Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland

Mary B. Kolozsvary and Robert K. Swihart

Abstract: We studied the effects of agriculturally induced fragmentation of forests and wetlands on amphibian assemblages and their distribution in a landscape of the midwestern United States. Potential breeding pools and upland areas in 30 forest patches of various sizes and degrees of isolation were intensively sampled for amphibians during April through August 1996 and March through August 1997 in Indiana. Species presence was documented using pitfall traps, anuran vocalization surveys, and cover-board sampling for adults and minnow traps and dip nets for larvae. Amphibians, anurans, and salamander assemblages were nonrandomly distributed across the landscape. American toads (Bufo americanus) and gray treefrogs (Hyla versicolor) were ubiquitous, whereas the distributions of several other species were ordered in a predictable manner. Logistic regression was used to develop predictive models of probabilities of occurrence for species in response to forest and wetland patch and landscape variables. Occurrence of redback salamanders (Plethodon cinereus) was positively associated with the area of a forest patch. Occurrence of rana frogs was positively associated with proximity of wetlands for three of four species, and occurrences of smallmouth salamanders (Ambystoma texanum), spring peepers (Pseudacris crucifer), and western chorus frogs (Pseudacris triseriata) were related to the degree of wetland permanency. Multiple linear regression revealed that species richness was greatest for wetlands with intermediate degrees of permanency. The observed nonrandom distribution exhibited by several amphibians suggests that they respond to landscape-level attributes. Moreover, species differed substantially in the nature of their responses to fragmentation, consistent with differences in their life history and ecology.

Résumé : Nous avons étudié les effets de la fragmentation des forêts et des terres humides due aux opérations agricoles sur les associations d’amphibiens et leur répartition dans un paysage du Midwest américain. Nous avons échantillonné les amphibiens dans les cuvettes présumées de reproduction et dans les terres hautes dans 30 boisés de dimensions et de degrés d’isolement variés, d’avril à août 1996 et de mars à août 1997 en Indiana. La présence des adultes a été détectée par utilisation de pièges à fosses, par audition des cris des anoures et par échantillonnage sous des planches de bois, et celle des larves, par utilisation de nasses à mânes et de prises. Les associations d’amphibiens, anour és et salamandres, n’étaient pas réparties au hasard à l’échelle du paysage. Les Crapauds d’Amérique (Bufo americanus) et les Rainettes versicolores (Hyla versicolor) ont été trouvés partout, alors que plusieurs autres espèces étaient réparties selon un ordre prévisible. Une régression logistique a été utilisée pour élaborer des modèles prédictifs de probabilité de la présence des espèces en fonction des variables reliées à des parcelles de forêt ou de terres humides, ou au paysage. La présence des Salamandres rayées (Plethodon cinereus) était associée à la surface d’une parcelle de forêt. Les Ranidés étaient associées à la proximité des terres humides chez trois des quatre espèces et la présence des Salamandres à nez court (Ambystoma texanum), des Rainettes cruciferes (Pseudacris crucifer) et des Rainettes faux-grillons (Pseudacris triseriata) était reliée au degré de permanence des terres humides. Une régression linéaire a révélé que la richesse en espèces était plus élevée dans les terres humides de permanence intermédiaire. La répartition non aléatoire observée chez plusieurs amphibiens indique que les animaux choisissent leur domaine en fonction d’attributs à l’échelle du paysage. En outre, les espèces diffèrent considérablement par la nature de leurs réactions à la fragmentation, à cause de différences dans leur cycle biologique et leur écologie.

Introduction

During recent years, much attention has focused on apparent declines of amphibian populations worldwide (Stebbins and Cohen 1995). The intensity of these declines varies regionally, and suggested causes differ (e.g., ultraviolet radiation, habitat loss, parasites, introduction of predaceous fish). Two species in particular, which occur in the midwestern United States, are declining in parts of their range: the northern leopard frog (Rana pipiens) and cricket frog (Acris crepi-
Table 1. Hypothesized importance of forest and wetland patch and landscape attributes as predictors of amphibian species presence and relative abundance, based on the species’ general life history.

<table>
<thead>
<tr>
<th>Species</th>
<th>Degree of sensitivity to:</th>
<th>forest area and (or) proximity</th>
<th>wetland area and (or) proximity</th>
</tr>
</thead>
<tbody>
<tr>
<td>American toad</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Fowler’s toad</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Western chorus frog</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Smallmouth salamander</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Eastern tiger salamander</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Northern leopard frog</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Pickerel frog</td>
<td>Low</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Gray treefrog</td>
<td>Moderate</td>
<td>Low–moderate</td>
<td></td>
</tr>
<tr>
<td>Redback salamander</td>
<td>High</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Bullfrog</td>
<td>Low</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Southern two-lined salamander</td>
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<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>Green frog</td>
<td>Moderate</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Northern spring peeper</td>
<td>Low</td>
<td>High</td>
<td></td>
</tr>
</tbody>
</table>


The exact causes of their decline are unknown, but anthropogenic disturbances that have resulted in a loss or diminished quality of habitat are thought to be major factors (Stebbins and Cohen 1995; Lannoo 1998).

The most important direct negative effects of humans on amphibian populations are habitat modification and destruction (Pough et al. 1998). In the midwestern United States, much of the historic habitat modification has resulted from massive land-clearing and draining of wetlands for cultivation during the mid-1800s. For example, Indiana in the early 1800s consisted of >85% forest, with smaller amounts of wetlands and prairie (Petty and Jackson 1966). As a result of agricultural practices and an increasing trend towards urbanization, Indiana’s forests and wetlands have been reduced by approximately 78 and 86%, respectively (Miller 1993; Harmon 1994). In northwestern Indiana, Brodbands and Kilmurry (1998) found species richness and abundance of amphibians to be positively associated with adjacent woodlands (>1 ha) and permanent ponds and wetlands and negatively associated with adjacent agricultural areas. They suggested that the loss of breeding habitat for amphibians since agricultural use was introduced into this area has been about 94–97%, and should have resulted in a range reduction in at least 3–5 species.

