# Amphibian Distributions in a Landscape of Forests and Agriculture: an Examination of Landscape Composition and Configuration

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Abstract: Landscapes can be described by two essential features: the composition and spatial arrangement of patches. We considered the roles of these basic landscape descriptors by examining how the occurrence of nine amphibian species in breeding ponds was associated with the area of forested babitat and the proximity of ponds to forested habitat. We used visual and call surveys to compare the composition of amphibian assemblages in 116 ponds adjacent to or separated from forest and surrounded by different amounts of forested land. The area of forest and pond adjacency to forest were not associated (t = -0.13,  $n_{isolated} = 64$ ,  $n_{connected} = 52$ , p = 0.21), which means these factors can manifest their effects separately. We used logistic regression to test predictions about associations between each species and forest area and to test for associations with pondforest adjacency. Seven of nine species were associated with forest area. Wood frogs (Rana sylvatica), green frogs (Rana clamitans), eastern newts (Notopthalmus viridescens), spotted salamanders (Ambystoma maculatum), and salamanders of the blue-spotted/Jefferson's complex (Ambystoma laterale/A. jeffersonianum) were more likely to occupy ponds in more forested areas, whereas leopard frogs (Rana pipiens) and American toads (Bufo americanus) were negatively associated with forest area. Three species were associated with pondforest adjacency. Spotted salamanders and salamanders of the blue-spotted/Jefferson's complex were more likely to occupy ponds that were adjacent to forest. In areas with little forest, leopard frogs were more likely to occur in adjacent ponds, but the reverse was true for areas with extensive forests. Our results suggest that the composition of the landscape surrounding breeding ponds is associated with the likelihood of occurrence of most of the species examined and that landscape configuration is also important for a smaller subset of species.

Distribución de Anfibios en un Paisaje de Bosques y Agricultura: un Análisis de la Composición y Configuración del Paisaje

**Resumen:** Los paisajes pueden ser descritos por dos características esenciales: la composición y la disposición de fragmentos. Consideramos la función de estos descriptores básicos de paisaje analizando como se asoció la presencia de nueve especies de anfibios en estanques de reproducción con el área de hábitat boscoso y la cercanía de estanques a hábitat boscoso. Utilizamos registros visuales y auditivos para comparar la composición de comunidades de anfibios en 116 estanques adyacentes a un bosque o separados del mismo y rodeados de diferentes cantidades de terreno boscoso. El área de bosque y la distancia de los estanques del al bosque no estuvieron asociados (t = -0.13,  $n_{aislado} = 64$ ,  $n_{conectado} = 52$ , p = 0.21) lo que significa que estos factores pueden manifestar sus efectos por separado. Utilizamos regresión logística para probar predicciones referentes a asociaciones entre cada especie y el área de bosque y para comprobar si las asociaciones si relacionaban con la adyacencia de los estanques al bosque. Ranas de bosque (Rana sylvatica), ranas verdes (Rana clamitans), tritones del este (Notopthalmus viridescens), salamandras manchadas (Ambystoma maculatum) y salamandras del complejo manchas azules/Jefferson (Ambystoma laterale/A. jeffersonianum) ocuparon más estanques en áreas más boscosas, mientras que ranas leopardo (Rana pipi-

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ens) y sapos americanos (Bufo americanus) se asociaron negativamente con el área de bosque. Tres especies se asociaron con la adyacencia al bosque. Salamandras manchadas y salamandras del complejo manchas azules/Jefferson tenian mayor probabilidad de ocupar estanques adyacentes a bosque. En áreas con poco bosque, ranas leopardo ocurrieron en estanques adyacentes, pero lo contrario sucedió en áreas con bosques extensos. Nuestros resultados sugieren que la composición del paisaje que rodea a los estanques de reproducción se asocia con la probabilidad de ocurrencia de la mayoría de las especies analizadas y que la configuración del paisaje también es importante para un subconjunto de especies más pequeño.

