

Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape

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Abstract

We investigated the influence of landscape and wetland characteristics on pond-breeding amphibian assemblages in south-central New Hampshire, a relatively low populated and heavily forested region of the northeastern United States. This allowed us to better understand landscape influences in less disturbed areas, and to determine critical landscape disturbance thresholds, above which amphibians are negatively impacted. We sampled 61 wetlands for larval amphibians in 1998 and 1999 to examine the influence of forest cover and road density (at seven buffer distances between 100 and 2000 m) and wetland characteristics on larval amphibian assemblages. Assemblages were influenced primarily by forest cover and wetland hydroperiod. Species richness was most strongly influenced by the proportion of forest cover within 1000 m of the wetland. Several species were also influenced by forest cover, but were differentially influenced by buffer widths. Our study suggests that, at least in the northeast US, wetlands with <40% forest cover within a 1000 m radius may have depauperate larval amphibian assemblages, and forest cover above 60% within a 1000 m radius is likely to ensure species rich and abundant larval amphibian assemblages. Given the above, current federal and state regulations that focus amphibian protection efforts on narrow terrestrial buffers surrounding wetlands are likely to be inadequate.

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1. Introduction

Research efforts focused on amphibian conservation are increasing in light of amphibian sensitivity to environmental perturbations and the corresponding declines, range constrictions, and extinctions worldwide (Blaustein et al., 1994; Wake, 1998). These trends are strongly linked to the fragmentation and modification of habitat by humans for agriculture, forestry, urbanization, or development (Blaustein et al., 1994; Skelly et al., 1999; Semlitsch, 2000), although disease, pathogens, global climate change, invasive species, chemical contamination, and commercial trade are also threats

(Blaustein et al., 1994; Lips, 1998, 1999; Wake, 1998; Carey et al., 1999).

Landscape-scale amphibian research has often examined the relationship between amphibian assemblages and the degree of surrounding landscape or wetland modification (e.g., Laan and Verboom, 1990; Hecnar and M'Closkey, 1996; Lehtinen et al., 1999; Knutson et al., 1999). These studies have typically included a significantly urbanized (Reh and Seitz, 1990; Richter and Azous, 1995; Gibbs, 1998a,b) or agricultural (Lehtinen et al., 1999; Knutson et al., 1999; Guerry and Hunter, 2002) component, or a strong contrast between forested and non-forested areas (deMaynadier and Hunter, 1998). Indeed, such studies suggest that amphibians in altered landscapes are susceptible to forest fragmentation (Laan and Verboom, 1990; Fahrig et al., 1995; Gibbs, 1998a,b; Bunnell and Zampella, 1999), urbanization

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(Orser and Shure, 1972; Richter and Azous, 1995) agriculture (Lehtinen et al., 1999; Knutson et al., 1999), presence of roads (Reh and Seitz, 1990; Findlay and Houlahan, 1997), and isolation from other wetlands (Laan and Verboom, 1990; Sjögren, 1991; Vos and Stumpel, 1995).

The combined efforts of these studies indicate that anthropogenic land-use negatively impacts most amphibians by reducing the quantity and quality of suitable wetland and upland habitats and by reducing the ecological connectivity (permeability) of the landscape. These factors in turn may breakdown critical metapopulation processes and alter the structure and persistence of amphibian populations (Gill, 1978; Berven and Grudzien, 1990; Sjögren, 1991; Hecnar and M'Closkey, 1996; Beebee, 1997; reviewed in Semlitsch, 2000 and Marsh and Trenham, 2001). Although amphibians may be adversely affected by high-intensity landscape changes, little is known about the influences of more subtle landscape gradients in less disturbed or predominantly forested areas. In such landscapes, it may be possible to detect early changes to amphibian assemblages and populations, thus taking a more proactive approach to conservation management and protection of amphibian biodiversity.

Currently, New Hampshire is 83% forested; and ranks as the 2nd most forested state in the nation (Thorne and Sunquist, 2001). However, the state is experiencing the fastest population growth rate in New England, and after several decades of increasing forest cover following farm abandonment and forest succession following logging (Litviatis, 1993), percent forest cover has begun to decrease (Thorne and Sunquist, 2001). This decrease is largely driven by suburban development. The southern portion of New Hampshire is experiencing the highest population growth, and a concomitant loss of forest cover and increase in fragmentation. It is also the area of highest herpetofaunal species richness in the state.

Our goal was to assess the influence of anthropogenic landscape changes and abiotic wetland characteristics on amphibian assemblages and populations, in a heavily forested landscape in south-central New Hampshire. We determined the relationship between landscape (% surrounding forest cover, % surrounding wetland habitat, river density, and road density) and wetland (wetland area, hydroperiod, pH, conductivity, and temperature) characteristics, and amphibian species richness and species density estimates. Because we measured landscape characteristics at different spatial scales (100–2000 m) around each wetland, we were able to determine at what, if any, scale(s) amphibian species richness and individual species respond to anthropogenic landscape change (e.g., loss of forest cover and increased road densities).

This study has important conservation implications for amphibians. Strategies to conserve amphibians have recently emphasized the importance of maintaining adequate areas (buffers) of suitable terrestrial habitat sur-

rounding isolated wetlands, which are vital for the feeding, growth, maturation, and maintenance of amphibians (Semlitsch, 2000). Evaluating critical land-use thresholds for maintaining amphibian species richness and individual species will provide regulators with biologically-based guidelines for conservation management to better ensure the persistence of pond-breeding amphibians in the northeastern United States, and possibly other regions.

2. Methods

2.1. Study area

This study was conducted within a 3300 km² region of the Merrimack River watershed in south-central New Hampshire. The study area is predominantly northern hardwood forest, with red oak (*Quercus rubra*), maple (*Acer* spp.), and white pine (*Pinus strobus*) as dominant species (Beltz et al., 1992); silver maple (*Acer saccharinum*) is often found along river floodplains. Much of the land consists of mature secondary forest, although there are scattered patches of agriculture and urban development along the rivers. Most wetlands are palustrine and include forested, scrub-shrub, and emergent wetlands (Cowardin et al., 1979). Typical wetland plants included *Pontederia cordata*, *Nymphaea* spp., and *Cephalanthus occidentalis*. Temporary wetlands also supported *Carex* spp.

