
A Resistant-Kernel Model of Connectivity for Amphibians that Breed in Vernal Pools

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Abstract: Pool-breeding amphibian populations operate at multiple scales, from the individual pool to surrounding upland habitat to clusters of pools. When metapopulation dynamics play a role in long-term viability, conservation efforts limited to the protection of individual pools or even pools with associated upland habitat may be ineffective over the long term if connectivity among pools is not maintained. Connectivity becomes especially important and difficult to assess in regions where suburban sprawl is rapidly increasing land development, road density, and traffic rates. We developed a model of connectivity among vernal pools for the four ambystomatid salamanders that occur in Massachusetts and applied it to the nearly 30,000 potential ephemeral wetlands across the state. The model was based on a modification of the kernel estimator (a density estimator commonly used in home range studies) that takes landscape resistance into account. The model was parameterized with empirical migration distances for spotted salamanders (*Ambystoma maculatum*), dispersal distances for marbled salamanders (*A. opacum*), and expert-derived estimates of landscape resistance. The model ranked vernal pools in Massachusetts by local, neighborhood, and regional connectivity and by an integrated measure of connectivity, both statewide and within ecoregions. The most functionally connected pool complexes occurred in southeastern and northeastern Massachusetts, areas with rapidly increasing suburban development. In a sensitivity analysis estimates of pool connectivity were relatively insensitive to uncertainty in parameter estimates, especially at the local and neighborhood scales. Our connectivity model could be used to prioritize conservation efforts for vernal-pool amphibian populations at broader scales than traditional pool-based approaches.

Keywords: Ambystomatidae, *Ambystoma opacum*, *Ambystoma maculatum*, amphibian conservation, metapopulation, pond-breeding amphibian, resistant-kernel model, seasonal pond, vernal pool

Un Modelo de Núcleo Resistente de la Conectividad para Anfibios que se Reproducen en Charcos Vernales

Resumen: Las poblaciones de anfibios que se reproducen en charcos operan en escalas múltiples, del charco individual al hábitat circundante al grupo de charcos. Cuando la dinámica de la metapoblación juega un papel en la viabilidad a largo plazo, los esfuerzos de conservación limitados a la protección de charcos individuales o aun charcos asociados con hábitat circundante pueden ser inefectivos a largo plazo si no se mantiene la conectividad entre charcos. La conectividad se vuelve especialmente importante y difícil de evaluar en regiones donde la expansión urbana esta incrementando rápidamente el desarrollo de tierras, la densidad de caminos y las tasas de tráfico. Desarrollamos un modelo de conectividad entre charcos vernaes para las cuatro especies de salamandras ambystomoideas que ocurren en Massachusetts y lo aplicamos a los casi 30,000 potenciales humedales efímeros en el estado. El modelo se basó en una modificación del estimador de núcleo (un estimador de densidad utilizado comúnmente en estudios de rango de hogar) que toma en consideración la resistencia del paisaje. El modelo fue parametrizado con distancias de migración empíricas para *Ambystoma maculatum*, distancias de dispersión para *A. opacum* y de la resistencia del paisaje derivada de estimaciones por expertos. El modelo clasificó los charcos vernaes en Massachusetts por la conectividad local,

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vecinal y regional y por una medida integrada de la conectividad, tanto estatal como dentro de ecoregiones. Los complejos de charcos más conectados funcionalmente ocurrieron en el sureste y noreste de Massachusetts, que son áreas con desarrollo suburbano en rápida expansión. Mediante análisis de sensibilidad, las estimaciones de la conectividad de charcos fueron relativamente insensibles a la incertidumbre en la estimación de los parámetros, especialmente en las escalas local y vecinal. Nuestro modelo de conectividad podría ser utilizado para priorizar los esfuerzos de conservación de poblaciones de anfibios de charcos vernaes a escalas más amplias que las basadas tradicionalmente en charcos individuales.

Palabras Clave: Ambystomatidae, *Ambystoma opacum*, *Ambystoma maculatum*, anfibios que se reproducen en charcos, charcos vernaes, conservación de anfibios, metapoblación, modelo de núcleo resistente

Introduction

Conservation of vernal-pool amphibians must account for the multiple spatial scales of population dynamics. Vernal-pool amphibians such as the ambystomatid salamanders typically exist in local populations associated with discrete breeding pools. With low dispersal rates and the potential for asynchronous dynamics among local populations, metapopulation dynamics may play an important role in long-term population persistence (Semlitsch 2003; Gamble 2004; Smith & Green 2005). Conservation efforts limited to the protection of individual pools or even pools with associated upland habitat may be ineffective over the long term if connectivity among pools is not maintained (e.g., due to the loss of individual wetlands or because of intervening roads or development; Gibbs 1993; Gibbs & Shriver 2005). Nevertheless, broad-scale efforts to address pool connectivity can be complicated because of the large number of ephemeral wetlands in a region and the difficulty of prioritizing pools and surrounding uplands for conservation.

Vernal pools in eastern North America support diverse faunal communities. These small fishless wetlands provide habitat for many obligate invertebrates and amphibians, including ambystomatid salamanders (Colburn 2004). Conservation of vernal pools has usually focused on protecting pool basins themselves, often with small terrestrial buffers. Although this strategy may accommodate flying or wind-dispersed invertebrates, it is inadequate for vernal-pool amphibians, which spend most of their lives in uplands and must disperse overland (Semlitsch 1998; Gamble et al. 2006). In Massachusetts conservation concern is focused on salamanders in the family Ambystomatidae, including marbled salamanders (*Ambystoma opacum*), spotted salamanders (*A. maculatum*), Jefferson's salamanders (*A. jeffersonianum*), blue-spotted salamanders (*A. laterale*), and a number of clonal lineages of *A. jeffersonianum* × *A. laterale* hybrids. At the state level the marbled salamander is listed as threatened and Jefferson's and blue-spotted salamanders are listed as special concern (Kenney & Burne 2000). All four of these species breed in vernal pools, which support the egg and larval life stages, but upland forests provide habitat for juveniles and adults.