# Introduction

Landscapes can be characterized by both the area and types of patches they contain and by the spatial arrangement of those patches (Turner 1989; Dunning et al. 1992). Landscape composition reflects only the types and amounts of landscape components without reference to their spatial arrangement, whereas measures of landscape configuration are spatially explicit but lack information about patch type and extent. Both composition and configuration can variously affect the individuals, populations, and communities that inhabit a landscape (see review by Kareiva 1990). Understanding the separate influences of each of these landscape features on the ecology of certain taxa may inform conservation planning. For example, if the effects of landscape composition predominate, conservation efforts should focus on protecting as much suitable habitat as possible, but if the effects of configuration are also important, attention to the spatial arrangement of habitat patches is also necessary.

Disentangling the roles of composition and configuration has proven difficult because the two are often correlated. For example, habitat loss (a composition feature) and habitat isolation (a configuration feature) are often confounded (Lynch & Whigham 1984; Fahrig 1997; Hargis et al. 1997; Bowers & Dooley 1999). Organisms that require two different habitat types to complete their life cycles offer a unique situation in which to separately examine the roles of these essential landscape features. For such organisms, Dunning et al. (1992) defined landscape complementation as the process by which the proximity of two critical habitat patches of different types complements occupancy, abundance, or persistence in each patch. Therefore, landscape complementation is a result of landscape configuration. Landscape composition can be examined independently from configuration by looking at the effects of variation in the amount of habitat of one type in the vicinity of a focal patch of the other type.

It may prove particularly important to understand the response of amphibians to landscape composition and configuration. Most pond-breeding amphibians depend on two types of habitat: wetlands for reproduction and upland forests for foraging, hibernating, and/or traveling (Zug 1993; Stebbins & Cohen 1995). Consequently, both the proximity of breeding habitat and terrestrial habitat and the area of terrestrial habitat may play a key role in the determination of occupancy of a focal patch (Pope et al. 2000). At the individual level, most amphibians are likely to respond to landscape complementation because they are small and slow moving (Stebbins & Cohen 1995), have limited dispersal capabilities (Sinsch 1990) and small home ranges (Stebbins & Cohen 1995), and are tied to moist microclimates because of their highly permeable skin that must remain cool and moist for efficient respiration (Feder 1983; Larson et al. 1984).

At the population level, if amphibians exhibit metapopulation structure (Gill 1978; Sinsch 1992; Gulve 1994; Marsh & Trenham 2001), then reduced immigration and emigration rates resulting from the disconnection of required habitat patches could have severe repercussions. Laan and Verboom (1990) demonstrated a negative association between amphibian occupancy of breeding ponds and the distance from the ponds to the nearest patch of forest. Similarly, research on adult amphibians in terrestrial habitats has shown that forest patch area and isolation of forest patches from one another are important influences on occupancy (Marsh & Pearman 1997; Gibbs 1998a; Kolozsvary & Swihart 1999). The area of forest surrounding breeding ponds can also influence amphibian assemblages (Laan & Verboom 1990; Vos & Stumpel 1995; Findlay & Houlahan 1997; Hecnar & M'Closkey 1996, 1998; Lehtinen et al. 1999). To our knowledge, however, the influences of upland habitat extent (an aspect of landscape composition) and pondforest adjacency (an aspect of landscape configuration) on amphibian distributions have not been separated.

Our objective was to examine landscape composition and configuration separately by looking at associations between amphibian species occurrence and forest extent and pond-forest adjacency in a landscape of forests and agriculture in northeastern Maine. In this landscape, a relatively inhospitable agricultural matrix that separates many ponds from the surrounding uplands has replaced much of the forest that once dominated the area. We looked at landscape composition by examining amphibian species occurrence in 116 breeding ponds surrounded by different amounts of forest. We examined landscape configuration by classifying each pond as either adjacent to or disconnected from the nearest tract of forest. Because the area of forest and pond-forest adjacency were not associated, we were able to examine associations with both landscape composition and configuration.