2.2. Field methods

Sixty-one palustrine wetlands were chosen randomly within the Merrimack River watershed in south-central New Hampshire (Fig. 1) using National Wetlands

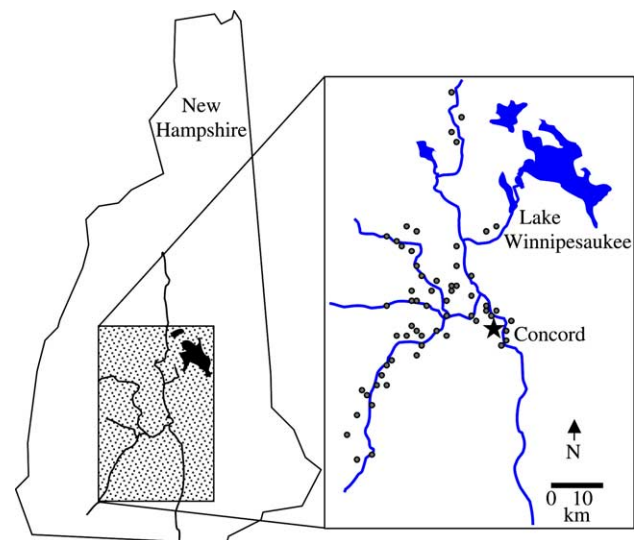


Fig. 1. Study area within the Merrimack River watershed, New Hampshire, USA. Dots indicate individual study sites.

Inventory maps divided into Universal Transverse Mercator grid blocks for stratified random selection. We sampled wetlands four times: July 15–August 31 in 1998 (heavy flooding in May and June precluded an early sample in 1998), and May 17–June 18, July 5–July 28, and August 9–August 28 in 1999. Sampling was conducted from south to north to follow advancing spring weather. Because wetland hydroperiod can influence amphibian use of wetlands as breeding sites (Wellborn et al., 1996; Babbitt et al., 2003), we classified wetlands as temporary or permanent. At the end of each sampling season, we checked wetlands to determine if they had dried. Wetlands that were dry at the end of a field season (November) were classified as temporary and wetlands that did not dry were considered permanent.

We divided each wetland into four microhabitats based on a combination of water depth (greater or lesser than 0.5 m deep) and the presence or absence of aquatic vegetation. We sampled each microhabitat in a spatially stratified manner so that all areas in the wetland were equally represented. The number of available wetland microhabitats during each sampling period ranged from 1 to 4. Fifteen 1 m² sweeps were made in each microhabitat (i.e., up to 60 total sweeps per sampling period) using a dipnet (30 × 45 cm). Sampling curves showed that 15 sweeps per microhabitat was likely to ensure that all species were detected within a wetland in the region (Tarr, 2000). Amphibian larvae were identified in the field where possible. Individuals that we could not identify in the field were preserved in 10% buffered formalin and later identified to species in the laboratory using appropriate keys (Orton, 1939; Altig, 1970; Travis, 1981). For the red-spotted newt (*Notophthalmus viridescens*) the presence of adults and larvae were recorded, since *N. viridescens* typically use a single aquatic habitat throughout adulthood (Albert and Albert-Knopp, 1999), and thus the presence of adults is a likely indicator that a wetland is used for breeding.

Amphibian survival and distribution can be influenced by pH (Freda and Dunson, 1986), ion concentrations (Rowe and Dunson, 1993; Turtle, 2000), and temperature (Seale, 1982). Thus, measurements of pH, conductivity, and temperature were taken within each microhabitat. Calibrated, portable meters (Orion model 230A pH and Orion model 128 conductivity) were used to measure these abiotic factors. Although predatory fish are known to influence the distribution of pond-breeding amphibians, we did not determine fish presence. Dipnet sampling is a rapid sampling technique, which allowed us to sample numerous wetland habitats over a short period; however, this was not expected to be an effective sampling method for determining the presence of predatory fish (particularly larger species). Moreover, working in the same area, Babbitt et al. (2003) found that, among permanent wetlands, predatory fish did not influence larval amphibian species richness.

2.3. GIS methods

All GIS analyses were conducted using ArcInfo software (ESRI Inc., 1999). Black and white USGS National Aerial Photography Program 1:40,000 photos of the study area (taken in 1996) were used to delineate forest vs. non-forest, and were digitized into the GIS. Other GIS layers (National Wetlands Inventory, hydrology, roads and railroads) were obtained from the University of New Hampshire Complex Systems GRANIT database.

The size of each wetland was computed from the GIS. Seven buffers were generated around each study wetland, encompassing 0–100, 0–250, 0–500, 0–750, 0–1000, and 0–2000 m from the wetland. These buffers were chosen to represent incremental distances covering the range of published migration distances for amphibians in the northeastern United States (Healy, 1975; Gill, 1978; Ber-ven and Grudzien, 1990; Dodd, 1996; Madison, 1997; Semlitsch, 1998; Lamoureaux and Madison, 1999). Buffer rings were also measured and analyzed. Each buffer ring included the land between the edge of one buffer and the edge of the next smallest buffer (i.e., 0–100, 100–250, 250–500, 500–750, 750–1000, 1000–1500, and 1500–2000 m). Measuring forest cover in buffers and buffer rings allowed us to examine the extent to which buffers were correlated. For example, by examining amphibian response to forest cover in buffer rings of 0–100, and 100–250 m, we were able to determine if a significant amphibian response at the 250 m buffer was dependent on the response at the 100 m buffer. Within each buffer and buffer ring we measured the percent area covered by forest, the percent areas covered by wetlands, and the density of rivers and roads (meters per square meter of area) using the GIS. For wetlands, we included the percent of the area covered by wetlands of hydrologic regime other than temporarily flooded, saturated, or seasonally flooded (because these three wetland classes did not hold water through the first sampling period in the spring which followed a flood period). We included river densities in the analyses because some of the wetlands were located adjacent to rivers, whereas others were a considerable distance away, and we considered it possible that these high-volume, fast-flowing rivers could create a migration barrier to amphibians and could mask other landscape influences.