Population dynamics of vernal-pool amphibians may be evaluated at four discernable ecological scales: (1) the breeding pool or basin, (2) the breeding pool with surrounding upland habitat, (3) neighboring pools and upland habitat, and (4) clusters (groups of groups) of pools in a broader regional framework. The pool itself is likely a primary determinant of population size and stability. Because adults exhibit high breeding-site fidelity (Whitford & Vinegar 1966; Pechmann et al. 1991; L.R.G., unpublished data), each vernal pool generally supports a distinct breeding population. Pools vary in habitat quality, supporting populations that vary widely among pools and across years (Pechmann et al. 1991; Skelly et al. 1999). Pool hydroperiod seems to be the most important variable structuring vernal-pool communities (Semlitsch et al. 1996; Skelly et al. 1999; Snodgrass et al. 2000; Colburn 2004).

The second scale is the pool with its surrounding upland habitat, or the "life zone" (Semlitsch 1998). Ambystomatids spend 90–95% of their lives in upland forests, up to several hundred meters from breeding pools (Semlitsch 1998), and upland habitat may overlap for several breeding pools. Clearly, protecting pools without this upland habitat does little for even the short-term persistence of populations. Although the details of upland habitat use is an area of active research (e.g., see Madison & Farrand 1998; Faccio 2003; Regosin et al. 2003; McDonough-Haughley & Paton 2007), a reasonable surrogate for the availability of upland habitat is simply the amount of forested area surrounding a pool that is accessible to individual salamanders (e.g., not across a major road; Guerry & Hunter 2002; Homan et al. 2004).

At a third scale, connectivity among populations represents the degree to which dispersal may support metapopulation processes. If dispersal (defined as demographic and genetic exchange among populations, as opposed to migration, which is annual upland movement within a population) among pool-centered populations is low but not zero, then pools and their surroundings represent discrete populations with the potential for occasional gene flow and demographic interactions (such as colonization and the rescue effect; Brown & Kodric-Brown 1977). If all populations have a high potential for extinction over time, and if these extinctions are

neither synchronized nor deterministic, then populations show metapopulation structure (Hanski & Gilpin 1991). Recent research on ambystomatid salamanders provides evidence for metapopulation structure in at least some populations (Gamble 2004; Smith & Green 2005; but see references in Marsh & Trenham 2001). If ambystomatids do generally operate in metapopulations, conservation at the scales of pool and local upland habitat is insufficient to ensure persistence over the long term because even in the absence of anthropogenic stressors, many (or even all) populations are expected to become extinct due to stochastic fluctuations over decades or centuries. If connectivity among pools is interrupted, natural dispersal that enables recolonization, rescue effects, and gene flow will not support metapopulation processes. Over long time periods connectivity takes place at even broader spatial scales because the contribution of dispersers from neighboring pools depends in part on how connected these pools are to more distant pools. Metapopulations in broader connected clusters may be more likely to persist than those in smaller clusters. Thus, regional connectivity is structured by the connectivity among clusters of pools at multiple spatial scales. For the sake of convenience, we lump these poorly understood broader scales into a fourth, broadly defined, "regional scale."

A number of strategies have been used to assess the functional connectivity (organism based, see Calabrese & Fagan 2004) of amphibian populations at one or more of these scales. For example, Ray et al. (2002) used a least-cost path approach to evaluate migratory connectivity ("local" scale) for the common toad (*Bufo bufo*) and the alpine newt (*Triturus alpestris*) for 127 ponds in Geneva, Switzerland. Their model showed some success in predicting presence and absence of toads across their study ponds. Rustigian et al. (2003) developed spatially explicit population models integrating multiple scales for four common amphibians in two Iowa watersheds. This approach allowed comparison of the effects of alternative land-use scenarios on populations of these species. In a third approach Pyke (2005) used graph theory to model linkages ("neighborhood" scale) among 122 wetlands used by the California tiger salamander (*A. californiense*) as part of a fuzzy-logic-based decision-support system for conservation action.

We present a modeling framework for assessing the three broader scales of connectivity. These scales are the most intractable to assess in the field; in fact, empirically assessing connectivity is unlikely to be feasible for more than a handful of pools in any region due to the costs and time required for mark-recapture or genetic studies. We applied our model to all four Massachusetts ambystomatids because of their relatively similar breeding and upland habitat associations. A new metric, the resistant-kernel estimator, is used to assess functional interpool connectivity at the neighborhood and regional scales, and a modification of this metric is used to assess connectiv-

ity of pools to local upland habitat. We used empirically based migration and dispersal parameters, expert-derived landscape resistance values, and statewide land-use coverages to rank almost 30,000 photointerpreted potential vernal pools in Massachusetts by their modeled level of connectivity at each scale. The resulting rank scores can be used to help identify vernal pools that have intact upland habitat and are highly connected across the landscape for groundtruthing and focused conservation action.

Methods

The resistant-kernel estimator is a hybrid between two existing approaches, the kernel estimator and least-cost paths with resistant surfaces. The kernel estimator (Silverman 1986; Worton 1989) is a density estimator commonly used for home range analysis in radiotelemetry studies. Given two-dimensional data (e.g., x, y points) it produces a three-dimensional surface representing an estimate of the underlying probability distribution by summing across bivariate curves centered on each sampled point. Resistant surfaces are being increasingly used in landscape ecology, replacing the binary habitat/nonhabitat classifications of island biogeography and classic metapopulation models with a more nuanced approach that represents variation in habitat quality (Ricketts 2001). A resistance value is typically assigned to each cover type in a land-cover map, representing a divisor of the expected dispersal or migration distance of animals moving through that cover type. Least-cost path analysis is then used to find the shortest functional distance between two points. This least-cost path approach can be extended to a multidirectional approach that measures the functional distance from a focal cell to every other cell in the landscape within a maximum dispersal or migration distance. Such a least-cost "kernel" is a surface that can be scaled to represent the probability of an individual dispersing from the focal cell arriving at any other point in the landscape. The resistant kernel estimator is calculated by creating a least-cost kernel for each focal cell that represents a source of dispersers (i.e., each vernal pool) and summing across all kernels at each cell (Fig. 1).