# Methods

## Study Area

We conducted our research from May through August in 1998 and 1999 in a 4500-km<sup>2</sup> area of northeastern Aroostook County, Maine (U.S.A.), that was approximately 50% forested and 50% agricultural (Fig. 1). The study area was within the hardwoods-spruce forest section of the Laurentian mixed-forest province (Bailey 1995). Glacial till derived from limestone and shale was the dominant soil parent material (Arno 1958), which yields soils suitable for agriculture. The most common crop was potatoes, but broccoli, peas, and numerous grains were also cultivated.

Because forest tracts and agricultural fields were the dominant land-cover types, the study area constituted a fairly simple landscape that approximated the pixel-based binary landscapes often used to model the effects of landscape pattern (e.g., With & Crist 1995; Hargis et al. 1997). Contrary to most pixel-based landscape simulations, in this real landscape, forest "patches" were almost entirely large tracts. What varied was whether or not a particular pond was adjacent to forest and the overall amount of forest nearby. Because the loss of forests in this region occurred decades ago, we examined one snapshot of forest extent at an endpoint of habitat loss through time.

We examined 116 ponds that were primarily small, permanent bodies of water. Many were farm ponds dug for agricultural purposes or fire suppression. Cattails (*Typha latifolia*), speckled alder (*Alnus incana*), willow (*Salix* spp.), and red-osier dogwood (*Cornus stolonifera*) were the most common emergent vegetation; duckweed (*Lemna* spp.) and algal mats were the most common floating vegetation. In 1998 we selected 73 ponds for study, and in 1999 we selected 43 additional ponds. In 1999 we resampled 18 of the 1998 ponds (chosen by stratified-random sampling based on the area of open land within a 1-km radius) to determine if there were differences between years.

Because we were primarily interested in the landscape context of breeding ponds, we used three basic selection criteria to minimize the variation in local pond characteristics: National Wetland Inventory (NWI) classification (Cowardin et al. 1979), wetland size, and distance to road. We selected only wetlands classified as palustrine unconsolidated bottom (PUB) or palustrine emergent vegetation (PEM); those <0.5 ha in size and not part of a larger wetland complex; and those within 200 m of roads. Sampling ponds near roads allowed for the



Figure 1. Location of the study area in northeastern Maine, including a land-use/land-cover map and a close-up view of the circles with 1-km radii centered on 5 of the 116 ponds. In the land-use/land-cover map, black is water, dark gray is forest, light gray is open land, and black circles are sample circles centered on ponds.

large sample size of ponds. Furthermore, it may have standardized ponds with respect to roads, which may filter amphibian movement (Reh & Seitz 1990; Vos & Chardon 1998; Gibbs 1998*b*; deMaynadier & Hunter 2000), although the effects of roads on amphibians are not well understood and are likely to be variable. After locating ponds that fit the criteria in a geographic information system (GIS), we field-checked them and excluded any pond that was not a PEM or a PUB or was likely to be temporary (although seven of the ponds we sampled dried by the end of the summer in at least one year).

To sample a continuum of forest extent, we stratified the ponds into three classes by the percentage of open land (0-33%, 34-66%, and 67-100%) within 1 km of the pond (an area of 314.16 ha) and strove to select an equal number of ponds in each class. These categories were used for selection only. Open land included crops, pastures, hay fields, and abandoned fields. Although we would have liked to examine a continuum of pond-forest distances, we were unable to locate many ponds at a great distance from forest. We classified ponds as either adjacent to forest (distance = 0) or nonadjacent (distance > 0) and attempted to represent both categories equally in each of the three classes of open land. We believed the use of the categorical variable was relevant to these species with limited vagility and was a conservative approach that would, if anything, bias the results against detecting a difference in occupation between adjacent and nonadjacent ponds.

To ensure that we were sampling independent landscapes (see landscape analysis), we selected ponds that were >2 km from other studied ponds, but because distances were initially estimated from maps in the field, 24 pairs of landscapes overlapped (maximum = 17%, median = 3%).