2.4. Data analyses

Data for 1998 and 1999 were combined in all analyses. Unusually wet weather in 1998 and a very dry season in 1999 may have eliminated certain species that normally breed in these wetlands; combining the two years of data reduced the influence of weather patterns on amphibian data. Total counts for each amphibian species were divided by the number of dipnet sweeps

taken in each wetland. This yielded an average number of individuals for each species per sweep (i.e., 1 m²) for the two years combined. We performed Spearman's rank correlations on wetland characteristics (wetland size, pH, conductivity, dissolved oxygen, depth, and temperature) and landscape characteristics (% forest cover, % wetlands, river density and road density for each buffer circle and buffer ring) to determine if strong relationships existed between these variables. Moreover, we determined whether wetland abiotic variables differed between temporary and permanent wetlands using non-parametric Mann–Whitney tests.

We used Generalized Linear Models (GLMs, McCullagh and Nelder, 1989) to determine which landscape and wetland variables had the greatest influence on amphibian species richness and individual species density estimates. We used individual species densities because such data may reveal relationships masked by simply analyzing species presence/absence (Guerry and Hunter, 2002). Generalized Linear Models present a major advantage over classical multiple regression approaches in that they integrate data from different statistical distributions with the appropriate modeling of statistical error (e.g., normal as in multiple regression, binomial for presence/absence data, ordinal for classes of abundance, poisson or negative binomial for species or individual counts). Amphibian species richness was analyzed using a normal response distribution with a canonical-link function, whereas individual species densities were best represented by a poisson regression and logarithmic-link function (McCullagh and Nelder, 1989). Road density and the proportion of forest cover were strongly correlated ($r > 0.6$) at buffer distances greater than 750 m. Thus for buffer distances >750 m the predictor variable forest cover represented a forest cover–road density covariate. It was necessary to construct separate models for each buffer circle and buffer ring to avoid collinearity. Exploratory univariate GLMs were first run to assess the importance of all predictors (i.e., hydroperiod category, water temperature, conductivity, pH, % forest cover, % wetlands, river density, and road density) for each buffer circle and buffer ring. The final models included non-collinear variables with significant ($P < 0.05$) deviance reduction (explained variance) values as determined by a χ^2 -test. Where necessary, we used a bonferroni-adjusted significance level to account for multiple testing. All statistical procedures were analyzed using SAS 8.0 (2001).

3. Results

3.1. Amphibian richness and density estimates

Nine species totaling 16,784 individuals (15,733 larval anurans and 1051 caudates) were captured during 1998

and 1999. Species richness among wetlands ranged from zero to six (4.03 ± 0.20 S.E.). The green frog (*Rana clamitans*) was the most ubiquitous species, occurring in 84% of the sites, followed by *N. viridescens*, which was found in 72% of the study wetlands. Other common species were the spring peeper (*Pseudacris crucifer*; 64% of sites), spotted salamander (*Ambystoma maculatum*; 56% of sites), wood frog (*Rana sylvatica*; 49% of sites), and the gray treefrog (*Hyla versicolor*; 41% of sites). American toads (*Bufo americanus*), and pickerel frogs (*Rana palustris*) were captured infrequently, both with tadpoles present in only six sites. Because these two species were encountered in so few wetlands, we did not perform any statistical analyses on them. The northern leopard frog (*Rana pipiens*), blue-spotted salamander (*Ambystoma laterale*), Jefferson's salamander (*Ambystoma jeffersonianum*), and hybrid *A. laterale* \times *jeffersonianum* were not captured despite being present (though not common) in the region. Mean amphibian density within wetlands was 2.25 ± 0.416 m² and ranged from 0.017 to 18.68 m². The most abundant species were *R. clamitans* (1.12 ± 0.019 m²) and *R. sylvatica* (0.561 ± 0.177 m²), whereas the least abundant species was *R. palustris* (0.0243 ± 0.012 m²).

3.2. Landscape and wetland characteristics

Landscape variable measurements varied little among buffer distances. Percent forest averaged 73.6% and ranged from 23.4% to 99.4% within a 1 km radius of each wetland. Road density varied from 0 to 0.016 m/m² within the seven buffers, with most of the zero values in the smaller buffers, particularly the 100 m buffer. The farther a buffer extended from the wetland, the greater was the chance of encountering at least a small segment of road. There was a negative correlation ($r < -0.6$) at distances of 750 m or larger between road density and the proportion of forest. As buffer distances increased, the mean % wetland habitat steadily decreased from 11.9% to 5.3%. River density ranged from 0 to 0.0082 m/m², with the widest range occurring within 100 m. At larger buffer distances, there were fewer wetlands lacking rivers within the buffer.

Wetland abiotic characteristics differed markedly among wetlands. Mean pH was 6.19 ± 0.07 (range 4.39–7.19), mean wetland temperature was 21.6 ± 3.9 °C (range 15.0–26.9 °C), and mean wetland conductivity was 138.14 ± 20.15 μ S (range 18.45–733.9 μ S). Of the 61 wetlands, 36 were permanent and 25 were temporary (all temporary wetlands had hydroperiods greater than four months). Conductivity ($U = 7.05$, $P = 0.008$), pH ($U = 7.28$, $P = 0.007$), and temperature ($U = 3.95$, $P = 0.046$) were significantly lower in temporary wetlands, whereas wetland size did not differ between hydroperiod categories ($U = 1.67$, $P = 0.197$).

3.3. Amphibian assemblage and environmental variables

Based on GLMs, amphibian species richness did not differ between permanent and temporary wetlands ($\chi^2 = 1.23$, $P = 0.46$), and densities of only two species differed significantly between wetland types (Fig. 2). *R. sylvatica* was found in higher densities in temporary wetlands ($\chi^2 = 11.84$, $P = < 0.001$), whereas *N. viridescens* attained higher densities in permanent wetlands ($\chi^2 = 5.99$, $P = 0.015$).

