<i>Rana clamitans</i>	0	0	0	-0.09	00	0.114	0.014
<i>Rana sylvatica</i>	0	0	0	1.34	10	0.027	0.011
<i>Rana pipiens</i>	0	0	0	1.02	01	0.036	0.010

*Niche breadth and range-edge boundary information obtained from Anthony and Kunz (1977), Black (1972), Conant and Collins (1998), Hall (1981), Hickey *et al.* (1996), Mumford and Whitaker (1982), Reich (1981), Stalling (1990), Streubel and Fritzgerald (1978), Swihart *et al.* (2003), Webster and Jones (1982), Whitaker (1972a,b; 1995), Whitaker and Hamilton (1998), and Whitaker and Weeks (2001).

†Range-edge boundary consisted of two indicator variables that defined proximity to range edge and the type of range edge. Three codes were used: 00 = not near a range edge, 01 = near a biotically induced range edge, and 10 = near an abiotically induced range edge.

‡Mean occupancy calculated across landscapes.

negative proportions could result when there are strong direct effects of non-orthogonal variable sets. In our case, non-orthogonality could result from spatial gradients in landscape attributes. Regressions were performed using SYSTAT version 11.0, and statistical significance was determined using permutation tests (Legendre, 2002). We used separate regressions for each species, because species occurred in the same landscapes throughout the basin, and therefore each landscape variable and spatial coordinate would otherwise have been replicated in the analysis 33 times.

RESULTS

The regression model based on species characteristics accounted for 47% of the variation in basin-wide occupancy rates ($R^2 = 0.47$, $P = 0.006$; Table 3). As predicted, niche breadth was positively related to basin-wide occupancy rates. Also as predicted, proximity to a geographical range boundary had a negative effect, reducing occupancy rate 11–16% (Table 3, Fig. 2). Rodents exhibited 2.9 times greater occupancy rates, on average, than the other taxonomic groups (Table 3).

Table 3 Parameter estimates and *P*-values for the regression of species occupancy on species life history characteristics ($R^2 = 0.47$, $P = 0.0061$)

Variable	Parameter estimate	<i>P</i> (permutation)
Intercept	0.129	0.0688
Taxon*		
Rodent	0.239	0.0071
Bat	0.072	0.2448
Reptile	0.095	0.1490
Niche breadth	0.076	0.0150
Proximity to north-west range edge	-0.110	0.1036
Proximity to south-east range edge	-0.156	0.0323

*Taxa were dummy coded; amphibians were coded zero for each taxon variable.

The landscape regression models accounted for between 23% and 60% of the residual variation in occupancy rates for four bats, one aquatic turtle, and one rodent (Table 4). At a nominal type I error rate of 0.05, only one or two models on average should result in statistical significance due to chance. Percentage cover of the primary habitat in a landscape was positively related to residual occupancy rates (Table 4). Landscape diversity was positively related and land-cover clumpiness negatively related to residual occupancy rates for *Chelydra serpentina* (Table 4). The models suggested a negative effect of both variables on residual occupancy rates for the other species considered (Table 4).

The spatial trend-surface model accounted for between 23.7% and 80.7% of the residual variation in occupancy rates for 13 species including all taxonomic groups (Table 4), far in excess of the one or two predicted by chance alone ($\alpha = 0.05$). For the five species in which it was a significant predictor, the first UTM (*x*) coordinate was negatively related to residual occupancy rates, indicating an east to west gradient of increasing occupancy across the basin (Table 4). Likewise, the second UTM (*y*) coordinate was positively related to residual occupancy for four species, indicating south to north gradient of increasing occupancy across the basin (Table 4). Variation in residual occupancy was explained by the cross-product term (*xy*) for six species, but with no discernible pattern.

Variation partitioning was conducted for the 16 species with regressions involving either strong contributions from landscape variables or spatial trend variables. On average, spatial trend variables accounted for 26% of the variation in residual occupancy rates, landscape variables accounted for 10%, and the joint effects of the two variable sets accounted for 8% (Fig. 3). Spatial trends alone explained more variation in residual occupancy rates than landscape variables alone in 13 of 16 species. Only for *C. serpentina* and *Myotis septentrionalis* did the variation explained by landscape variables exceed levels explained by spatial trends.