In west-central Indiana, native habitats occur as fragmented patches of various sizes and degrees of isolation surrounded by farmland. Amphibians, many species of which require aquatic sites for breeding and moist upland habitats for foraging or hibernation, might be especially susceptible to such agricultural fragmentation. Because life-history attributes vary greatly among species, they should be differentially affected by fragmentation. Species with high vagility, broad environmental tolerances, desiccation resistance, or general seasonal requirements for breeding (i.e., they breed in a wide variety of wetland types) should be less severely affected or may actually benefit (Noss and Csuti 1994). In contrast, species that have limited mobility, require large forest tracts, or have specific seasonal requirements for breeding (e.g., they breed only in ephemeral wetlands) are likely to be much more severely affected.

Our goal was to determine the extent to which local amphibian assemblages vary within an agricultural landscape of the midwestern United States, and to test whether this variation can be attributed to forest or wetland features. We compared amphibian assemblages sampled from localities that differed considerably with respect to the characteristics of the patch and of the surrounding landscape. We hypothesized that species composition at the local level would be influenced by fragmentation in a systematic manner. A review of life-history information for each species permitted us to develop general predictions concerning how their distributions might be affected in an agriculturally fragmented landscape (Kolozsvari 1998) (Table 1). We hypothesized that species which are specifically associated with forest, at least for a portion of their life cycle, should be more sensitive to the area and proximity of forest patches than those that can exploit several types of terrestrial habitat. It was suspected that vagile species potentially capable of exploiting forest patches isolated by farmland would be somewhat less susceptible to forest fragmentation. Aquatic breeders that can exploit a variety of wetland water regimes were considered less likely to be sensitive to wetland area and proximity than those species with specific wetland associations. It was also hypothesized that species which have rapidly developing larvae or use temporary wetlands for breeding are less affected than species that require semipermanent or permanent wetlands for breeding. because the latter regimes have a more restricted distribution across our landscape. Terrestrial breeders were not expected to be affected by wetland variables.

Materials and methods

Study area

Our study area is part of the Indiana Pine Natural Resources Area in west-central Indiana, in western Tippecanoe and eastern Warren counties. This region encompasses 259 km² and historically was dominated by forests, wetlands, and tall-grass prairie (Petty and Jackson 1966). Because intensive agriculture was introduced to the area of the midwestern United States in the mid-1800s, when clearing of land and draining of wetlands were widespread, remaining forest within Indiana Pine is restricted primarily to riparian areas or small woodlot fragments surrounded by farmland. Only 16% of the area remains forested (Shepherd and Swihart 1995). The primary agricultural crops in this region are corn and soybeans.

We sampled amphibian populations in 30 forest patches, 12 during April through August 1996 and 18 during March through August 1997. Forested study sites were selected according to three criteria: (1) the size of the patch, (2) the relative degree of isolation from other forest patches, and (3) the degree of permanency of potential breeding pools associated with the forest patch, if any. Woodlots were 0.6–143.5 ha in area and the distance to the nearest woodlot was 10–710 m. Four of the 30 study sites were representative of extensive wooded areas (>1400 ha). Potential breeding
areas were considered to be associated with a forest patch if they occurred on or within 30 m of the patch. Semlitsch (1998) concluded that 95% of the population of most pond-breeding anurans at study sites use terrestrial habitat <165 m from a breeding pond. To restrict our sampling to potential breeding pools within 30 m of a forest patch because of time limitations and in order to more confidently determine actual use of the forest patch. Forest patches that we selected contained wetlands with water regimes ranging from temporary to permanent. Nine study sites lacked wetlands entirely. We used the U.S. Fish and Wildlife Service classification system for examining specific wetland water regimes, with slight modification (Cowardin et al. 1979; Mitsch and Gosselink 1993). In particular, in temporary wetlands, surface water is present for brief periods during the growing season, but the water table is otherwise well below the soil surface. In seasonal wetlands, surface water is present for extended periods, especially during the early growing season, but is absent by the end of the season. In semipermanent wetlands, surface water persists throughout the growing season in most years. When surface water is absent, the water table is at or near the surface. Lastly, in permanent wetlands, as we defined them, water covers the land surface throughout the year in most, if not all, years.

To most accurately determine which species of amphibians were present in the study sites, we sampled by means of multiple methods. We installed drift fences leading to pitfall traps around breeding areas and in forested uplands. In addition, we surveyed for calling anurans, sampled amphibian larvae, and placed boards on the ground under which amphibians could seek refuge throughout the upland area of the woodlots.

Pitfall traps

Pitfall traps were operated for 15-day sessions each month during April through June 1996 and March through June 1997. We recorded length (total length for anurans and both total length and snout-vent length for salamanders) and body mass of all amphibians captured. All salamanders and most anurans were marked using unique toe clips. Pitfall traps were standard 18.9 L capacity plastic buckets connected by a 7.6-m plastic drift fence anchored approximately 15 cm below ground level and extending approximately 30 cm above the ground.