The cost assigned to each cover type in the resistant surface represents an integration of the willingness of an animal to cross this cover type, the physiological cost of moving, and the reduction in survival for an organism moving across the landscape. Empirical data on these costs for ambystomatid salamanders are sparse. In a field experiment in which metamorphs were released in enclosed runs, Rothermel and Semlitsch (2002) recaptured spotted salamander (*A. maculatum*) metamorphs at twice the rate in forested runs than open fields, suggesting that survival rates in forests are approximately

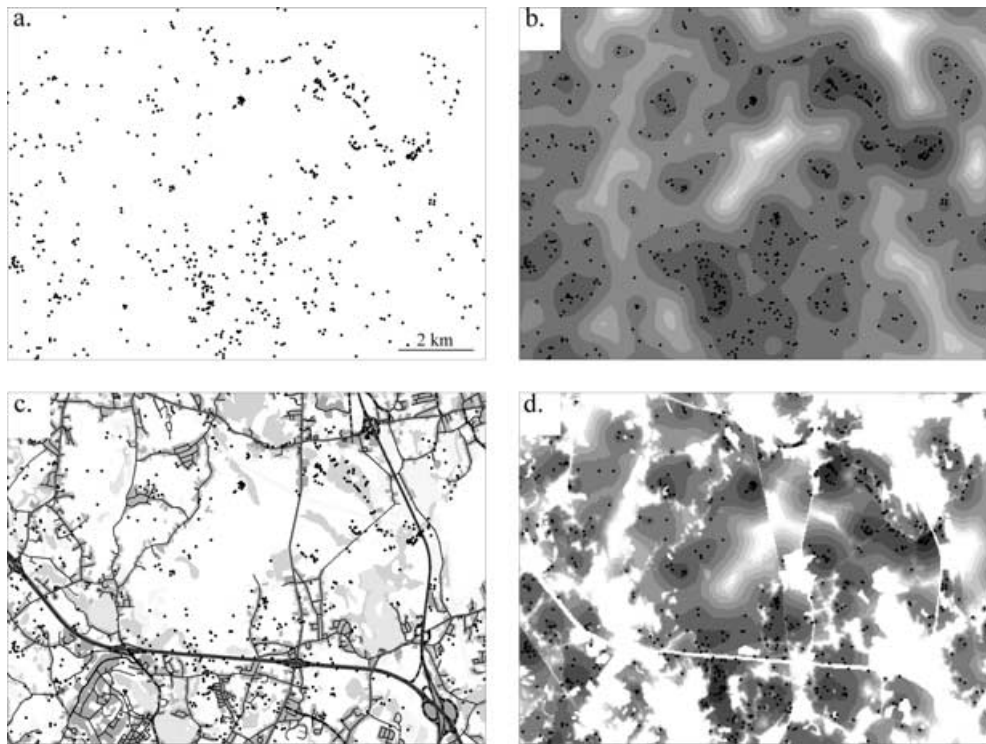


Figure 1. An example of standard versus resistant-kernel estimator applied to a number of potential vernal pools: (a) potential vernal pools represented as points on the landscape, (b) standard-kernel estimator ($h = 399.6\text{ m}$) applied to these pools (darker shading represents higher probability of a dispersing salamander arriving at a particular point and thus higher connectivity), (c) pools with roads and land use included in representation, (d) resistant-kernel estimator ($h = 399.6\text{ m}$) applied to pools, taking roads and land use into account. Resistant-kernel values are reduced (in comparison with the standard-kernel estimator) by highly resistant land-cover types such as roads.

double that in fields. McDonough-Haughley and Paton (2007) similarly found reduced survival rates in radio-tracked adult spotted salamanders on golf courses compared with forests. deMaynadier and Hunter (1999) experimentally released wood frog (*Rana sylvatica*) metamorphs in artificial pools along a forest-powerline edge; recapture rates (interpreted as the result of habitat selection) were positively associated with canopy and understory density.

Given the paucity of empirical data, we used expert opinion to parameterize resistance values. We met with a group of seven researchers with field experience on ambystomatid salamanders in southern New England. After discussing our land-cover types and the meaning of resistance values, each expert team member independently assigned a resistance value for each land-cover type for juvenile and adult marbled salamanders. The team then discussed how these values might differ for other ambystomatids in Massachusetts. For each cover type we took a trimmed mean (by dropping the lowest and highest value before taking the mean). These were the landscape resistance values we used in the model (Table 1). Resistance values for vernal pool and forest were fixed

at 1.0, the optimal value, and all other values were relative to this optimum. Given our cell size, resistances > 40 act as an absolute barrier. When running the model the resistance value for each cell was multiplied by the three-dimensional Euclidean distance between cell centers to account for diagonally adjacent cells and slopes.

Local Connectivity

We modeled local connectivity (Fig. 2a) between breeding pools and upland habitat by setting the kernel bandwidth b (the standard deviation of a bivariate normal curve) to the expected upland migration distance, based on radiotelemetry data for spotted salamanders in Rhode Island (McDonough-Haughley & Paton 2007). We set b to the 66th percentile of maximum migratory distances from pools for 28 spotted salamanders tracked through forests, or 124 m. As a check on this parameter estimate, we compared percentiles of maximum migratory distances with those of eight spotted and eight Jefferson salamanders tracked in Vermont (Faccio 2003). Percentiles were generally similar; the 66th percentile was 97 m.