DISCUSSION

Our results confirm the importance of niche breadth and geographical range boundary as determinants of occupancy rates

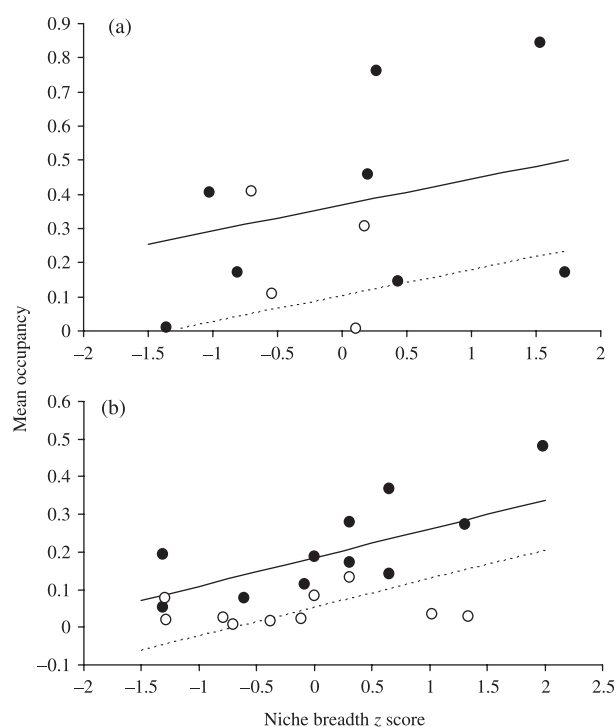
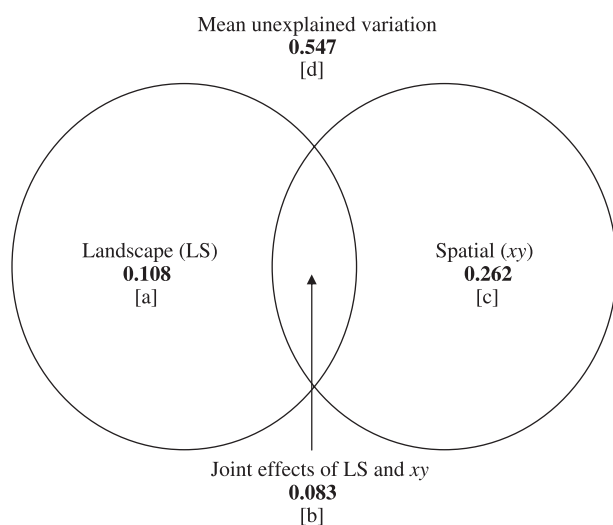


Figure 2 Plots of the regressions of mean occupancy rates against the *z* score of niche breadth for rodents (a) and other vertebrates (b). A dashed line represents the regression for species in proximity to their range boundary (hollow circles), and a solid line represents the regression for species not in proximity to their range boundary (solid circles).

first suggested by Swihart *et al.* (2003). Only 36% of the species of vertebrates that we studied also were used in the analysis by Swihart *et al.* (2003), and aquatic turtles and bats were entirely new taxa. The severe habitat loss and modification that have occurred over the past 150 years in the upper Wabash River basin undoubtedly have exerted a major influence on the current community composition. Our analysis indicates that extant species with an ability to rely on a broad array of food and habitat types across their geographical ranges are associated with tolerance to habitat alteration by humans at the population level, irrespective of taxonomic affiliation. For instance, white-footed mice (*Peromyscus leucopus*), red bats (*Lasiurus borealis*), and snapping turtles (*C. serpentina*) exhibited the greatest niche breadth in their respective taxa and either the highest or the second highest mean occupancy rates (Table 2). Conversely, species with low niche breadth (e.g. southern flying squirrel — *Glaucomys volans*, hoary bat — *Lasiurus cinereus*, and eastern red-backed salamander — *Plethodon cinereus*) were among the rarest species within their respective taxa (Table 2). The southern flying squirrel requires cavity trees and habitat suitable for gliding, and the minimum suitable area of a forest patch may be limited by thermoregulatory requirements associated with huddling (Stapp *et al.*, 1991; Nupp & Swihart, 2000). The hoary bat relies on forest areas for summer roost sites (Jung *et al.*, 1999) and primarily consumes large moths during foraging (Black, 1972; Hickey *et al.*, 1996).