Potential breeding pools were sampled with two-bucket arrays (Heyer et al. 1994); the number of arrays installed was approximately proportional to the rank of the wetland perimeter. When multiple arrays (range 2–5) were installed at the pools, they were placed equidistant from each other when possible. Also, for breeding pools located ≤30 m outside the woodland, only the wetland perimeter that faced the woodlot was considered when the arrays were established. We set up four-bucket arrays connected by three drift fences to sample the upland areas of the study sites (Jones 1981). The number of arrays (range 0–4) installed was approximately proportional to the rank of the logarithmic upland area associated with each study site. We initially attempted to locate the upland arrays in completely random locations within each forest patch, provided that they were at least 15 m from potential breeding areas, forest edge, or other arrays. Because many of the woodlots had poorly drained soils, for most sites we had to limit potential locations to the driest areas. This was necessary to ensure adequate numbers of functional pitfall trap night (i.e., to minimize the number of floating buckets during wet conditions). Some forest sites lacked pools, therefore only four-bucket upland arrays were used; other sites contained wooded pools with limited upland area, in which case only two-bucket arrays were used.

Call surveys

Anuran call surveys were conducted monthly, after sunset and before midnight, during April through July of 1996 and 1997. We listened for 10 min at each study site, recording any calling anurans on site, either at the breeding pools or in the upland areas.

Sampling of larvae

Larvae were sampled at potential breeding areas at all of the study sites in May and June 1997. Pools were actively searched and dip-netted for a period of time that was roughly proportional to the area and complexity of the pool (range 20–80 min per site). Standard plastic minnow traps were also operated and checked daily for 5 days. The number of these traps was approximately proportional to the area of the pool and individual traps were placed in the various habitat types in each pool. For example, if a pool contained approximately 25% deep-water and 75% shallow-water habitat, we placed traps in the deep area and shallow portions of the pool in a 1:3 ratio. Amphibian larvae were collected and preserved. The following keys for amphibian larvae and general guides were used to aid in identification: Dickerson (1969), Pfenning and Downs (1989), Conant and Collins (1991), and Wright and Wright (1995).

Cover boards

A grid of cover-board objects was placed at 30-m spacing within the upland areas of the forest patches. Each station consisted of four pine boards (each approximately 15 × 30 × 1.25 cm), with 5-cm spacing between boards. The intensity of the sampling corresponded to the ordered rank of the patch size, with more cover-board stations in larger patches (range 4–50). Cover boards were checked weekly for 9 weeks during June through August in 1996 and 1997. Cover boards were checked by turning them over to see if any amphibians had taken refuge under them. All salamanders captured were measured, uniquely marked, and then released.

Data analysis

To examine whether species richness varied predictably in the landscape, we measured the degree to which species were distributed in a nested pattern. Nestedness refers to nonrandom distributions of species among habitat sites. The initial development of the concept of nestedness dealt with isolates, although the concept is applicable to terrestrial fragments of habitat that may vary in their degree of isolation (Wright et al. 1998). For illustrative purposes, consider an array of isolated fragments that, before fragmentation, had been occupied by a common assemblage of species. If extinctions of species occurred in an identical, entirely predictable fashion on each isolate, then each smaller isolate would eventually contain only a proper (i.e., nested) subset of the species found on larger isolates. The nestedness could be depicted by a matrix in which rows (isolates) and columns (species) were arranged in descending order of richness and prevalence, respectively, resulting in a matrix that documented a species’ presence on isolates in the upper left portion and its absence in the lower right portion (Atmar and Patterson 1993). By contrast, if extinctions were entirely stochastic and independent of either isolate or species identity, a nested pattern of species distributions would not arise, and the resulting matrix of presence and absence would resemble a checkerboard (Patterson and Atmar 1986).

Numerous measures of nestedness have been developed (reviewed by Wright et al. 1998). We used the metric T, which measures deviations from perfect nestedness in the form of unexpected absences or presences of species in the isolate–species matrix described above (Atmar and Patterson 1993). An increasing value of T is analogous to an increase in entropy of the system, i.e., the percentage of the system’s energy that is lost as unrecycled heat (Patterson and Atmar 1993). T ranges from 0° for assemblages that are perfectly nested (no disorder) to 100° for assemblages that are randomly ordered. We used the nestedness temperature calculator (Atmar and Patterson 1993) to calculate T among the study sites for all amphibian species, as well as separately for anurans and salamanders.
amanders. We also used the program to calculate the probability of randomly generating the observed species distribution among study sites. Monte Carlo trials (n = 500) were used to generate the null distribution from which the probability was computed.

We digitized forest patches within the Indian Pine watershed from 1992 colored aerial photographs (1:30,000) and then transformed the data into an ARC/INFO forest coverage. The computer program FRAGSTATS (McGarigal and Marks 1995) was then used to calculate a variety of landscape metrics describing patch attributes and spatial structure of patches. We chose to include two forest metrics in our analysis: area (AREA) and proximity (PROX). PROX is inversely related to the isolation of a forest patch and is the sum of patch area (m²) divided by the nearest squared edge-to-edge distance (m²) between a neighboring patch and the focal patch for all neighboring patches whose edges are within a specified radius from the focal patch, i.e., PROX = (∑Aᵢ/j²), where a is the neighboring forest patch area and j is the nearest squared edge-to-edge distance between a neighboring forest patch and the focal forest patch, summed over all patches within a specified radius (j = 1, ..., n). We chose 1 km as the radius for our analysis. We calculated PROX in a slightly different manner for the four study sites that represented extensive wooded areas. Because the area of such an extensive forest tract was large (approximately 1480 ha), PROX revealed little about proximity to other forest sites. Thus, we calculated PROX using a 1-km radius around the actual sampling site.