Table 1. Resistance values* (trimmed mean with range in parentheses) assigned by seven expert team members to each land-cover type for dispersing *Ambystoma opacum* juveniles and for migrating *A. maculatum* adults.

| Cover type | Dispersal | Migration |
|--------------------------|------------------|------------------|
| Vernal pool | 1.0 (1-1) | 1.0 (1-1) |
| Forest | 1.0 (1-1) | 1.0 (1-1) |
| Old field | 3.4 (2-5) | 3.2 (2-5) |
| Powerline | 3.2 (2-5) | 3.0 (2-5) |
| Pasture | 9.2 (5-20) | 8.6 (5-20) |
| Row crop | 10.2 (4-15) | 9.7 (4-15) |
| Orchard | 6.4 (3-15) | 6.2 (2.3-15) |
| Nursery | 6.8 (4-15) | 6.6 (3-15) |
| Pond/lake | 22.0 (10-40) | 10.6 (5-20) |
| Salt marsh | absolute barrier | absolute barrier |
| Nonforested wetland | 3.0 (2-5) | 2.5 (2-5) |
| Low-density residential | 6.8 (4-15) | 6.4 (2-15) |
| High-density residential | 12.6 (4-30) | 9.8 (3-30) |
| Urban | 26.0 (10-40) | 24.0 (10-40) |
| Expressway | 39.0 (30-40) | 37.0 (30-40) |
| Major highway | 32.6 (20-40) | 30.6 (20-40) |
| Major road | 16.4 (10-35) | 14.9 (7.5-31.5) |
| Minor street or road | 7.2 (2-20) | 6.6 (1.5-20) |
| Unpaved road | 4.8 (1-10) | 4.4 (1-10) |
| Railroad | 15.0 (4-40) | 14.2 (3.8-40) |
| Stream: 1st order | 1.3 (1-3) | 1.3 (0.8-3) |
| Stream: 2nd order | 2.8 (2-5) | 2.6 (1.5-5) |
| Stream: 3rd order | 12.6 (8-30) | 12.0 (6-30) |
| Stream: 4th order | 33.0 (15-40) | 32.4 (11.3-40) |

*Resistance values represent the estimated integrated costs of movement and survival through each cover type. A resistance value of 1 indicates minimal resistance (i.e., movement through preferred habitat, a resistance of 2 means that an individual would be expected to successfully move half as far as the preferred habitat, and a maximum resistance of 40 indicates a complete barrier.

A single resistant kernel for each pool represented the expected probability distribution of terrestrial habitat use. We summed the cell values of each pool's kernel across forested and vernal-pool cells (rather than sum

across all kernels at each cell, as in the kernel estimator) to give the proportion of upland habitat available relative to a kernel in intact optimal habitat (i.e., a pool surrounded by continuous forest). This quantity ranged from near 0 (for a pool with no accessible upland habitat) to 1 (for a pool with optimal upland habitat). This approach differs from simply counting the amount of forest in a circle around each pool in two ways. First, for each pool, forested cells were scaled by the distance from the pool to account for the distribution of expected migratory distances. Second, this approach accounted for differential survival and willingness to cross different land-cover types such as golf courses or roads.

Neighborhood Connectivity

We modeled neighborhood connectivity (the number of dispersers each pool was expected to receive directly from populations associated with neighboring pools; Fig. 2b) with the estimated dispersal distance of marbled salamanders as the kernel bandwidth b . Dispersal distances were fit to empirical data from a 7-year study of marbled salamander dispersal among 14 vernal pools in South Hadley, Massachusetts (L.R.G., unpublished data). Dispersal distances are typically fit to a negative exponential distribution (Berven & Grudzien 1990; Trenham et al. 2001) to represent both philopatric and dispersing individuals. We chose to fit dispersal distances to a normal curve for two reasons. First, kernel estimators require a rounded, rather than sharply peaked, distribution (Silverman 1986). Second, observed philopatry in our study population was so high (>90%; L.R.G., unpublished data) that a single exponential curve fit the data poorly. Therefore, we separated the philopatric and dispersing animals. For our purposes only the dispersing animals were of interest.

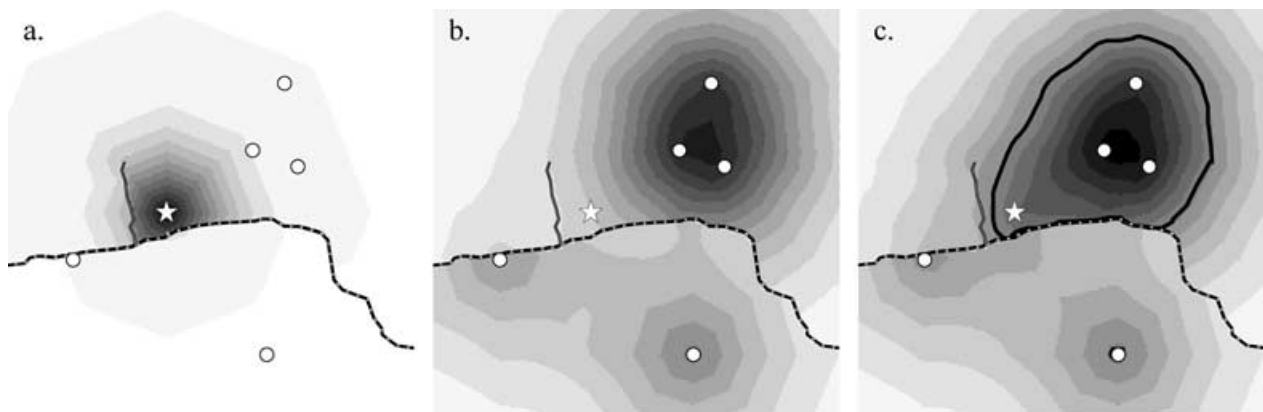


Figure 2. Examples of the resistant-kernel estimator at three scales in a landscape with a focal pool (star), five neighboring pools (circles), and two roads: (a) local scale, showing connectivity to upland habitat from the focal pool; (b) neighborhood scale, showing the probability of the focal pool receiving dispersing animals from each neighboring pool; and (c) regional scale, with dark outline indicating pools that are interconnected by a specified level of dispersal. Darker shading indicates greater connectivity at each scale.