Table 4 Parameter estimates for significant ($\alpha = 0.05$) regressions of residual species occupancy (i.e., after accounting for variation due to species attributes) on either landscape variables only or spatial trend variables only. Coefficients with an * were significant at $P = 0.05$

			Predictor variables		
	R ²	Intercept	1	2	3
Landscape regressions			SHDIV	PERCOV	CLUMPY
<i>Sciurus carolinensis</i>	0.231	5.01	−0.06	0.02*	−0.07
<i>Myotis septentrionalis</i>	0.293	0.73	−0.43	0.02*	−0.01
<i>Myotis sodalis</i>	0.281	−1.40	−0.38	0.02*	0.02
<i>Pipistrellus subflavus</i>	0.358	4.13	−0.160	0.01*	−0.05
<i>Eptesicus fuscus</i>	0.274	2.96	−0.50	0.00	−0.03
<i>Chelydra serpentina</i>	0.602	8.07	2.31*	0.07	−0.15*
Spatial trend regressions			<i>x</i>	<i>y</i>	<i>xy</i>
<i>Sciurus carolinensis</i>	0.345	−0.16	−0.10*	−0.06	0.04
<i>Tamiasciurus hudsonicus</i>	0.274	0.06	0.10	0.04	0.04
<i>Spermophilus tridecemlineatus</i>	0.251	−0.01	−0.10*	0.15*	−0.10
<i>Microtus ochrogaster</i>	0.332	0.35	−0.08	−0.11	−0.06
<i>Microtus pennsylvanicus</i>	0.237	0.16	0.11	−0.06	0.15*
<i>Peromyscus maniculatus</i>	0.302	−0.28	−0.06	0.13*	−0.08*
<i>Myotis sodalis</i>	0.320	0.04	−0.04	−0.03	0.09
<i>Pipistrellus subflavus</i>	0.368	−0.02	−0.05*	−0.00	0.03
<i>Emydoidea blandingii</i>	0.807	−0.08	−0.01	0.01	0.04*
<i>Trachemys scripta</i>	0.733	0.03	−0.16*	0.27*	−0.16*
<i>Rana clamitans</i>	0.309	−0.01	−0.05*	0.04*	0.00
<i>Rana pipiens</i>	0.383	−0.04	0.00	0.01	0.03*
<i>Rana sylvatica</i>	0.272	−0.12	−0.01	0.00	0.04*

**Figure 3** Venn diagram of mean proportion of variation accounted for by the pure effects of spatial (fraction [c]) and landscape (fraction [a]), and the joint effects of spatial and landscape variable sets for the 16 species in which at least one variation partitioning regression was significant.

Red-backed salamanders are lungless and prefer moist forest conditions containing fallen woody debris (Grover, 1998; Kolozsvary & Swihart, 1999). The importance of niche breadth also should extend to taxa other than vertebrates. For instance, Thuiller *et al.* (2005) predicted niche breadth to be an important

determinant of plant species sensitivity to environmental alteration created by climate change.

Proximity of a species to its geographical range boundary exerted a significant negative influence on patch occupancy rates (Fig. 2). This is seen most easily by examining occupancy rates for species whose niche scores were greater than the average for their taxonomic group. Considering only those species which also were proximal to a geographical range boundary yielded six species: *Tamiasciurus hudsonicus*, *Reithrodontomys megalotis*, *Pipistrellus subflavus*, *Trachemys scripta*, *Rana pipiens*, and *Rana sylvatica* (Table 2). None of the mean observed occupancy rates of these species were as great as predicted by niche breadth, nor did their mean occupancy rates exceed the mean occupancy rate for their respective taxa. Thus, proximity to a geographical range boundary appears capable of mitigating positive influences on occupancy associated with niche breadth. Our findings suggest that conservation strategies that ignore the effects of range boundaries on occupancy may expend limited financial resources inefficiently by concentrating efforts on populations responding principally to adaptive regimes operating at a geographical scale rather than to disturbance regimes imposed by humans. Specifically we agree with Gaston *et al.* (2001) that selection of a core reserve network based on minimum complementary sets of species will be inadequate if several species are represented in marginal or peripheral areas of their ranges.

Effects of range boundaries in Swihart *et al.* (2003) were dominated by amphibians, whereas the taxonomic distribution in the current study was more uniform. Moreover, the effect of

proximity to southern or eastern range boundaries was more pronounced in the current study (Table 3), suggesting that biotic factors may exert an influence on patterns of occupancy. Detailed studies of biotic effects are lacking for the species in our study occurring near their southern or eastern range boundaries, except for *T. hudsonicus*. In this tree squirrel with a predominantly boreal distribution, predation is greater in deciduous forest habitats (Goheen & Swihart, 2005), and evidence for a competitive disadvantage with grey squirrels (*Sciurus carolinensis*) also exists (Nupp & Swihart, 2001; Goheen *et al.*, 2003b; Moore & Swihart, 2005). Red squirrels likely persist in fragmented agricultural landscapes because of their ability to use suboptimal forest habitat (Bayne & Hobson, 1998; Moore & Swihart, 2005) and to move successfully through the agricultural matrix separating forest patches (Goheen *et al.*, 2003b).