We used digitized National Wetlands Inventory (NWI) maps to obtain comparable metrics for wetlands. Because some of our forested study sites contained wetlands that did not appear on the NWI maps, we digitized several additional wetlands for inclusion in the final wetlands coverage. We calculated two wetland metrics for each of our study sites: wetland area (WET) and wetland proximity (WETPR). Wet is the sum of total wetland area (ha) that is either on or within 30 m of each forest patch. WETPR is inversely related to the isolation of a forest patch from wetlands and is the sum of wetland area (m²) divided by the nearest squared edge-to-edge distance (m²) between a neighboring wetland and the focal forest patch for all wetlands whose edges are within a 1-km radius of the focal forest patch, i.e., WETPR = (∑Aᵢ/j²), where a is the neighboring wetland area and j is the nearest squared edge-to-edge distance from the neighboring wetland and the focal forest patch, summed from a = 1 to n. FRAGSTATS was not able to calculate WETPR and WETPR, so we calculated these measures by hand. An additional variable, WETWGT, was calculated and represents a weighted degree of wetland permanency associated with each forest patch. The degree of permanency for a particular wetland was categorized in rank order: temporary (1), seasonal (2), semipermanent (3), and permanent (4). WETWGT for each forest patch is the sum of the wetland regime rank multiplied by the proportion of the total wetland area associated with that patch which was composed by that rank, for all wetland ranks. For example, if a forest patch had 50% temporary wetlands and 50% semipermanent wetlands, WETWGT would be (1 x 0.5) + (3 x 0.5) = 2. A forest patch lacking wetlands was assigned a WETWGT value of 0. In addition, fish presence (FISH) was documented during larval sampling with minnow traps. A value of 1 was assigned to sites where fish were present and 0 to sites that lacked fish. The presence of a stream associated with the forest patches was also tallied (STREAM). A STREAM value of 1 was assigned to forest patches that had streams on or within 30 m of a forest patch and 0 if no streams were present.

AREA, PROX, WET, and WETPR ranged over several orders of magnitude. Accordingly, we transformed them logarithmically (base 10) (Table 2). We squared the transformed patch and landscape variables centered on mean values to reduce collinearity between the first-order and second-order terms (Neter et al. 1990). Although this substantially reduced the correlations between these terms, correlations remained significant for three of the five pairs. The transformed patch and landscape variables and their squared terms centered on mean values, as well as the variable STREAM, were used in best possible subsets multiple regression models to predict amphibian, anuran, and ranid species richness (Table 2; Neter et al. 1990). We used both R² and adjusted R² criteria to select several potential models. These models were fitted and final regression models selected on the basis of the overall adjusted R² value combined with the levels of significance of the independent variables. Predictive models were developed for species richness of amphibians, anurans, and ranids (i.e., bullfrog, Rana catesbeiana; green frog, Rana clamitans; pickerel frog, Rana palustris; and northern leopard frog, Rana pipiens). Because fish was significantly correlated with WETWGT (r = 0.378, p < 0.05), we initially used only WETWGT in this analysis. Including fish as an independent variable did not affect the outcome of our model selection. We also used these patch and landscape metrics to predict the presence or absence of selected amphibians, using logistic regression and a stepwise model selection algorithm with a 0.05 values of 0.3 to enter the model and 0.1 to stay in the model (SAS Institute Inc. 1994). After a logistic model was fitted, we calculated predicted probabilities of occurrence for all possible, pairs of occupied and unoccupied sites. If the predicted probability was greater for the occupied site, the pair was considered concordant. The predictive ability of the logistic model was then estimated using Somers’ D (SAS Institute Inc. 1994): D = (number of concordant pairs – number of discordant pairs) / total number of pairs.

Results
We captured a total of 1804 amphibians (284 salamanders and 1520 anurans) in 13031 effective pitfall-trap-nights. Cover boards yielded an additional 42 salamanders. The remaining contribution to the species richness estimates for the sites was obtained using the other sampling methods, or occasionally from opportunistic hand capture or calling anurans heard while we were on the study site. We documented the presence of 14 amphibian species across the 30 forested study sites, represented by 5 salamanders and 9 anurans, using all sampling techniques (Table 3). Species richness on the sites was 6.3 ± 1.2 (mean ± SE), ranging from 3 to 11, for amphibians; 4.8 ± 0.9, ranging from 3 to 8, for anurans; and 1.5 ± 0.3, ranging from 0 to 4, for ranids. All sites contained anurans, but salamanders were absent from 6 of the 30 sites.

Nestedness
Amphibian, anuran, and salamander assemblages all exhibited a highly ordered and nested distribution among the study sites (Table 3). The nested temperature calculator calculated temperatures of 16.45°C (P < 0.0001), 7.29°C (P < 0.0001), and 21.53°C (P = 0.01) for amphibians, anurans, and salamanders, respectively.