Although we assumed that prebreeding juveniles are the primary dispersers, our empirical measures were of lifetime dispersal (individuals marked as juveniles breeding at non-natal pools as adults). Thus, the lifestage at which dispersal takes place did not have a major effect on the model. The standard deviation of the normal dispersal curve (corresponding to the kernel bandwidth b) was 399.6 m (L.R.G., unpublished data).

At the neighborhood scale connectivity represents the expected number of dispersing animals arriving at a pool from neighboring pools annually. We modeled neighborhood connectivity by applying a resistant kernel (scaled to sum to 1, thus representing the probability of a single individual dispersing to each point surrounding the pool) to each pool and summing across kernels, creating a cumulative kernel surface (as in a standard kernel estimator). The value at the center of each kernel was subtracted from each pool so that the model represented the contribution of dispersers from neighboring pools. We sampled this surface at each pool to yield the neighborhood connectivity metric.

Regional Connectivity

Connectivity at a regional scale measured the size of pool clusters with a specified level of dispersal among pools. This was simply a matter of slicing the cumulative kernel surface at a selected height and counting the number of pools in each cluster (Fig. 2c). If populations and expected numbers of dispersers were consistent among pools, a regional slice could be taken at, for instance, one arriving disperser per generation (Mills & Allendorf 1996). Nevertheless, breeding populations of ambystomatid salamanders vary considerably among pools, and many pools do not support populations at all. Without an estimate of pool-based populations (which would require at least some knowledge about individual pools), determination of regional-scale connectivity becomes somewhat arbitrary. Because our goal was to differentiate among pools for conservation prioritization, we selected the scale that best distinguished among the top 50% of pools. We did this by taking a number of slices, throwing out the 50% of pools with the worst scores, and selecting the scale that gave the largest number of distinct values.

Pool Scores

To score pools across the landscape, we took the geometric mean of the three metrics (local, neighborhood, and regional connectivity) for each pool. Each metric was first rescaled by percentiles to give a qualitative ranking. The geometric mean, often used to integrate limit-

ing factors, was used because a pool that is poorly connected at any one scale will be less likely to contribute to a viable metapopulation. We then rescaled this geometric mean by percentiles across the state, to give a final score for each pool of between 0 and 0.99. A second score was calculated for each pool by rescaling these final scores by percentile within each of the 13 Environmental Protection Agency Level III ecoregions (epa.gov/bioindicators/html/usecoregions.html) that fall within Massachusetts, to give a measure of the most connected pools within each ecoregion. Thus, each pool had a percentile for local, neighborhood, and regional connectivity and for these three metrics combined at the statewide and ecoregional levels. These results can be used to select, for instance, the 5% of pools across the state with the highest scores to be used for conservation prioritization. Full results are available (both as a text file and GIS coverage) at the University of Massachusetts Landscape Ecology Program Web site (www.umass.edu/landeco).

Sensitivity Analysis

There was a high degree of uncertainty in model parameters, due both to the difficulty of obtaining empirical measures of migration and dispersal, and the nature of our expert-derived resistance values. We performed a sensitivity analysis designed to bracket likely parameter values to assess robustness of model results. The sensitivity analysis was conducted at the three scales by altering each parameter or set of parameters one at a time and comparing results with those from the standard model. At the local scale we altered migratory distance $\pm 50\%$ (to 62 and 186 m) and used the lowest and the highest expert-supplied resistance values (Table 1; these extreme values were omitted in calculating the trimmed mean resistance for the standard model). At the neighborhood scale we altered dispersal distance $\pm 50\%$ (to 200 and 600 m) and used lowest and highest resistance values. At the regional scale we altered dispersal and resistance as for the neighborhood scale and maximized differentiation among the top 25% and top 75% of pools. For each sensitivity run we calculated the coefficient of determination (r^2) between the results at the chosen scale (transformed to percentiles) with the results from the standard model. High values of r^2 indicated that the chosen parameter had little leverage on the ranking of pools, whereas low values indicated that the results were sensitive to the parameter in question. To address the question of whether results were affected by resistance values at all (as opposed to simply the arrangement of pools on the landscape), we also compared the standard model run to a run with all resistance values set to 1.0, thus removing the effect of landcover resistance from the model. Finally, to assess the effect of

the geographic scope on pool scaling, we calculated the correlation between pools scored across the entire state and scores rescaled within each ecoregion.

GIS Data

The GIS data consisted of potential vernal pools, land use, roads, streams, and slope. Potential vernal pools were photointerpreted from 1:12,000 color infrared aerial photographs by the Massachusetts Natural Heritage and Endangered Species Program (Burne 2001). These data consist of point locations of nearly 30,000 potential vernal pools across the state and have not been extensively field validated. Known errors of omission include pools <40 m across, pools under conifer canopy and pools embedded in larger wetlands; errors of commission include tree shadows, small permanent ponds, and seeps and shallow pools with extremely short hydroperiods (Burne 2001). Land-use data were photointerpreted from 1999 aerial photographs by the University of Massachusetts Resource Mapping Unit and included 24 cover classes (Table 1). Road data were photointerpreted by the Massachusetts Highway Department and categorized into six classes. Streams were classified by order on the basis of stream center lines. All data layers were converted to a 30-m grid and combined into a comprehensive land cover with each potential vernal pool represented by a single cell. Source data are available from the Massachusetts Office of Geographic and Environmental Information (www.state.ma.us/mgis).

We completed GIS and statistical analyses with ArcInfo (version 9.1, Environmental Systems Research Institute, Redlands, California), JMPIN (version 3.0.2, SAS Institute,

Cary, North Carolina), and programs written by B.W.C. in APL+Win (version 6.0, APLNow, Brielle, New Jersey) and by E. Ene in Visual C++ (version 6.0, Microsoft, Redmond, Washington, D.C.).

Results

Potential vernal pools across Massachusetts were ranked at each of the three scales of connectivity and given a combined score. Pools and their combined rankings were distributed unevenly across the state, with the highest concentrations of high-valued pools generally following the highest concentrations of potential vernal pools. These were located mostly in the coastal plain, particularly in Bristol, Middlesex, Essex, and Plymouth counties.