## **Amphibian Sampling and Predictions**

We restricted our study to nine amphibian species that lay their eggs and undergo larval development in palustrine wetlands. To generate a priori predictions about associations between each species and forest area, we grouped them into four classes based on ecological characteristics (Table 1): "forest" species require forests for part of their life cycle, "aquatic" species stay primarily in the water but occasionally disperse from natal ponds, "open" species use meadows and fields, and "generalists" are widespread (Hunter et al. 1999).

We sampled ponds for amphibians with two methods: auditory night surveys and visual day surveys. For the night surveys, we identified each species heard calling during a 3-minute survey, following a 1-minute pause between arrival and commencement of the survey. We surveyed two routes in different parts of the study area each night. We sampled each pond three times during each period of optimal breeding time for the expected species, for a total of nine night surveys per pond. We recorded environmental variables that might have affected frog calling: air temperature, precipitation, cloud cover (as a percentage of the sky filled with clouds), and wind (with the Beaufort Wind Scale) (Heyer et al. 1994). Surveys were conducted only when wind did not interfere with our ability to hear calls (<5 on the Beaufort scale). This protocol was modified from those of the North American Amphibian Monitoring Program (NAAMP) for callinganuran surveys (A. J. K. Calhoun, personal communication).

Visual day surveys involved searching the entire perimeter of the pond to a depth of approximately 1 m, the habitat used by most amphibians. Two observers started at one point and searched in opposite directions until they met. We recorded the presence of all adults, tadpoles, and metamorphs seen. We also recorded numbers of spotted salamander egg masses, the only species for which we were confident we could obtain accurate counts. Day surveys provided the only data for salamanders and newts, because these species do not call.

Most species did not show a marked difference in occurrence between the 2 years at the 18 ponds sampled in both years. We used Fisher's exact tests to test whether or not the proportion of ponds for which oc-

Table 1. Grouping of the nine amphibian species by ecological characteristics and predictions of their associations with forest area.

Ecological group (prediction for association with forest area)*	Species
Forest (+)	wood frog (Rana sylvatica)
	spring peeper (Pseudacris crucifer)
	spotted salamander (Ambystoma maculatum)
	blue-spotted/Jefferson's salamander complex (Ambystoma laterale/A. jeffersonianum)
	eastern newt (Notopthalmus viridescens)
Aquatic (+)	green frog (Rana clamitans)
	mink frog (Rana septentrionalis)
Open (0)	leopard frog (Rana pipiens)
Generalist (0)	American toad (Bufo americanus)

\*A (+) represents the expectation of a significant, positive association between occupancy of a pond and the area of forest; a (0) represents the expectation of no significant association. See the text for rationale of the groupings.

currence data agreed (either present in both years or absent in both years) was different from perfect agreement (18/18). American toads were the only species for which occurrence across years was significantly different from perfect agreement (p = 0.046). Therefore, we treated the 2 years separately for American toads and pooled both years for all other species.

### Landscape Analysis

We defined the "landscape" surrounding a pond as the area within a circle with a 1-km radius centered on the pond. This 1-km radius is biologically relevant because most estimates of migration and dispersal distance for the species in our study (or closely related species) range from 249 m to 1 km (Healy 1975; Semlitsch 1980; Kleeberger & Werner 1983; Berven & Grudzien 1990; Sinsch 1990; Madison 1997; Waldick et al. 1999). Individuals of some species are capable of moving beyond 1 km (e.g., the maximum expected dispersal distance for leopard-frog metamorphs is 5 km; Dole 1971), but most individuals move much less than the maximum distance reported (Semlitsch 1998). We also calculated the area of forest in circles with radii of 500 and 300 m to allow for an examination of associations at these scales. Because of the large degree of overlap and the ensuing lack of independence of landscapes defined by circles with radii of >1 km, we were unable to examine associations at larger scales.

We analyzed landscape composition within this sample circle in a GIS (Arc-Info, Environmental Research Systems 1998) with a vegetation and land-cover map developed by the Maine Gap Analysis Project (Hepinstall et al. 1999). The map was created from 1991 and 1993 satellite imagery and ancillary GIS layers, had a 30-m pixel size, and contained 37 classes of vegetation. We simplified the vegetation classes to include only four types: open (crops, pastures, hay fields, and abandoned fields), forest (all forest types and wetlands), water (lakes, rivers, and large ponds), and urban (residential, commercial, and industrial). Although we designed the study to examine pond-forest adjacency as a binary variable, we also measured the distance to forest from each pond on aerial photographs and in the field to determine whether or not continuous distance data provided more information than the categorical parameter.