How do factors other than taxonomic affiliation and autecology affect variation in occupancy rates across landscapes? Spatial context played a significant role for nearly half of the species in our study, explaining for these species an average of 45% of among-landscape variation in occupancy rates after removing effects due to species attributes (Fig. 3). Of this variation, spatial trends alone were 2.6 times more influential than landscape variables alone, suggesting that species are responding to broad-scale environmental gradients across the basin. Some of this variation appears related to range boundary phenomena occurring at a finer resolution than captured in the indicator variables for proximity to range edge. For instance, occupancy rates of red-eared sliders (*T. scripta*) increased in a south-westerly direction corresponding to the core of the species' range. Similarly, increased occupancy rates for landscapes located in the direction of the interior of geographical ranges were noted for *R. sylvatica*, *Microtus pennsylvanicus*, and *Emydoidea blandingii*. The upper Wabash River basin represents a confluence of ecoregions (Swihart & Slade, 2004), which also may contribute an historical component to the broad spatial trends. For instance, the northwestern portion of the basin resides in the Grand Prairie natural region (Homoya, 1997). Although the basin has been dominated by agriculture for over a century (Parker, 1997), occupancy rates of grassland specialists such as *Spermophilus tridecemlineatus* and *Peromyscus maniculatus* are greater in north-western landscapes (Table 4).

Among landscape variables, percentage cover was the most important variable accounting for variation in occupancy rates. This is not too surprising, as percentage cover provides a measure of a landscape's capacity (*sensu* Vos *et al.*, 2001) for supporting the species that rely on the cover type in question. Thus, greater values for percentage of a preferred cover type indicate that less of the habitat has been lost due to human modification of the landscape, resulting in a greater capacity. For instance, forests offer both roosting cover and a diverse array of insect prey for foraging bats (Pierson, 1998). Increased forest cover also is more likely to address the needs of more specialized species when compared to simpler urban and agricultural land covers. Prior work has documented the adverse effect of forest loss on

S. carolinensis, a species that moves poorly through farmland and is confined in the basin to landscapes containing a relatively high percentage of forest cover and large forest patches (Goheen *et al.*, 2003a; Moore & Swihart, 2005).

Occupancy rates also varied across vertebrate taxa, and even within taxonomic groups. In the upper Wabash River basin, species have experienced profound changes in landscapes over the past 150 years, and several extinctions have occurred. Nonetheless, the extant species that we studied were not uniformly resistant to habitat loss and fragmentation; on the contrary, they varied enormously in their patterns of occupancy. For a given landscape context, resistance was affiliated with species exhibiting broad niches and occurring in the core of their geographical range.

Regarding the variation that was unexplained in our analysis, stochastic effects on occupancy levels likely play a large role at the landscape scale. In addition, weak patch selection for the species we studied could have contributed to reduced explanatory power. Hepinstall *et al.* (2002) found that niche breadth was inversely related to predictive power of their occurrence models, and many of the species that we modelled may be considered generalists. Finally, non-detection error also may have reduced explanatory power of our models (MacKenzie, 2005) and contributed to variation in occupancy between species. We did not consider measures of local habitat or patch quality, although such variables in aggregate should be expected to influence a landscape's suitability to a species. Sorting out the role of stochastic events relative to deterministic factors in patterns of landscape occupancy will require improved specification of species-based models (MacKenzie *et al.*, 2003, 2006; Thogmartin *et al.*, 2004; Moore & Swihart, 2005).

Researchers too often base conclusions of studies at a landscape scale on patterns derived from a single landscape. As demonstrated here, occupancy patterns of many species vary according to the composition and configuration of land cover within landscapes. From a practical standpoint, this finding suggests that predicting species responses to landscape change at one site by extrapolating findings from another landscape may be difficult. Conceptually, the causes of variation in occupancy among landscapes could be due to at least two factors. Given the significant effect of spatial context on species prevalence, variable patterns of occupancy among landscapes could reflect either differing rates of relaxation to a common equilibrium state or divergent trajectories in terms of metapopulation viability. Although we cannot rule out the former explanation, we suspect that divergent metapopulation dynamics occur and are driven by differences in landscape capacity and connectivity (Vos *et al.*, 2001). Consistent with this notion, Radford and Bennett (2004) identified thresholds of woodland cover below which patches were not occupied by white-browed treecreepers. A similar threshold response in bird species richness was noted when multiple landscapes were examined (Radford *et al.*, 2005). Addressing the role of landscape capacity and connectivity in species conservation will require longitudinal data to be collected at replicate landscapes, rather than the snap-shot approach used in our study.