Species richness was most strongly associated with the proportion of forest cover within 1000 m of the wetland (Table 1). The proportion of forest cover within 100 m of a wetland had little influence on species richness, but influence of forest cover on species richness was relatively high for buffer rings between 100 and 1000 m (Fig. 3(a)). Species richness was low in wetlands surrounded by less than 40% forest cover (Fig. 4(a)). Of the seven species analyzed, four were significantly influenced by the proportion of forest cover within at least

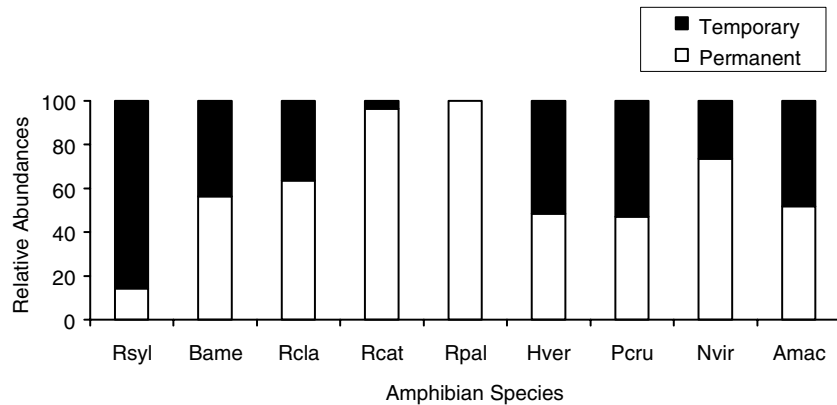


Fig. 2. Mean species richness (a) and relative abundance (%) of each species (c) in temporary and permanent wetlands in southern and central New Hampshire in 1998 and 1999: Rsyl, *R. sylvatica*; Bame, *B. americanus*; Rcla, *R. clamitans*; Rpal, *R. palustris*; Hver, *H. versicolor*; Percu, *P. crucifer*; Nvir, *N. viridescens*; Amac, *A. maculatum*.

Table 1

Generalized Linear Models showing the most important variables influencing amphibian assemblages (species richness, and species densities) in southern and central New Hampshire in 1998 and 1999

Dependent variable	Independent variable	Model deviance (%)	χ^2	P-value
Species richness	Forest 500 m	6.3	3.93	0.047
	Forest 750 m	6.4	4.06	0.044
	Forest 1000 m	6.8	5.10	0.024
<i>Rana sylvatica</i>	Hydroperiod	20.8	11.84	<0.001*
<i>Rana catesbeiana</i>	Hydroperiod	24.7	3.53	0.060
	Forest 1000 m		4.54	0.033
<i>Pseudacris crucifer</i>	Wetland size	17.7	8.19	0.004*
	Forest 1000 m		6.36	0.012
<i>Notophthalmus viridescens</i>	Hydroperiod	22.2	5.99	0.015
	Forest 250 m		7.46	0.005
	Hydroperiod	22.9	5.91	0.015
	Forest 500 m		7.46	0.006
	Hydroperiod	19.4	5.64	0.018
	Forest 750 m		5.93	0.015
	Hydroperiod	20.4	6.20	0.013
	Forest 1000 m		6.46	0.011
	Hydroperiod	17.5	6.63	0.010
<i>Ambystoma maculatum</i>	Forest 1500 m		4.85	0.028
	Forest 250 m	12.4	6.63	0.010
	Forest 1000 m	10.6	5.40	0.020

Models shown exhibited the highest deviance (explained variance) value and thus indicate the most important variables including the buffer zone with the strongest influence on each particular amphibian parameter. Bold denotes strongest response to buffer for each respective dependent variable.

Note: *Rana palustris* and *Bufo americanus* were not analyzed due to inadequate sample sizes.

* Denotes significance at the bonferroni adjusted alpha level.