#### **Ancillary Pond and Landscape Attributes**

Although we attempted to minimize variation among wetlands, pond attributes may have varied in ways that were correlated with pond isolation and forest extent. Therefore, we collected information about the pond and the landscape surrounding the pond that was likely to be correlated with these two factors. For the surrounding landscape this information included the area of wetlands, length of forest edge, and distance to crops. For the ponds, we recorded pH and conductance (Guerry 2000).

#### Statistical Analyses

We tested for associations between amphibian occupancy and forest area and pond-forest adjacency with logistic regression models for each species. In ecology, logistic regression is most often used as a predictive modeling tool, but we used it here to test our hypotheses about the association between amphibian species occurrence and forest extent and pond-forest adjacency. We used the area of forest in the landscape and whether or not the pond was adjacent to the nearest patch of forest as explanatory variables and the presence or absence of a species as the binary response. We began with a full model, including interactions, and to find the best model we used backward elimination with a p-to-remove of 0.05, always removing higher-order terms before main effects (Hosmer & Lemeshow 1989; Agresti 1996; SYSTAT, SPSS 1998). We determined overall model significance using the likelihood-ratio statistic and assessed goodnessof-fit with the Hosmer-Lemeshow (H-L) statistic (Hosmer & Lemeshow 1989). We used odds ratios (Agresti 1996) to describe the strength of the associations and to allow for interpretation of the influence of both variables on occupancy.

To further assess model fit, we plotted the observed proportions of ponds (grouped by forest area in classes of equal size) in which each species was present against the area of forest and compared these data points to the fitted model. We also examined residual plots. Because goodness-of-fit statistics can only show lack of evidence of a poor model fit but not prove model fit when the pvalues are between 0.05 and 0.95, we also conducted univariate tests—multiresponse permutation procedures (MRPP; Slauson et al. 1994) and Fishers' exact tests— to ensure that the relationships outlined by the logistic regressions were not statistical artifacts.

To examine whether or not the distance to forest provided more information than the binary adjacency variable, we built a second set of logistic regressions for each species based on the categorical variable for adjacency and the continuous variable for distance and its square. If either of the continuous terms was significant, then the continuous-distance data added explanatory power beyond that explained by the categorical variable.

Because occurrence data are relatively coarse, we used the egg-mass abundance of the spotted salamander to refine our study of this species, focusing only on ponds in which spotted salamanders occurred. Because transformations failed to normalize the right-skewed distribution, we examined the relationship between eggmass abundance of spotted salamanders and forest area with a Spearman's rank-correlation test with Spearman's rho ( $\rho$ , Conover 1980) and between egg-mass abundance and adjacency with a Mann-Whitney *U* test.

We used Pearson's correlation coefficients to examine correlations between forest area and the ancillary independent variables and Mann-Whitney *U* tests to examine associations between pond isolation and these variables. For the correlation analysis, we defined as highly correlated pairs of variables with correlation coefficients of >0.6. For the Mann-Whitney *U* tests we used  $\alpha = 0.05$ . By using  $\alpha = 0.05$  instead of a Bonferroni-corrected  $\alpha$  of 0.006, we were more likely to detect confounding variables.

To provide a more holistic view of the amphibian assemblages, we also examined the relationship between the number of species present in the ponds and the area and adjacency of forests. Because counts of species are less meaningful when species with different requirements are treated equally, we examined this relationship without leopard frogs and American toads. We used linear regression to model the number of forest and aquatic species present. We started with a full model including interactions and employed a backward step-wise procedure to remove insignificant variables. We examined residuals visually with normal probability plots and by plotting them against model estimates.