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Appendix Landscape indices and sampling effort for 35 landscapes occurring in the upper Wabash River basin of Indiana, USA.

Landscape	Shannon diversity	Forest (%)	Forest clumpiness	Wetland (%)	Wetland clumpiness	Grassland (%)	Grassland clumpiness	Sampling effort (# of Sites) ^a			
								Rodents ^b	Bats	Aquatic turtles	Amphibians
295	1.57	12.16	0.96	7.31	0.96	14.83	0.96	17/6	—	9	38
365	1.41	16.04	0.96	1.38	0.87	13.00	0.96	14/8	—	—	36
366	1.38	15.23	0.96	2.14	0.90	11.73	0.96	16/2	—	9	25
400	1.56	7.90	0.96	6.18	0.97	12.76	0.96	12/8	—	—	33
456	1.18	12.31	0.96	2.08	0.87	7.10	0.96	34/11	8	21	41
459	1.31	13.13	0.96	1.36	0.86	9.64	0.95	10/4	—	—	19
464	1.03	10.56	0.96	1.86	0.80	5.35	0.96	10/16	7	9	43
561	1.48	18.85	0.97	6.37	0.98	10.76	0.96	16/8	—	18	31
580	1.32	17.17	0.96	6.66	0.96	8.08	0.95	35/5	18	10	40
613	1.20	21.21	0.96	1.99	0.87	7.77	0.96	22/8	15	—	27
654	1.41	18.61	0.96	9.07	0.98	7.12	0.95	37/12	16	13	11
691	0.72	1.10	0.95	1.34	0.85	8.85	0.97	6/10	13	—	—
720	0.98	10.93	0.97	0.70	0.73	4.65	0.96	16/3	15	—	32
763	1.46	19.53	0.96	0.92	0.82	8.10	0.94	10/6	32	—	17
790	1.38	16.39	0.95	1.67	0.86	8.31	0.94	—	31	—	31
793	1.15	12.37	0.97	0.64	0.82	10.85	0.96	12/6	22	—	19
803	1.16	11.36	0.97	0.70	0.80	7.52	0.97	19/4	21	—	42
821	1.38	22.15	0.95	2.30	0.88	6.83	0.93	11/6	39	—	11
826	0.57	2.62	0.96	0.51	0.63	2.64	0.96	—	25	—	31
831	1.20	18.71	0.96	1.66	0.89	11.00	0.96	16/2	23	—	19
833	1.31	13.43	0.95	1.86	0.89	6.35	0.94	14/6	37	8	19
836	1.44	31.42	0.96	2.80	0.93	15.63	0.96	13/6	18	—	17
844	1.41	24.11	0.96	1.40	0.80	12.70	0.96	11/5	20	10	22
845	1.59	14.59	0.95	2.44	0.90	10.90	0.95	14/8	24	—	13
854	1.44	21.71	0.96	2.43	0.94	15.90	0.96	13/5	17	—	28
856	1.20	15.46	0.96	1.06	0.80	8.15	0.95	20/6	22	—	22
865	1.54	29.29	0.96	2.59	0.90	11.82	0.96	12/5	21	—	20
869	1.33	25.97	0.96	1.14	0.79	8.46	0.95	13/7	28	—	37
870	1.13	14.49	0.96	0.93	0.79	5.38	0.95	11/6	31	—	25
875	0.79	6.15	0.95	0.57	0.65	3.65	0.94	17/2	24	—	22
896	1.49	24.26	0.96	2.10	0.91	13.17	0.96	16/8	25	—	38
898	0.98	2.90	0.95	0.62	0.73	3.57	0.96	9/—	11	—	15
905	0.85	5.54	0.96	0.43	0.66	7.72	0.96	6/10	7	—	—
920	1.38	38.26	0.96	2.26	0.89	7.76	0.95	12/4	11	—	13
960	1.33	24.00	0.96	3.21	0.93	8.26	0.95	10/9	10	—	—

^aLandscapes designated by a “—” fell below thresholds of sampling effort established for inclusion in analysis.^bValues represent forest and grassland sites sampled for rodents, respectively.