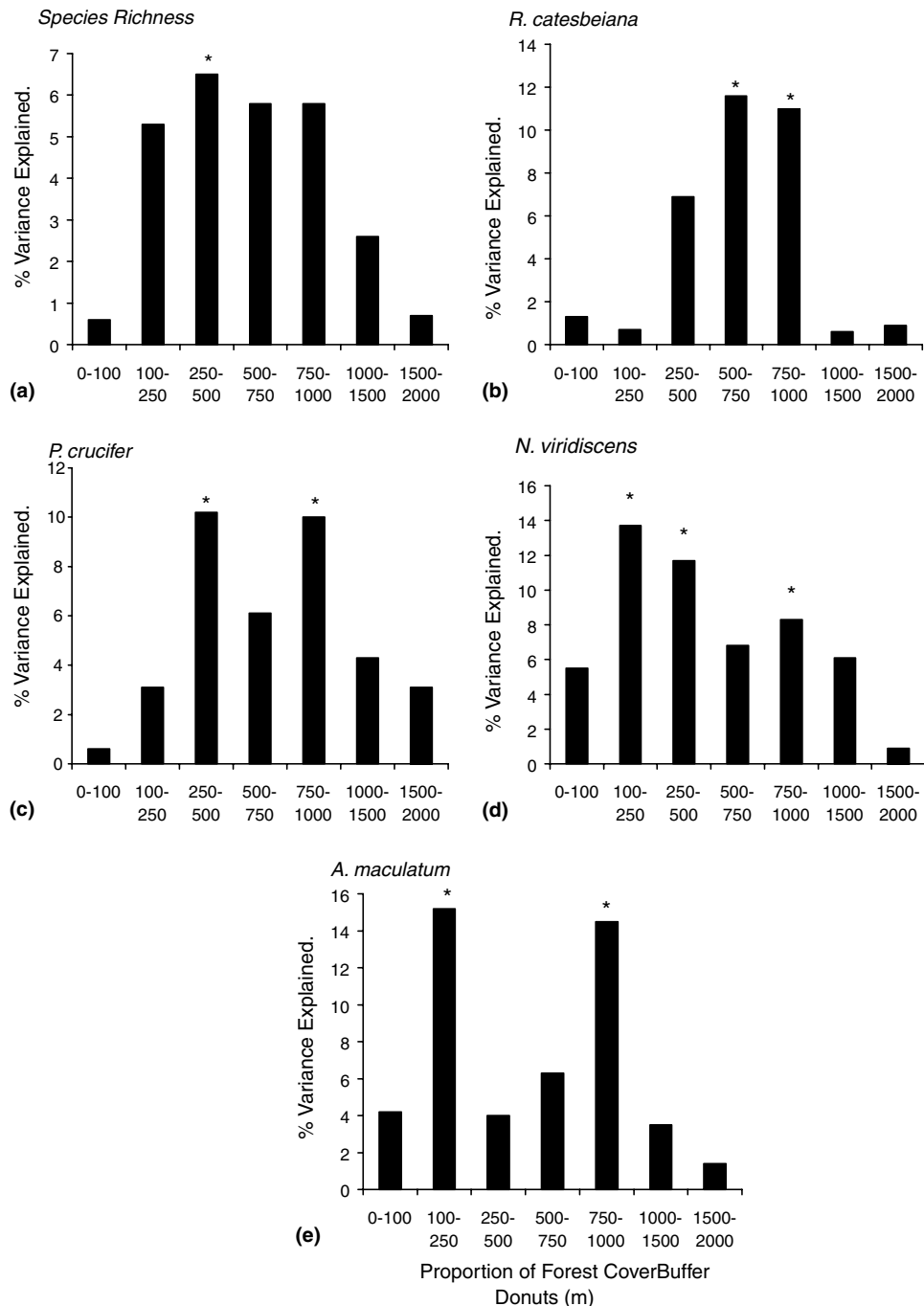


Fig. 3. The relationship between species richness (a), and species densities (b–e) and the proportion of forest cover in each buffer ring. The strength of the relationship is indicated by the % explained variance for each buffer ring (based on Generalized Linear Models). * $P < 0.05$. No relationships were significant after a bonferroni adjustment for multiple significance testing.

one buffer circle (Table 1) and one buffer ring (Fig. 3(b)–(e)). For the four species significantly influenced by forest cover, all showed a similar pattern to species richness in that the buffer rings (Fig. 3(b)–(e)) with the strongest influences tended to be at intermediate distances from the wetland (100–1000 m). Conversely, the proportion of forest cover in the 0–100 m and 1000–2000 m rings generally had little influence on amphibians. Most spe-

cies were influenced by the proportion of forest cover (Fig. 4(b)–(i)) and the species most strongly influenced by this variable were *N. viridescens* and *A. maculatum*. Both these species attained their highest densities when the surrounding forest cover was greater than 80% (Fig. 4(h) and (i)). Furthermore, *R. sylvatica* and *R. clamitans* did not occur or were at extremely low densities in wetlands surrounded by less than 60% and 40%

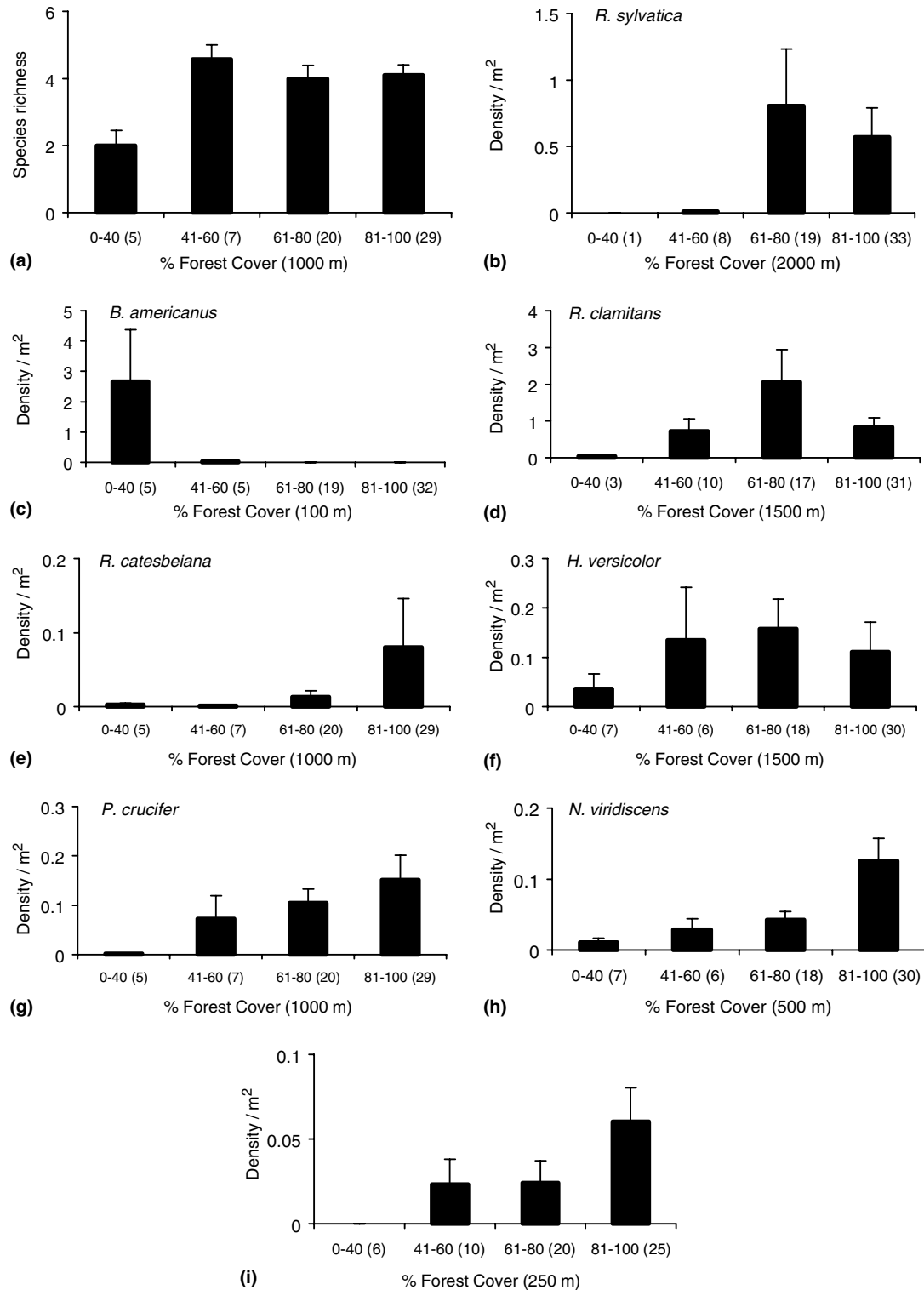


Fig. 4. Amphibian species richness (a), and species densities/m² (b–i) in wetlands that differ in the proportion of surrounding forest cover. Buffer distance used represented the buffer size that most influenced the respective amphibian parameter. Data were collected in southern and central New Hampshire in 1998 and 1999. * $P < 0.05$. The proportion of forest cover did not significantly influence any dependent variables after bonferroni adjustments for multiple testing.

cover, respectively (Fig. 4(b) and (d)), despite the fact that densities of these species were not significantly influenced by forest cover. Because road density was strongly

correlated with forest cover at buffer distances greater than 750 m, it is possible that road density concomitantly impacted amphibian assemblages at greater distances.