Values for local connectivity were distributed uniformly (values vs. ranks, $r^2 = 1.000$). Values for neighborhood connectivity were long tailed (reciprocal of values vs. ranks, $r^2 = 0.991$). The regional scale also had a long tail, with clumping at the upper end, because all pools in larger clusters had the same value (log of value vs. ranks, $r^2 = 0.974$). Values were rescaled by percentiles at each scale to yield uniform distributions. Each pool was assigned a combined score by taking the geometric mean across the three scales (Figs. 3 & 4).

Sensitivity Analysis

Results of the sensitivity analysis (Table 2) indicated that pool rankings were relatively insensitive to the parameter values we used, suggesting that the model was robust to modest estimation errors in migration and dispersal distances and to the expert-based estimates of resistance

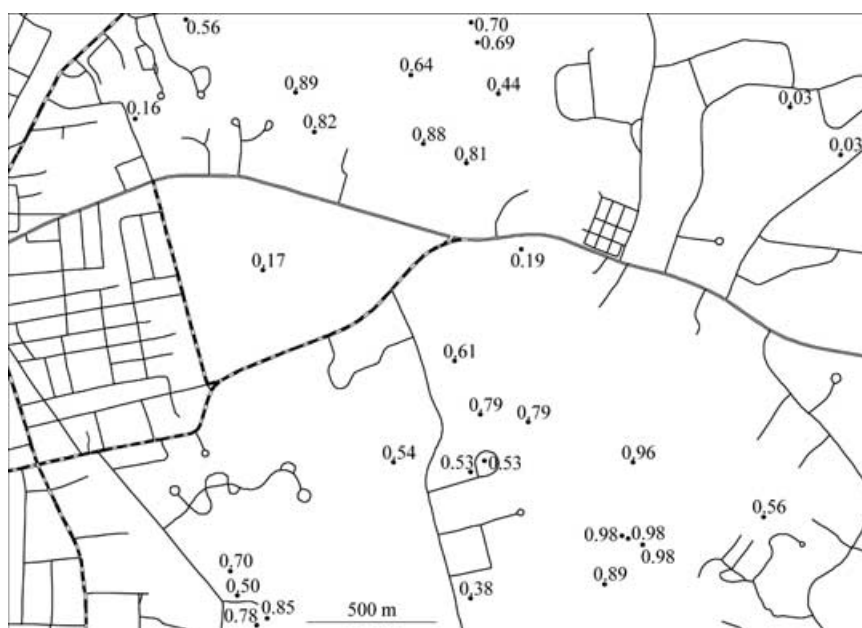


Figure 3. Combined pool scores (integrated level of vernal-pool connectivity across all three scales) for a small area, with roads for context. Scores represent the percentile for each pool based on all three scales of connectivity. A score of 0.99 represents the 1% most connected pools in the landscape (across scales).

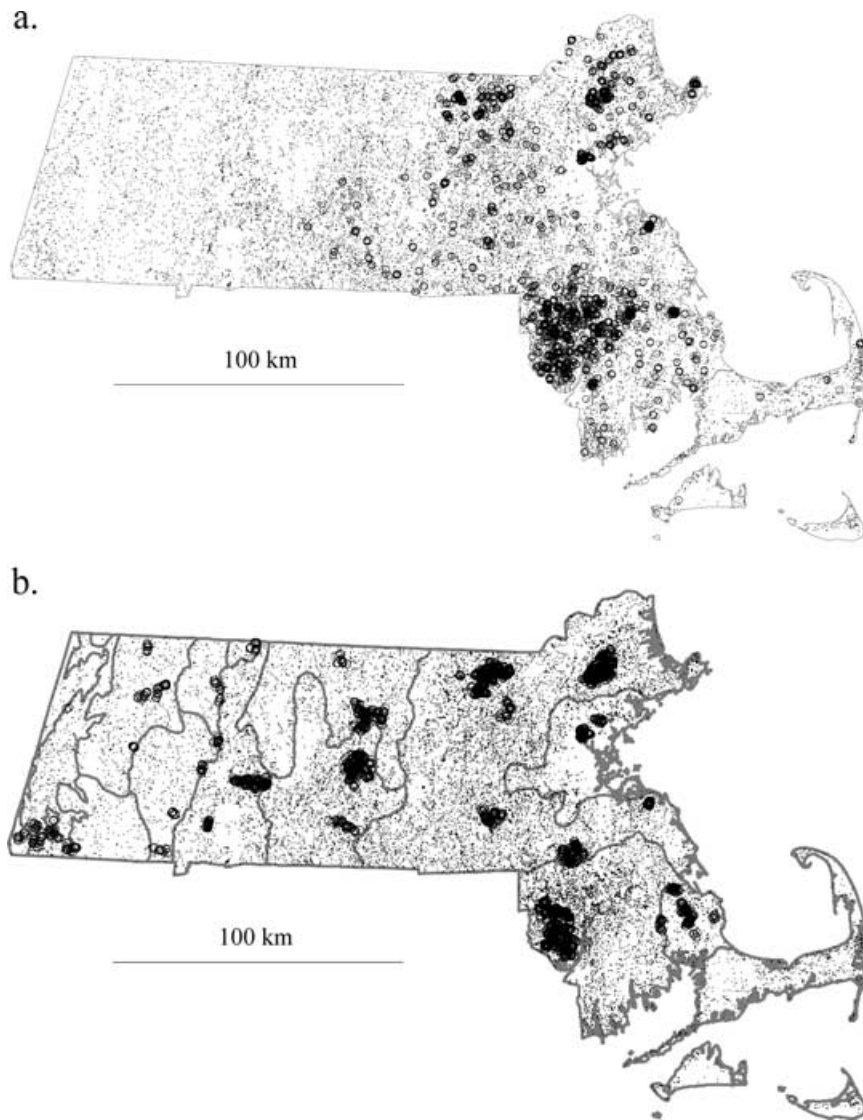


Figure 4. Vernal-pool connectivity scores (integrated across all three scales) for all pools across Massachusetts: (a) combined pool scores across Massachusetts and (b) pool scores by ecoregion (black circles, 10% most connected pools; small dots, 90% least connected pools; gray lines [in b], ecoregion boundaries).

values. Local and neighborhood rankings were quite stable (all $r^2 \geq 0.86$), whereas rankings at the regional scale were less so. The greater instability of regional rankings was not surprising because scores were assigned on the basis of the number of pools in a cluster, so changes in parameters that resulted in large clusters being split or joined could radically change the scores for many pools.