## Results

Wood frogs occurred in 95 ponds, spring peepers in all 116, spotted salamanders in 60, blue-spotted/Jefferson's salamanders in 29, eastern newts in 6, green frogs in 98, mink frogs in 101, leopard frogs in 49, and American toads in 83. (Table 1 provides scientific names.) Seven of the nine species showed an association (five positive

and two negative) with forest area in the surrounding landscape. Of these, three species also showed an association with pond-forest adjacency (two positive and one complicated by an interaction) (Table 2). The area of forest in the landscape and pond-forest adjacency were not associated (t = -0.13,  $n_{isolated} = 64$ ,  $n_{connected} = 52$ , p = 0.21). Spring peepers occurred in all 116 ponds and thus showed no association with forest area and pond-forest adjacency in the range of landscapes studied here. Similarly, the presence of mink frogs was not associated with the area of forest or with pond-forest adjacency.

Leopard frogs, spotted salamanders, and salamanders of the blue-spotted/Jefferson's complex were associated with both adjacency and area. In addition, leopard-frog occurrence was dependent on a significant interaction between adjacency and area. Spotted and blue-spotted/ Jefferson's salamanders were more likely to occupy ponds with more forest and were more likely to be in ponds adjacent to the nearest forest patch. A significant interaction term in the leopard-frog model complicated the interpretation of main effects. When there was little forest (<160 ha), nonadjacent ponds were less likely to be occupied by leopard frogs than adjacent ponds (Fig. 2). When there was a larger area of forest in the surrounding upland, however, ponds that were adjacent to forest were less likely to be occupied by leopard frogs. For all of these species, the associations with forest area were more significant than those with pond-forest adjacency (Table 2).

Wood frogs, American toads, green frogs, and eastern newts were associated only with the area of forest surrounding the pond (American toads in 1998 only). Wood frogs, green frogs, and eastern newts were positively associated with forest area, whereas American toads were negatively associated with forest area.

Table 2.	Logistic regression results for an	phibian species occurrence in	preeding ponds in relation to	forest area and pond-forest adjacency.

Species	Sign of FOREST <sup>b</sup> coefficient (p)	Sign of ADJ <sup>c</sup> coefficient (p)	Sign of interaction coefficient <sup>d</sup> (p)	Odds ratio <sup>e</sup> FOREST (95% CI)	Odds ratio <sup>e</sup> ADJ (95% CI)	Likelihood ratio ( p)
Wood frog	+(0.009)			1.01 (1.003-1.018)		7.985 (0.005)
Green frog	+(0.027)			1.009 (1.001-1.017)		5.585 (0.018)
Eastern newt	+(0.023)			1.017 (1.002-1.032)		7.039 (0.008)
American toad (1998) <sup>f</sup>	- (0.012)			0.990 (0.983-0.998)		7.020 (0.008)
Spotted salamander Blue-spotted/lefferson's	+ (<0.001)	- (0.006)		1.013 (1.007-1.02)	0.304 (0.130-0.711)	30.235 (<0.001)
salamander Northern leopard frog	+ (0.001) - (0.001)	- (0.027) - (0.055)	+ (0.037)	1.011 (1.005-1.018) 0.983 (0.975-0.993)	$\begin{array}{c} 0.349 \ (0.137 \text{-} 0.888) \\ 0.144 \ (0.020 \text{-} 1.024)^g \end{array}$	19.873 (<0.001) 16.022 (0.001)

<sup>a</sup>In empty cells the term was not significant and therefore not in the final model.

<sup>b</sup>FOREST is the area of forest (ba) within a 1-km radius of the pond.

<sup>c</sup>ADJ is a binary variable coding for whether or not the pond was adjacent to (1) or disconnected from (0) the nearest patch of forest.

<sup>d</sup> The interaction is FOREST  $\times$  ADJ.

<sup>*e*</sup>*The odds ratio is* ( $e^{\beta}$ ), *where*  $\beta$  *is the coefficient.* 

<sup>f</sup>Years were treated separately for American toads, and a significant model could be built only from the 1998 data.

<sup>g</sup>This odds ratio includes 1, but the term is included in the model because the higher-order interaction term that included it was significant.