Other landscape variables measured (i.e., % wetlands and river density) had no significant effect on species richness or abundance of individual species.

4. Discussion

4.1. Landscape characteristics and amphibians

Our study suggests that ponds surrounded by >60% forest within a 1000 m radius may be necessary to support species rich amphibian assemblages and that ponds surrounded by <40% forest within a 1000 m radius generally contained depauperate larval amphibian assemblages in southern New Hampshire. Forested habitat is critical to many pond-breeding amphibians because the vegetation creates diverse habitats, provides shade, moderates temperature, retains moisture, and contributes to organic matter (Corn and Bury, 1991; Waldick, 1997; Naughton et al., 2000); although some amphibians are more likely to utilize non-forested habitats as adults (e.g., *B. americanus* and *R. pipiens*, Guerry and Hunter, 2002).

Despite finding significant influence of forest cover on larval amphibian species richness and species densities, the amount of variance explained was weak (6.8%). With a mean forest cover of 74%, our study area in south-central New Hampshire represents a more heavily forested landscape than found in similar studies that have examined the effects of landscape characteristics on amphibian assemblage structure (e.g., Hecnar and M'Closkey, 1996; Lehtinen et al., 1999; Kolozsvary and Swihart, 1999; Guerry and Hunter, 2002). It is unclear whether the low explanatory power of forest cover in this dataset may be attributed to the relatively high availability of forested habitat in the landscape, or other processes not measured in this study, such as variation among wetlands in forest structure, biotic interactions (e.g., predator composition or competition), or the use of density estimates instead of species presence. Other researchers have also documented that landscape variables alone account for a relatively small percentage of the statistical variation (<35%) in their data sets (Bonin et al., 1997; Hecnar, 1997; Knutson et al., 1999).

Amphibian species richness was most strongly influenced by the proportion of surrounding forest within a 1000 m radius of the wetland; however, there were some differences among species in the scale of response. *N. viridiscens* was most strongly associated with forest within 500 m (but up to 1000 m), and *A. maculatum* was most strongly associated with forest within 250 m (but up to 1000 m) of the wetland. These distances are generally larger than the reported migration distances for *A. maculatum* (Douglas and Monroe, 1981; Kleeberger and Werner, 1983; Madison, 1997), and *N. viridiscens* (Gill, 1978). Our findings are generally similar to Guerry and Hunter (2002) based on larval amphibian assem-

blages in northeastern Maine, where the proportion of forest cover is $\approx 50\%$.

In addition to differences in the spatial scale of response, amphibian species also varied in their sensitivity to forest attributes and responded to critical forest cover thresholds, below which they were absent from wetlands or at extremely low densities. Conversely, Guerry and Hunter (2002) failed to find critical forest cover thresholds for all but one species (*N. viridiscens*), but they partially attribute this to their use of presence-absence data, which may mask relationships. In the current study, *A. maculatum* did not occur in the 6 wetlands with less than 40% cover (within a 250 m radius) and occurred at lower densities in wetlands with (<80%) forest cover. Similarly, Guerry and Hunter (2002) found the presence of *A. maculatum* was influenced by the amount of forest area around a wetland. This species is generally considered susceptible to forest fragmentation (deMaynadier and Hunter, 1998; Madison and Farrand, 1998; Guerry and Hunter, 2002). Neither Gibbs (1998b) nor Guerry and Hunter (2002) found *N. viridiscens* in ponds surrounded by less than 50% forest. In this study, *N. viridiscens* occurred at low densities when surrounding forest cover (within 500 m) was <80%. Gibbs (1998b) found that *N. viridiscens* behaviorally avoid forest edge habitats, which may help explain the response of this species to forest fragmentation (Gibbs, 1998b; Guerry and Hunter, 2002). Overall, our study supports previous research, which has shown that high forest cover is associated with higher herpetofaunal richness (Findlay and Houlihan, 1997), amphibian species richness (Hecnar and M'Closkey, 1996), and presence and density of *A. maculatum* (Hecnar and M'Closkey, 1996; deMaynadier and Hunter, 1998; Guerry and Hunter, 2002) and *N. viridiscens* (Hecnar and M'Closkey, 1996; Gibbs, 1998b; Guerry and Hunter, 2002).

Road density did not appear to influence amphibian species richness and density estimates at smaller scales; however, because this variable was strongly correlated with forest cover at larger scales (>750 m), it was difficult to statistically interpret the effect of roads on amphibians. Nevertheless, a growing body of work suggests that roads negatively affect amphibian persistence through mortality and fragmentation of populations (Fahrig et al., 1995; Findlay and Houlihan, 1997; Vos and Chardon, 1998; Carr and Fahrig, 2001). Studies suggest that roads can negatively influence amphibians up to 2 km from breeding sites (Findlay and Houlihan, 1997; Vos and Chardon, 1998; Carr and Fahrig, 2001).