Results of the null resistance model (Table 2) were not highly correlated with results of the standard model at the local and regional scales; however, at the neighborhood scale, the standard and no-resistance runs were correlated ($r^2 = 0.79$). The median reduction in raw neighborhood pool scores in the standard versus the null resistance model was 5.5% (interquartile range = 1.4–13.5%).

Finally, the correlation between combined pool scores rescaled within each ecoregion to scores scaled across the entire state was relatively low ($r^2 = 0.24$). This was an expected result of changing the scope of the analysis; such a rescaling elevates scores of pools in ecoregions

with relatively low scores overall at the expense of higher-scoring pools in ecoregions with generally higher scores (Fig. 4).

Discussion

The density of potential vernal pools was strongly reflected in the connectivity metrics. Although it was not possible to explicitly partition variance between landscape resistance and pool configuration, the null resistance model (Table 2) suggested that, at the neighborhood scale, pool scores reacted primarily to pool configuration rather than landscape resistance. Unfortunately, the densest groupings of potential vernal pools and thus the largest clusters of highest-ranked pools were in the coastal plains of Essex, Middlesex, Bristol, and Plymouth counties, on the leading edge of suburban sprawl from

Table 2. Correlations between pool scores (rankings of connectivity among pools for ambystomatids at each scale) from standard-model run and scores from sensitivity-analysis runs.^a

| Scale | Parameter | r^2 | | |
|--------------|--------------------------------|--------------------|--------------------|-------------------|
| | | lower ^c | upper ^d | null ^e |
| Local | migratory distance (±50%) | 0.90 | 0.96 | |
| | resistance values ^b | 0.96 | 0.99 | 0.02 |
| Neighborhood | dispersal distance (±50%) | 0.86 | 0.95 | |
| | resistance values | 0.96 | 0.97 | 0.79 |
| Regional | dispersal distance (±50%) | 0.55 | 0.72 | |
| | resistance values | 0.56 | 0.57 | 0.15 |
| | top 25% / top 75% ^f | 0.72 | 0.59 | |

^aHigh correlations indicate the model is insensitive to parameter values.

^bResistance values are estimates of costs of moving through each cover type set by expert opinion. The resistance values used in the standard model were the trimmed mean for each cover type. In the sensitivity analysis, results of the standard model were compared with those from a model based on the minimum resistance across experts for each cover type and with the maximum resistances.

^cCorrelation between results of standard model and those from runs with minimum parameter values.

^dCorrelation between results of standard model and those from runs with maximum parameter values.

^eCorrelation between results of standard model and those from run with all resistance values set to 1.0.

^fFor the standard model, the scale was chosen to maximize differentiation among the top 50% of pools. In this sensitivity analysis, scales were chosen to maximize the top 25% and top 75% of pools.

the Boston metropolitan area (Fig. 4a). The model suggested that despite current levels of development, pools in these areas may still offer the most connected habitat for ambystomatids in Massachusetts and should be a priority for conservation action.

The resistant-kernel estimator we used was a functional measure of connectivity that realistically modeled movement across different cover types while avoiding the complexity and computational costs of an individual-based model. As a functional metric, the resistant-kernel estimator is parameterized on the basis of the biology of particular organisms, as opposed to structural metrics, which measure connectivity as a feature of the landscape (Calabrese & Fagan 2004). We used resistant kernels to explicitly model connectivity at multiple scales, thus allowing separate assessment of each scale, trade-offs among scales, and integration across scales.

Sensitivity Analysis

The sensitivity analysis suggested that the model results at the regional scale were less reliable for ranking pools

than the local and neighborhood scales. Therefore, a user may choose to omit the regional scale when ranking pools for conservation action. The relative insensitivity of pool rankings to changes in resistance values at the local and neighborhood scales suggested that expert-based resistance values need not be precise (a clearly unattainable goal), but it did bring up the question of whether resistance values (and thus land cover) have any effect on model results. Were pool rankings primarily a reflection of the arrangement and density of pools on the landscape? A comparison of results of the null resistance model with the standard model indicated that at the local and regional scales landscape resistance played a large role in pool rankings. At the local scale the null model simply reflected the amount of upland habitat available to each population; the low agreement with the standard model suggested that habitat configuration (and thus landscape resistance) played a major role. Likewise, at the regional scale, the null model simply reflected the density and configuration of pool clusters; the low agreement with the standard model suggests that land-cover patterns in the intervening landscape between clusters of pools has the potential to significantly affect connectivity at these broader scales. However, at the neighborhood scale, there was fairly strong agreement between the standard and null resistance models in ranking of pools (Table 2). At this scale, the null model reflected the density and configuration of nearby pools; the agreement with the standard model suggested that landscape resistance between pools in a cluster had relatively little effect on connectivity at this scale.

Pool rankings were sensitive to the geographic scope of analysis. Rescaling by percentiles within each ecoregion provided an assessment of the most connected pools within each region. These geographically nested analyses allow targeting of both the most connected pools across the state (which were skewed heavily to eastern Massachusetts) and the most connected pools within each ecoregion.

Conservation Application

The large number of potential vernal pools across Massachusetts would preclude site visits to more than a small fraction. At the same time landscape-scale issues such as connectivity and, to some extent, availability of upland habitat, are difficult to assess objectively in the field. Current regulatory protection mechanisms focus on the pool basin and a small (31 m) buffer around each pool, leaving upland habitat and connectivity to be assessed on a case-by-case basis. As a result, at these broader scales, there is little effective protection from the cumulative effects of development.