Species-richness regressions
Species richness of amphibians had a curvilinear relationship to WETWGT (F₁,₂₇ = 18.68, P = 0.0001) (Table 4). Anuran species richness was related to WETWGT in a similar fashion (F₁,₂₇ = 12.51, P = 0.0001) (Table 4). In both instances, species richness tended to be highest at sites with intermediate values of weighted wetland permanency (Fig. 1). In contrast, ranid species richness was positively related to LOGPRWE and WETWGT (F₁,₂₇ = 9.18, P = 0.0009) (Table 4).
Table 2. Abbreviations of dependent and independent variables for the linear regression and logistic regression analyses.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>RICH</td>
<td>LOGAR</td>
</tr>
<tr>
<td>RICHANUR</td>
<td>LOGAR2</td>
</tr>
<tr>
<td>RICHAN</td>
<td>LOGPR</td>
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</tr>
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<td></td>
<td>WETWGETC2</td>
</tr>
<tr>
<td></td>
<td>FISH</td>
</tr>
<tr>
<td>Amphibian species richness</td>
<td>Log_{10} of forest patch area</td>
</tr>
<tr>
<td>Anuran species richness</td>
<td>Squared term for LOGAR after centering around the mean</td>
</tr>
<tr>
<td>Ranid species richness (bullfrog, green frog, pickerel frog, northern leopard frog)</td>
<td>Log_{10} of forest proximity index</td>
</tr>
<tr>
<td>Presence/absence of a stream on or within 30 m of a forest patch</td>
<td>Squared term for LOGPR after centering around the mean</td>
</tr>
<tr>
<td>Presence/absence of wetland area on or within 30 m of a forest patch</td>
<td>Log_{10} of wetland area on or within 30 m of a forest patch</td>
</tr>
<tr>
<td>Presence/absence of wetland permanency</td>
<td>Squared term for LOGWET after centering around the mean</td>
</tr>
<tr>
<td>Weighted degree of wetland permanency</td>
<td>Log_{10} of wetland proximity index</td>
</tr>
<tr>
<td>Presence/absence of fish</td>
<td>Squared term for LOGPRWE after centering around the mean</td>
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Table 3. Matrix representing presence (+) or absence (blank) of amphibian species documented across 30 forest patches in west-central Indiana.

<table>
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<tr>
<th>Site</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
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Note: Species are denoted as follows: A. American toad; B. gray treefrog; C. western chorus frog; D. green frog; E. northern spring peeper; F. eastern tiger salamander; G. smallmouth salamander; H. redback salamander; I. pickerel frog; J. northern leopard frog; K. bullfrog; L. southern two-lined salamander; M. Fowler's toad; N. Jefferson hybrid salamander.
Table 4. Multiple regression models of species richness of amphibians, anurans, and ranids based on patch and landscape variables in an agricultural landscape in west-central Indiana.

<table>
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<tr>
<th>Explanatory variable</th>
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Note: $B$ is the regression coefficient for an explanatory variable; $P$ is the level of significance. For an explanation of abbreviations see Table 2.

Fig. 1. Relationship between species richness of amphibians (A) and anurans (B) and the weighted degree of wetland permanency (wetwgt, wetwgtC2) for 30 forest patches studied in 1996 and 1997 in west-central Indiana.

Logistic models of presence/absence

Logistic regression models were developed for smallmouth salamanders (Ambystoma texanum), eastern tiger salamanders (Ambystoma tigrinum tigrinum), redback salamanders (Plethodon cinereus), northern spring peepers (Pseudacris crucifer crucifer), western chorus frogs (Pseudacris triseriata), bullfrogs, green frogs, northern leopard frogs, and pickerel frogs (Table 5). American toads (Bufo americanus) and gray treefrogs (Hyla versicolor) were documented at all sites and therefore no predictive models could be constructed. Southern two-lined salamanders (Eurycea cirrigera), Jefferson hybrid salamanders (Ambystoma laterale-jeffersonianum), and Fowler’s toads (Bufo woodhousii fowleri) occurred at too few sites for significant predictive models to be constructed.

The probability of occurrence of redback salamanders increased with forest patch area (Fig. 2). The probability of occurrence of tiger salamanders was negatively associated with forest proximity and positively associated with wetwgt. Tiger salamanders were more likely to occur at more isolated forest patches or sites containing wetlands of a greater degree of permanency (Fig. 3). Presence of leopard frogs was positively associated with logprwe and negatively associated with logpr. They were more likely to occur at more isolated forest patches that were in close proximity to wetlands (Fig. 4). Presence of smallmouth salamanders, chorus frogs, and spring peepers had a curvilinear relationship with wetwgt; in addition, presence of spring peepers was associated with stream. In general, this illustrates a curvilinear relationship between wetwgt and the probability of occurrence of these species (Fig. 5). The probability of occurrence of bullfrogs and green frogs increased with both wetwgt and logprwe. As proximity to wetlands increased and the wetlands on-site became dominated by more permanent water regimes, the probability of occurrence of bullfrogs and green frogs increased (Fig. 6). Lastly, the probability of occurrence of pickerel frogs was positively associated only with wetwgt (Table 5).

Discussion

Nestedness and species richness of amphibians

Our results indicate that amphibians exhibit a high degree of nestedness in the agricultural landscape of west-central Indiana. Such an ordered pattern likely has formed since massive land-clearing and alteration of wetlands were initiated in the mid-1800s. Species-specific life histories and habitat preferences may have contributed to differential extinction or recolonization rates of species in response to the severe alteration and fragmentation of the landscape. Lower matrix temperatures may reflect greater predictability in the...
Table 5. Logistic regression models of amphibian presence based on patch and landscape variables in an agricultural landscape in west-central Indiana.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Northern leopard frog</th>
<th>Redback salamander</th>
<th>Western chorus frog</th>
<th>Bullfrog</th>
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Note: B is the regression coefficient for an explanatory variable; P is the level of significance. For an explanation of abbreviations see Table 2.

Fig. 2. Logistic model for probability of occurrence of redback salamanders in relation to forest patch area determined from 30 forest patches studied in 1996 and 1997 in west-central Indiana.

Fig. 3. Logistic model for probability of occurrence of eastern tiger salamanders in relation to forest proximity for various WETWGT values determined from 30 forest patches studied in 1996 and 1997 in west-central Indiana.