4.2. Wetland characteristics and amphibians

Amphibian assemblages often differ across the hydrologic gradient in relation to species-specific adaptations for avoiding desiccation risk in temporary aquatic hab-

itats or predation risk in more permanent aquatic habitats (reviewed in Wellborn et al., 1996; Babbitt et al., 2003). Although landscape characteristics predominately influenced larval amphibian species richness, wetland characteristics had a stronger influence on species density estimates. Most notably, *R. sylvatica* dominated temporary wetlands, whereas *R. clamitans* dominated permanent wetlands. Moreover, *R. palustris*, *R. catesbeiana* and *N. viridescens* were more likely to occur in permanent wetlands. This highlights the importance of factoring in amphibian compositional differences between temporary and permanent wetlands in wetland protection conservation initiatives (Babbitt et al., 2003). Moreover, wetlands surrounded predominately by forest were more likely to have temporary hydroperiods than wetlands surrounded by lower proportions of forested habitat, which may be due to the loss (i.e., filling) of smaller temporary wetlands to development. Thus, anthropogenic landscape changes may also impact amphibian assemblages by acting directly on wetland hydroperiod and possibly associated changes in wetland characteristics (e.g., temperature and pH) (Babbitt et al., 2003).

4.3. Management implications

Increasingly, focus has been placed on the protection of isolated wetlands (particularly seasonally inundated wetlands) in recognition of their importance to the ecological integrity of forested landscapes. Because the quality of habitat surrounding breeding wetlands is important to most amphibians, it is necessary to consider the surrounding upland landscape in conservation strategies. Although many state and federal policies have resulted in the regulation of impacts to wetlands and hydric soils, they have not extended adequate protection to surrounding terrestrial areas (Semlitsch, 1998; Semlitsch and Bodie, 1998). For example, New Hampshire requires only a 50-foot (15.25 m) buffer around wetlands with hydric B (poorly drained) soils, and a 75-foot (22.88 m) buffer around wetlands with hydric A (very poorly drained) soils for activities involving wastewater disposal (Chase et al., 1995). A buffer of 100 feet (30.5 m) is recommended but not required for wildlife and water quality (Chase et al., 1995).

Based on published studies of Ambystomatid salamanders, Semlitsch (1998) recommended a buffer zone of 164 m, which is likely to encompass 95% of the population of some salamanders. Dodd (1996) found that 82.9% of amphibians captured were within 600 m of the nearest potential breeding site in northern Florida. Burke and Gibbons (1995) found that only 44% of mud turtle (*Kinosternon subrubrum*) nest sites in a South Carolina wetland were within a 30.5 m buffer around the wetland, and all of the nest sites were outside of the federally delineated wetland boundary.

Interestingly, our findings suggest that neither amphibian richness nor individual species densities were strongly influenced by the degree of disturbance (forest cover) within 100 m of wetlands. Thus, rather than a conservation strategy that focuses on exclusive protection of upland habitats immediately surrounding wetlands (e.g., 164 m, Semlitsch, 1998), it may be better to focus on protecting a large proportion of suitable upland habitat within a larger area. Furthermore, the concept of buffer zones may not safeguard amphibian metapopulation processes (Semlitsch, 1998; Marsh and Trenham, 2001). Amphibians may rely heavily on metapopulation dynamics (Hanski and Gilpin, 1991) and long-term persistence in the landscape may be driven largely by inter-wetland dispersal, colonization and recolonization (Sjögren, 1991; Marsh and Trenham, 2001).

When choosing wetlands that warrant protection, sites surrounded by a high degree of forest and low densities of roads should be given preference (Semlitsch, 2000). Amphibian assemblages may be able to tolerate some landscape alteration within the protected area, as long as a high percentage of forest is retained overall. We propose maintaining a matrix of suitable upland and wetland habitat, with a spatial configuration that emphasizes wetland connectivity and upland-wetland linkages. In the northeastern United States, to be most effective, this matrix should extend at least to a distance beyond breeding wetlands that is compatible with the scale of amphibian response (1000 m) (Guerry and Hunter, 2002, this study). Finally, efforts must be taken to ensure that smaller buffer zones immediately surrounding the wetland are protected to avoid direct impacts to the wetland itself.

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References

- Albert, E.H., Albert-Knopp, H., 1999. Eastern newt, *Notophthalmus viridescens*. In: Hunter, Jr., M.L., Calhoun, A.J.K., McCollough,