Figure 2. Fitted logistic-regression models displaying the probability of occurrence of each species (curves) and observed proportions of occupied ponds (points). Observed proportions were calculated from ponds grouped into categories based on ranks of forest coverage: nine groups of 13 for models for both years without pond-forest adjacency effects (a-c), six groups of 12 for the model for a single year (d), and quartiles stratified by adjacency status for models with pond-forest adjacency effects (e-g). On the x-axis, observed proportions are plotted against the median of forest coverage for each group.

With one exception (blue-spotted/Jefferson's salamander: H-L = 11.8, df = 6, p = 0.07), the models fit the data well (p > 0.23), suggesting that the documented associations drawn from these models are not artifactual. The plots of observed proportions and fitted curves support this conclusion (Fig. 2). Also, all conclusions from the MRPP and Fisher's exact tests were identical to those drawn from the logistic regressions. Forest area and pond-forest adjacency were uncorrelated (r <0.6) or unassociated (Mann-Whitney U tests, p > 0.05) with other characteristics of the pond or the pond landscape. Examining the distance to forest did not provide additional information that was not captured by the binary pond-forest adjacency variable (p > 0.1 for both distance and distance squared for all species). Finally, decreasing the radius of the sample circle to 500 and 300 m did not alter the results for any species, although strong correlations across scales precluded conclusions about any scale being more important than the other two.

The abundance of egg masses of spotted salamanders was correlated with the area of forest in the upland (n = 60,  $\rho = 0.236$ , p = 0.035) for the subset of ponds where spotted salamanders were present. There was no difference in the number of egg masses with respect to the adjacency of the pond (U = 331, p = 0.109). Examination of connected ponds with spotted salamanders present showed that egg-mass abundance was still correlated with the area of forest (n = 35,  $\rho = 0.307$ , p =0.037), whereas in isolated ponds the two were not correlated (n = 25,  $\rho = 0.081$ , p = 0.346). As the area of forest in the upland increased and when a pond was adjacent to the forest, there tended to be more forest-associated and aquatic species in the pond. The final linear-regression model included significant terms for both forest area and adjacency, but not the interaction between them (F = 22.35, p < 0.0001,  $R^2 = 0.28$ ).

## Discussion

Our results stress the importance of species-specific conservation strategies. The occurrences of many species were associated with the area of forest surrounding breeding ponds, whereas fewer species were associated with the adjacency of ponds and forest. Also, two species were negatively associated with forest area, highlighting the importance of open areas as habitat for these species. Our results strengthen the arguments of other investigators who have cautioned landscape planners—and wetland regulators in particular—to recognize the importance of the uplands surrounding wetlands (Dodd & Cade 1998; Semlitsch 1998; Pope et al. 2000). Because the association between occupancy and forest area remained strong in the cases in which adjacency was a significant factor, our results stress the primary importance of habitat area.

For the most part, associations with the area of forest in the surrounding uplands matched what is known about the ecology of each species. The positive associations between the occurrence of five species and the area of forest were generally consistent with other results for these forest-associated species (Hecnar & M'Closkey 1996, 1998; deMaynadier & Hunter 1998; 1999; Gibbs 1998*a*; Waldick et al. 1999). Although ranids have been documented to be associated with interior forest conditions (deMaynadier & Hunter 1998), we found that mink frogs were almost ubiquitous and were not associated with the area of forest. Similarly, the spring peeper, a species we expected to be tied to forest area, was clearly distributed independently of forest area and pond-forest adjacency.

The affinity of leopard frogs and American toads for open areas likely explains the negative associations between these species and the area of forest (Pais et al. 1988; Kolozsvary & Swihart 1999). The insignificance of the negative association between American toad occurrence and forest in the second year of the study may indicate that this relationship is not consistent and may be swamped by other factors. Although forest is generally considered good foraging, hibernating, and traveling habitat for many amphibians, the importance of open areas for American toads and leopard frogs should be considered in strategies for their conservation.