Fig. 4. Logistic model for probability of occurrence of northern leopard frogs in relation to wetland proximity for a variety of forest proximity values determined from 30 forest patches studied in 1996 and 1997 in west-central Indiana.
strong sensitivity to forest patch area, which suggests that extinction events could limit their occurrence in small patches (Fig. 2). In contrast, three species of *Rana* exhibited sensitivity to isolation from wetlands, which suggests an important role of recolonization ability in determining their distribution in the landscape (Figs. 4 and 6).

Wright et al. (1998) examined 279 matrices of species presence/absence for a broad range of taxa and geographic regions. They suggested that some degree of nestedness appears to be the rule in nature. The results were within the ranges of matrix temperatures (*T*) for studies in fragments that they examined, as well as for oceanic and land-bridge situations. Wright et al. (1998) also ranked the results of one study which examined several taxa and showed that amphibians exhibited greater levels of nestedness than either bird or mammal assemblages.

Nupp (1997) examined the spatial distribution of small mammals across forested areas within our study area. He calculated matrix temperatures of 12.14° (*P* < 0.0001) and 8.25° (*P* < 0.0001) for all small mammals and for forest-dwelling granivores, respectively. These values are comparable to our values for amphibians (16.45°) and anurans (7.29°). The results of these studies indicate that amphibian and small-mammal assemblages show a highly ordered distribution, with the specialized subgroup (i.e., anurans and granivores) having a lower matrix temperature. Our salamander assemblages, however, have a higher matrix temper-
ature (21.53°) than our amphibian assemblages, perhaps because the salamander species are more variable in their life-history characteristics.

Local persistence and metapopulation dynamics can often be modeled satisfactorily by examining the effects of patch area and isolation (Mollanen and Hanski 1998). However, predictable changes in local species composition and richness may also result from factors that influence habitat suitability independently of area or isolation effects. For instance, amphibian species richness was highest for sites dominated by seasonal and semipermanent wetlands or sites containing a mixture of wetlands with various water regimes, resulting in intermediate wetter values (Table 4, Fig. 1). As a group, amphibian species exploit a variety of different sites for breeding. Many species, however, require water regimes of seasonal or longer duration for eggs to hatch and larvae to develop (Collins and Wilbur 1979; Pfingsten and Downs 1989; Tying 1990; Conant and Collins 1991). However, sites that are dominated by permanent water bodies may support predatory species of fish, or for that matter other amphibian species that may prey directly on amphibian eggs and larvae (Semlitsch 1987, 1988; Semlitsch and Gibbons 1988). Accordingly, the availability of seasonal and semipermanent wetlands appears to be important in sustaining high levels of species richness. Skelly and Meir (1997) used rule-based models to show that the distributions of 3 of 14 species of amphibians in southern Michigan were influenced significantly by pond permanence. We found a significant association of richness with wetland permanence, as measured using WET_P. Even more notable was the fact that wetland permanence was a significant predictor of occurrence for seven of nine species for which logistic models were constructed (Table 5). Thus, our findings support Skelly and Meir's (1997) conclusion that factors other than spatial effects are capable of altering the distribution of amphibians.

Few studies of amphibians have investigated the effects of patch area or isolation on their distributional patterns. In Sweden, however, Sjogren (1991) found that pond isolation was related to the probability of local extinction in a metapopulation of the pool frog (Rana lessonae). The rescue effect (i.e., immigration) played an important role in local and regional population persistence (Brown and Kodric-Brown 1977). Our results support the observations of Sjogren (1991). We found that species richness of ranids was positively related to proximity to wetlands (Table 4). Moreover, proximity to wetlands was a significant predictor of occurrence for three species of ranids (Table 5).

Our goal was to relate characteristics of amphibian assemblages to both forest and wetland patch and landscape attributes. Other studies have focused on the effects of wetland fragmentation in agricultural areas and have related species richness to such landscape variables as proximity to forest. For example, Hecnar and McCloskey (1998) sampled 180 ponds in southwestern Ontario and found that the area of regional woodlands was the most important variable in determining amphibian species richness. Laan and Verboom (1990) surveyed 77 potential amphibian breeding pools in the Netherlands and categorized them into old (>7 years) and new (<5 years). Important landscape predictors for amphibian species richness in old pools included pool size and depth as well as the area of woodland in the vicinity of the pond; for new pools, a greater area of woodland in close proximity to the pool was associated with greater species richness. Because woodlands served as part of the terrestrial habitat for these amphibians, they likely served as a measure of connectivity in the landscape (Laan and Verboom 1990; see also Dodd and Cade 1998). Vos and Stumpel (1996) found that presence of the tree frog (Hyla arborea) in the Netherlands depended on three isolation factors: density of ponds <750 m from the occupied pond and densities of shrubs and high herbs <1 km from the occupied pond. In both studies, upland features of the landscape were important determinants of amphibian occurrence in agricultural areas. The presence of three species in our study was influenced by proximity to wetlands, and two species were influenced by proximity to forest (Table 5).

Interspecific differences in sensitivity to habitat fragmentation

Our review of the literature suggested that amphibian species on our study area would display a range of sensitivities to habitat fragmentation in accordance with their life histories (Table 1). In general, our results confirmed this prediction. Rank correlations were computed between the hypothesized sensitivity reported in Table 1 (low = 0, moderate = 1, high = 2) and the frequency of associated explanatory variables appearing in regression models (Table 5). The American toad and gray treefrog were included in the analysis and assigned a value of 0 because they were ubiquitous. Species for which we predicted a low sensitivity to forest area or proximity yielded models containing fewer forest variables, on average, than species for which a high sensitivity had been predicted (Spearman's $p = 0.54$, $P < 0.05$). A similar but stronger correlation occurred between predicted and observed sensitivity to wetland area or proximity (Spearman's $p = 0.67$, $P < 0.025$).