- M. (Eds.), Maine Amphibians and Reptiles. University of Maine Press, Orono, ME, USA, pp. 49–52.
- Altig, R., 1970. A key to the tadpoles of the continental United States and Canada. *Herpetologica* 26, 180–207.
- Babbitt, K.J., Baber, M.J., Tarr, T.L., 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. *Canadian Journal of Zoology* 81, 1539–1552.
- Beebee, T.J.C., 1997. Changes in dewpond numbers and amphibian diversity over 20 years on chalk Downland in Sussex, England. *Biological Conservation* 81, 215–219.
- Beltz, R.C., Cost, N.D., Kingsley, N.P., Peters, R.J., 1992. Timber volume distribution maps for the Eastern United States. General Technical Report WO-60. U.S. Forest Service, Washington, DC.
- Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44, 2047–2056.
- Blaustein, A.R., Wake, D., Sousa, W.P., 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8, 60–71.
- Bonin, J., DesGranges, J.L., Rodrigue, J., Ouellet, M., 1997. Anuran species richness in agricultural landscapes of Quebec. Foreseeing long-term results of road call surveys. In: Green, D.M. (Ed.), *Amphibians in Decline; Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St Louis, Missouri, USA, pp. 141–149.
- Bunnell, J.F., Zampella, R.A., 1999. Acid water anuran communities along a regional forest to agro-urban ecotone. *Copeia* 1999, 614–627.
- Burke, V.J., Gibbons, J.W., 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. *Conservation Biology* 9, 1365–1369.
- Carey, C., Cohen, N., Rollins-Smith, L., 1999. Amphibian declines: an immunological perspective. *Developmental and Comparative Immunology* 23, 459–472.
- Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15, 1071–1078.
- Chase, V.P., Deming, L.S., Latawiec, F., 1995. *Buffers for Wetlands and Surface Waters: a Guidebook for New Hampshire Municipalities*. Audubon Society of New Hampshire, Concord, New Hampshire, USA.
- Corn, P.S., Bury, R.B., 1991. Logging in western Oregon: responses of headwater habitat and stream amphibians. *Forest Ecology and Management* 29, 39–67.
- Cowardin, L.M., Carter, V., Golet, F.C., LaRoe, E.T., 1979. *Classification of Wetlands and Deepwater Habitats of the United States*. U.S. Fish and Wildlife Service, Washington, DC.
- deMaynadier, P.G., Hunter Jr., M.L., 1998. Effects of silvicultural edges on the distribution and density of amphibians in Maine. *Conservation Biology* 12, 340–352.
- Dodd, C.K., 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. *Alytes* 14, 42–52.
- Douglas, M.E., Monroe Jr., B.L., 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). *Copeia* 1981, 460–463.
- ESRI Inc., 1999. ArcInfo User's Manual, Version 7.2.1. Environmental Systems Research Institute Inc., Redlands, CA, USA.
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73, 177–182.
- Findlay, C.S., Houlahan, J., 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* 11, 1000–1009.
- Freda, J., Dunson, W.A., 1986. Effects of low pH and other chemical variables on the local distribution of amphibians. *Copeia* 1986, 454–466.
- Gibbs, J.P., 1998a. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62, 584–589.
- Gibbs, J.P., 1998b. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* 13, 263–268.
- Gill, D.E., 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48, 145–166.
- Guerry, A.D., Hunter Jr., M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16, 745–754.
- Hanski, I., Gilpin, M.E., 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42, 3–16.
- Healy, W.R., 1975. Breeding and postlarval migrations of the red-spotted newt, *Notophthalmus viridescens*, in Massachusetts. *Ecology* 56, 673–680.
- Hecnar, S.J., 1997. Amphibian pond communities in southwestern Ontario. In: Green, D.M. (Ed.), *Amphibians in Decline; Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St Louis, Missouri, USA, pp. 1–15.
- Hecnar, S.J., M'Closkey, R.T., 1996. Regional dynamics and the status of amphibians. *Ecology* 77, 2091–2097.
- Kleeberger, S.R., Werner, J.K., 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. *Journal of Herpetology* 17, 176–177.
- Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., Lannoo, M.J., 1999. Effects of landscape composition and wetland fragmentation on frog and toad density and species richness in Iowa and Wisconsin, USA. *Conservation Biology* 13, 1437–1446.
- Kolozsvary, M.B., Swihart, R.K., 1999. Habitat fragmentation and the distribution of amphibians: patch and landscape correlates in farmland. *Canadian Journal of Zoology* 77, 1288–1299.
- Laan, R., Verboom, B., 1990. Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54, 251–262.
- Lamoureaux, V.S., Madison, D.M., 1999. Overwintering habitats of radio-implanted green frogs, *Rana clamitans*. *Journal of Herpetology* 33, 430–435.
- Lehtinen, R.M., Galatowitsch, S.M., Tester, J.R., 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* 19, 1–12.
- Lips, K.R., 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* 12, 106–117.
- Lips, K.R., 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology* 13, 117–125.
- Litvatis, J.A., 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* 7, 866–873.
- Madison, D.M., 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31, 542–551.
- Madison, D.M., Farrand III, L., 1998. Habitat use during breeding and emigration in radio-implanted tiger salamanders, *Ambystoma tigrinum*. *Copeia* 1998, 402–410.
- Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15, 40–49.
- McCullagh, P., Nelder, J.A., 1989. *Generalized linear models*, second ed. Chapman & Hall, London.
- Naughton, G.P., Henderson, C.B., Foresman, K.R., McGraw, R.L., 2000. Long-toed salamanders in harvested and intact Douglas-fir forests of western Montana. *Ecological Applications* 10, 1681–1689.
- Orser, P.N., Shure, D.J., 1972. Effects of urbanization on the salamander *Desmognathus fuscus*. *Ecology* 53, 1148–1154.
- Orton, G., 1939. Key to New Hampshire amphibian larvae. In: Warfel, H.E. (Ed.), *Biological Survey of the Connecticut Watershed*. New Hampshire Fish and Game Department, Concord, New Hampshire, USA, pp. 218–219.

- Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54, 239–249.
- Richter, K.O., Azous, A.L., 1995. Amphibian occurrence and wetland characteristics in the Puget Sound Basin. *Wetlands* 15, 305–312.
- Rowe, C.L., Dunson, W.A., 1993. Relationships among abiotic parameters and breeding effort by three amphibians in temporary wetlands of central Pennsylvania. *Wetlands* 13, 237–246.
- SAS 2001. SAS/STAT Software, Version 8 Edition. SAS Institute, Cary, NC, USA.
- Seale, D.B., 1982. Physical factors influencing oviposition by the wood frog, *Rana sylvatica*, in Pennsylvania. *Copeia* 1982, 627–635.
- Semlitsch, R.D., 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12, 1113–1119.
- Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64, 615–631.
- Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable?. *Conservation Biology* 12, 1129–1133.
- Sjögren, P., 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42, 135–147.
- Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80, 2326–2337.
- Tarr, T.L., 2000. Patterns of Larval Amphibian and Aquatic Insect Distribution: Effects of Hydroperiod. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.
- Thorne, S., Sunquist, D., 2001. New Hampshire's Vanishing Forests: Conversion, Fragmentation and Parcelization of Forests in the Granite State/Report of the New Hampshire Forest Land Base Study. Society for the Protection of New Hampshire Forests, Concord, New Hampshire, USA.
- Travis, J., 1981. A key to the tadpoles of North Carolina. *Brimleyana* 6, 119–127.
- Turtle, S.L., 2000. Embryonic survivorship of the spotted salamander (*Ambystoma maculatum*) in roadside and woodland vernal pools in southeastern New Hampshire. *Journal of Herpetology* 34, 60–67.
- Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* 35, 44–56.
- Vos, C.C., Stumpel, A.H.P., 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the treefrog (*Hyla arborea*). *Landscape Ecology* 11, 203–214.
- Wake, D., 1998. Action on amphibians. *Trends-in-Ecology-and-Evolution* 13, 379–380.
- Waldick, R., 1997. The impact of forestry practices upon amphibian populations in eastern North American. In: Green, D.M. (Ed.), *Amphibians in Decline: Canadian Studies of a Global Problem*. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri, USA, pp. 191–205.
- Wellborn, G.A., Skelly, D.K., Werner, E.E., 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27, 337–363.