Spotted salamanders and salamanders of the blue-spotted/Jefferson's complex were the least vagile species in our study, an indication that even small distances between upland and wetland habitats may serve as a barrier to their movement across the landscape. The positive association between salamander presence and pond-forest adjacency is generally consistent with the movement patterns of these species and congenerics (Semlitsch 1980; deMaynadier & Hunter 1998; Madison & Farrand 1998), but this contrasts with the findings of Gibbs (1998b), who found that the movements of both adult and juvenile spotted salamanders were not influenced by forest edges and open areas. Analysis of the abundance of spotted salamander egg masses indicated that adjacency intensifies the correlation with forest area.

The positive association between the number of forest and aquatic species and forest area and pond-forest adjacency, although not surprising given the species-specific relationships examined, allows for a more holistic perspective on amphibian assemblages in human-dominated landscapes such as this one. Competitive interactions and other community-level processes are likely at work in these assemblages, so this relationship does not simply follow from the species-by-species associations.

Although thresholds of habitat area within a landscape have been documented by some (e.g., Andrén 1994), we found little evidence of thresholds of upland forest area affecting occupancy by these nine species. Eight of nine species were present across almost the entire continuum of forest area (32.6 ha [10.4%] forest to 301 ha [98%] forest). There was weak evidence of a threshold for newts that were not present in any pond with <144.3 ha (46.2%) forest (n = 57). But because they were present in only 6 of 59 ponds above this apparent threshold, the small sample size of occupied ponds precludes much inference. We note this result here because newts may be particularly susceptible to the isolation of habitat patches (Healy 1975; deMaynadier & Hunter 1998; Gibbs 1998a, 1998b), despite their tolerance of dry upland habitats (Pough 1974). For the other species, it is possible that the minimum forest area we examined was above critical thresholds.

The discussion about associations between each amphibian species and forest area and pond-forest adjacency must be viewed in the context of three issues. First, it is possible that the relatively coarse nature of presence-absence data masks some relationships that data on population size, reproductive success, or some other measure might have revealed. Second, because amphibians tend to be faithful to the site of first breeding (Sinsch 1990), individuals may return to breeding ponds whose upland surroundings have recently become suboptimal. However, the extent of forested land in this region has been stable or increasing for the last several decades. Finally, agricultural practices in the uplands may adversely affect amphibians in wetlands, thereby enhancing the apparent association with forest area, for example, through more runoff of chemicals into wetlands surrounded by crops. Although investigators have documented the effects of agricultural chemicals on

the health of amphibians, such effects have often been shown to be sublethal and dependent upon concentrations, timing, and species sensitivity (Cooke 1977; Berrill et al. 1993; Materna et al. 1995). However, the lethal effects of commonly used levels of agricultural chemicals also have been documented (Hecnar 1995). Given the potential for cascading effects, an investigation of relative abundance or reproductive success may have been more susceptible to this confounding factor.

Populations of many amphibian species have declined in a variety of locations (Wake 1991; Blaustein & Wake 1995; Houlahan et al. 2000). There are likely multiple causes for these declines, but loss and degradation of both terrestrial and aquatic habitats are prominent on the list of potential problems. We have shown that occupancy of breeding sites by amphibians is associated with forest area, and, separately, that occupancy by some species is associated with adjacency of breeding sites and forested uplands. This descriptive examination of the roles of forest extent and pond-forest adjacency cannot lead to firm conclusions about the processes of habitat loss and landscape complementation as determinants of amphibian species' distributions. However, the consistent, strong associations between occupancy and forest area and pond-forest adjacency document a pattern, suggest a possible cause, and may encourage the development of experimental approaches that further examine the effects of habitat area and the spatial arrangement of habitat patches—both in concert and singly. Although it is possible that landscape configuration might in some cases mitigate the effects of changes in landscape composition, our results corroborate those of Fahrig (1997) and Villard et al. (1999), who caution conservation practitioners not to lose sight of the importance of habitat loss in the pursuit of mitigation by favorable habitat configuration. Both habitat extent and configuration need to be considered when landscape-level conservation plans are designed.

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