Two species, the spotted salamander (Ambystoma maculatum) and the wood frog (Rana sylvatica), occurred historically in our study area (Minton 1972), but we failed to detect their presence. Spotted salamanders, however, currently occur in areas to the east of our study area (R. Howard, personal communication). Their absence in our area was not surprising because spotted salamanders and wood frogs are closely associated with forests (Demaynadier and Hunter 1998) and are known to disappear rapidly from agricultural lands (Minton 1972). In contrast, the American toad and gray treefrog were ubiquitous across our study sites, and thus appeared to be the most stable species in terms of their probability of long-term persistence in this landscape. The life-history and ecological attributes of both of these species favor their survival in an agricultural landscape. Gray treefrogs are closely associated with woodlands, but they have a prolonged breeding season and can use a variety of wetland types for breeding. They also undergo migrations from upland woods to breeding pools (Tying 1990) and appear to persist in cultivated areas (Minton 1972). American toads prefer sites characterized by disturbance, such as grassland and sparse woods, and they can exploit a variety of temporary water bodies, which are not limiting in this landscape, for breeding (Minton 1972). They also undergo...
migrations to breeding areas, so wetlands do not need to be present on site. Our observations indicate that toads are very abundant in this landscape, probably because they are able to exploit a variety of breeding areas and are relatively mobile. We suspect that they can generally be found in dense concentrations in isolated woodlands that are surrounded by farmland.

Little information exists on the frequency or extent of movements of amphibians in agricultural areas, yet a species’ ability to move through a cropland matrix is widely believed to be critical to its persistence in farmland (Noss and Csuti 1994). Although our records of use of the matrix are limited, they support this notion. The most extensive actual or suspected movements we recorded were of tiger salamanders and American toads, which are among the most widely distributed and abundant salamander and anuran species, respectively, in our study area. We captured a tiger salamander at one of our smallest forest patches, >1 km from the nearest potential breeding site. This forest patch was surrounded almost exclusively by farmland within this 1-km radius. In addition, we documented interpatch movements of American toads. In one instance, we marked a toad at one of the smallest and most highly isolated forest patches and recaptured it 6 days later at another forest patch >2 km away. There were no forest patches within a straight-line distance between the two sites, only recently plowed agricultural land. Also, several individually marked American toads moved between a group of our study sites: one was captured at one site, then was captured 24 h later at another forest patch 250 m away.

We predicted that redback salamanders would be among those amphibian species that were most sensitive to forest patch area, occurring only at the largest sites (Table 1). The logistic regression model supported our prediction (Fig. 2). Redback salamanders were, in general, captured on moderately sized to the largest of forest patches. Interestingly, they were documented in the largest woodland in this study, the largest contiguous forested area, and in small or moderately sized woodlots that were in close proximity to the large forested tract. This distribution indicates that immigration of salamanders from the largest forest tract may rescue populations in these small to moderately sized woodlots, either preventing them from becoming extinct or increasing the likelihood of their recolonization.

Forest isolation was a significant predictor of the presence of both tiger salamanders and northern leopard frogs at sites that had higher wetwr values or were in close proximity to larger amounts of wetland, respectively. This is consistent with our predictions (Table 1), because neither of these species is strongly associated with forest; in fact both are likely to occur in open areas such as fields and grasslands (Dickerson 1969; Pfingsten and Downs 1989; Wright and Wright 1995). Tiger salamanders were highly associated with sites with higher wetwr values, that is, sites dominated by more permanent wetland water regimes (Fig. 3). This is reasonable, since their larvae typically require 3 months to develop (Tyler 1990). Leopard frogs were associated with isolated forest patches in close proximity to wetlands (Fig. 4). Although in summer they often forage in grassy areas or fields, often far from water, in spring and fall they often remain close to pools, marshes, or streams, where they overwinter (Dickerson 1969; Minton 1972; Wright and Wright 1995).

Tiger and smallmouth salamanders were both documented on 15 sites, but only 10 of these sites were shared. Our pitfalls-trapping data suggest that at many of the sites where they co-occur, one species is more abundant than the other. Unlike tiger salamanders, smallmouth salamanders were not sensitive to forest proximity. The probability of occurrence of smallmouth salamanders had a curvilinear relationship with wetwr, reaching a maximum at wetwr values between 2 and 3 (Fig. 5). Smallmouth salamanders were more likely to occur in sites dominated by seasonal wetlands or semipermanent wetlands or with a mixture of wetland water regimes resulting in a moderate wetwr value for the site. It appears that smallmouth salamanders are more associated with woodland pools than tiger salamanders (Pfingsten and Downs 1989), which are typically associated with pools in fields and meadows adjacent to forests (Tyler 1990). Smallmouth salamanders, however, typically exploit a variety of aquatic breeding sites, including vernal and semipermanent pools in fields as well as woodlands (Pfingsten and Downs 1989). The logistic model for smallmouth salamanders appears reasonable, in that their larvae would have sufficient time to develop in seasonal and semipermanent pools, without competition with fish or other amphibians that dominate permanent wetlands. Furthermore, it would be interesting to examine specific characteristics (i.e., habitat, water chemistry) of pools dominated by tiger salamanders versus those dominated by smallmouth salamanders. In this landscape, smallmouth salamanders may be more abundant in seasonal woodland pools, where they may experience less competition with or predation by tiger salamander larvae.

The probability of occurrence of both western chorus frogs and northern spring peepers had a curvilinear relationship with wetwr, with peepers more likely to occur at sites with no streams present. Spring peepers were more likely to occur in forest patches with wetwr values that were dominated by temporary wetlands, while chorus frogs had a high likelihood of occurrence over the entire range of temporary to permanent wetlands (Fig. 5). Although chorus frog larvae tend to have greater growth rates and larval survivorship than spring peepers in temporary regimes (Skelly 1995), our landscape-level analysis did not reflect this. Spring peepers are associated with woods in the nonbreeding season and are known to disappear from agricultural areas (Minton 1972), whereas chorus frogs can be found in a variety of habitats, some of which may be dry and greatly altered by humans (Conant and Collins 1991). Although our data did not indicate sensitivity of spring peepers to forest patch area or isolation, the fact that they had a narrower, more limited probability of occurrence along a wetwr gradient than chorus frogs (Fig. 5) suggests that they are generally less successful in this agricultural landscape.

Two species with strong aquatic affiliations, the bullfrogs and green frogs, were more likely to occur at sites with higher wetwr values or forest patches that were in close proximity to more wetland area, which concurs with our predictions (Tables 1 and 5, Fig. 6). Bullfrogs are more closely associated with larger, more permanent water bodies, whereas green frogs also can be found in smaller ponds and pools.
as well as in streams and rivers (Tyning 1990). These
differences were reflected by our data, which indicated that even
when there were few wetlands in proximity to a site, green
frogs had a high probability of occurrence. In contrast, only
low wetland proximity values combined with higher
wetland area values were associated with higher probabilities of
occurrence of bullfrogs (Fig. 6), probably because of their
more specific association with more permanent water bodies.

In conclusion, local assemblages of amphibians exhibited
a highly nested pattern in this agriculturally dominated mid-
western landscape. Forest and wetland patch and landscape-
level variables were good predictors of species richness of
amphibians, anurans, and ranids. Our results suggest that
seasonal and semipermanent wetlands associated with forest
patches are particularly important for conserving species
richness of amphibians in this landscape. Forest patches that
are associated with a variety of wetland water regimes also
are important. Some species, such as the American toad and
gray treefrog, appear to thrive in the presence of intensive
agriculture. Other species, such as the tiger salamander,
smallmouth salamander, and green frog, occur primarily in
the vicinity of suitable breeding habitat. Forest-dependent
species, such as the spotted salamander, wood frog, and
redback salamander, either were absent or showed the great-
est sensitivity to reductions in forest area.

Demographic data, coupled with studies of animal move-
ments and experimental manipulation of populations in patches,
will ultimately provide the most comprehensive under-
standing of the influence of agriculturally induced fragmenta-
tion on amphibians (Lima and Zoller 1996). More information
is needed on amphibian movements, both seasonal and dis-
spersal, if we are to understand the patterns exhibited in an
agriculturally fragmented landscape. We also need to exam-
ine the spatial scale to which amphibians respond, a scale
that may be quite different in fragmented versus continuous
landscapes. Such information could then be incorporated
into spatially explicit population models and used to aid con-
servation efforts by predicting the effects of landscape
change on populations (Dunning et al. 1995; Turner et al.
1995).

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References

Atmar, W., and Patterson, B.D. 1993. The measure of order and
disorder in the distribution of species in fragmented habitat.

Breden, F. 1987. The effect of pre-metamorphic dispersal on the pop-

northwestern Indiana. In Status and conservation of Midwestern
amphibians. Edited by M.J. Lannoo. University of Iowa Press,

biogeography: effects of immigration on extinction. Ecology,
58: 445-449.

of the amphibians of the Edwin S. George Reserve, Michigan,

Conant, R., and Collins, J.T. 1991. A field guide to reptiles and
amphibians. eastern and central North America. 3rd ed. Houghton

Classification of wetlands and deepwater habitats of the United

Cunjak, R.A. 1986. Winter habitat of northern leopard frogs, Rana

Dickerson, M.C. 1969. The frog brook, North American toads and
frogs, with a study of the habits and life histories of those of the

Demaynadier, P.G., and Hunter, M.L., Jr. 1998. Effects of silvi-
cultural edges on the distribution and abundance of amphibians

Dodd, K.D., Jr., and Cade, B.S. 1998. Movement patterns and the
conservation of amphibians breeding in small, temporary wet-

Dunning, J.B., Jr., Stewart, D.J., Danielson, B.L., Noon, B.R., Root,
explicit population models: current forms and future uses. Ecol.
Appl. 5: 3-11.

in north-central Indiana. M.S. thesis, Purdue University, West
Lafayette, Ind.

of amphibians in southeastern Ontario ponds. J. Biogeogr. 25:
763-772.

Heyer, W.R., Donnelly, M.A., McDermid, R.W., Hayek, L.C., and
Foster, M.S. (Editors). 1994. Measuring and monitoring biologi-
cal diversity: standard methods for amphibians. Smithsonian
Institute Press, Washington, D.C.

selection in American toads: a test of a good-genes hypothesis.
Evolution, 48: 1286-1300.

Jones, K.B. 1981. Effects of grazing on lizard abundance and diver-

Kolozsvary, M.B. 1998. Effects of agriculturally induced fragmenta-
tion on amphibian assemblages in west-central Indiana. M.S.
thesis, Purdue University, West Lafayette, Indiana.

Laan, R., and Verboom, B. 1990. Effects of pool size and isolation

Lannoo, M.J. 1998. Amphibian conservation and wetland man-
germent in the Upper Midwest: a catch 22 for the cricket frog?
Edited by M.J. Lannoo. In Status and conservation of Midwestern

Lima, S.L., and Zoller, P.A. 1996. Towards a behavioral ecology of

McGarrigle, K., and Marks, B.J. 1995. FRAGSTATS: spatial pattern
analysis program for quantifying landscape structure. U.S. Dep.