We propose a strategic framework for conservation of vernal pools at multiple scales. Our approach is hierarchical, starting from a broad landscape scale, and allows for flexibility in matching efforts to available resources. The model of habitat connectivity presented here would be used in the initial step. Conservation planners could use the results from our model statewide or across a smaller region of interest (e.g., ecoregion, watershed, or town). Pools with high scores for connectivity would be identified. Such identification could take other variables into account, such as proximity to protected open space. Depending on the resources available, this could include the top 1%, 10%, or more—such use of qualitative metrics is to some extent a political, rather than a biological decision (e.g., What percentage of vernal pools need protection at all scales?). The result of this step would be the identification of hotspots of potential vernal pools with high connectivity to other pools and intact upland habitat.

Once clusters of high-ranking potential vernal pools are identified, field validation could target these subsets of pools. Such efforts could make use of volunteers, as has been previously done effectively in Massachusetts. Depending on available resources, field validation could range from confirming the existence of standing water during various seasons as an estimate of hydroperiod (e.g., from aerial photos), to biologically based pool certification, to more intensive work targeted at confirming the presence of rare species (such as marbled salamanders) and estimating populations sizes. This two-step process is a highly efficient way to identify vernal pools with high conservation value for ambystomatids. Such work must, obviously, be linked to efforts to protect high-ranking pools, their surrounding upland habitat, and connections among pools.

Our model results allow assessment of pools at each of the three scales independently, assessment of pools based on the integrated score, or exploration of trade-offs among the different scales. Although our integrated score is based on equal weighting of the three scales, the scores at each scale may be given weights reflecting the purported importance of each scale before integration. If surveys allow assignment of a value that reflects breeding habitat quality of each pool in an area, these values can be easily incorporated as a fourth scale in the integrated score.

The results of the model were not scaled and parameterized appropriately to cover other taxa that use or require vernal pools (such as obligate vernal-pool invertebrates or turtles that feed on vernal-pool species). To some extent, by targeting clusters of vernal pools in intact uplands, other vernal-pool species may also be protected. This is less likely to be true for invertebrates with extremely patchy distributions and dispersal that is either strongly limited or takes place at much broader scales than salamanders. A pool is not necessarily a low conservation priority simply because it is poorly connected. Many iso-

lated pools or small clusters of pools may support rare species or genotypes, or may contain sufficiently robust salamander populations to persist over the long term despite their isolation. Isolated pools in urban areas can also provide important educational or “wilderness” values to humans.

When applying this model to individual ambystomatid species the output should first be clipped to the approximate range of the species within Massachusetts. The marbled salamander, for instance, apparently does not occur in north-central Massachusetts or in the higher elevations of western Massachusetts.

Assumptions and Limitations

A modeling effort such as ours carries a number of assumptions. We assumed that land use and road data were correct and that the categories assigned were meaningful. Roads, for example, were classified by size (Table 1), which is assumed to correspond to the more ecologically meaningful road width and traffic rate. In addition, land use does not correspond exactly to land cover. For instance, “low-density residential” includes both mowed lawns and small patches of forested areas. Finally, these data may carry positional errors. All of these potential sources of error may affect model results to some extent, but are unlikely to have a major effect. Gross misclassifications in land use, most likely caused by land-use changes since the coverage was created in 1999, are likely to have a larger effect.

The model relied heavily on the photointerpreted potential vernal pools coverage (Burne 2001), which has not been field validated extensively. Errors of omission and commission will affect our results. More important, each vernal pool was represented as a point in the landscape; thus, we assumed that all pools provide ecologically equal habitats (and essentially, equal population sizes) for the species under consideration. In reality the size, hydroperiod, water chemistry, and other features of vernal pools vary widely. These pool-scale factors are probably the primary determinants of local amphibian populations. In amphibian metapopulations there is a strong source-sink aspect to metapopulation dynamics among pools because pools vary in habitat quality. Representing these important pool-scale factors requires extensive local (and usually field based) information that is unavailable at the large extents we addressed. Thus, our model addressed connectivity among pools and to upland habitat, assuming that pools themselves are equal. We see this model as an important first step in estimating the relative conservation value of different pools that should be followed up with more intensive study of selected pools at the local scale.

Our model was static, based on a current snapshot of the landscape. Thus, it did not account for the effects

of land history or future changes in land use. Land-use history may have an important effect on the distribution of vernal-pool amphibians because more than half of the forests in Massachusetts were converted to agriculture during the eighteenth and nineteenth centuries and much of this land has since become reforested (Hall et al. 2002). Thus, many amphibian populations may have been extirpated because of the loss of upland habitat and have yet to recolonize currently available habitat. There is also likely to be a time lag as upland habitat is developed and connections are lost among pools because metapopulation dynamics play out over many generations, which in long-lived species such as spotted salamanders (Flageole & Leclair 1992) may take several decades or longer. Our model represents the current connectivity among pools, whereas past connectivity is likely a more important determinant of current population distribution (Findlay & Bourdages 2000). Finally, future changes in land use and traffic levels will continue to affect connectivity among pools.

Our model depended on several poorly known parameters: dispersal and migration distances and the resistance of different land uses and road types. We obtained estimates of movement and life-history parameters from empirical field studies of spotted and marbled salamanders and thus assumed that these data were representative of ambystomatid salamanders across Massachusetts. Although some variation is likely in migration and dispersal distances and landscape resistance among these four species, field work has not yet demonstrated such differences. Our model assumed that dispersal is random and nondirectional; thus it focused on available upland habitat and among-pool connections rather than predicted actual movements. We assumed the shape of the dispersal curve is normal. Sufficient data do not currently exist for these species to allow confident distinction among different dispersal distribution models. Finally, we used expert opinion to obtain resistance values for each land-use type and road size. Empirical resistance values are poorly known, although recent and current field experiments are addressing this issue (Rothermel & Semlitsch 2002). Sensitivity analysis suggests, however, that the model responded more strongly to pool arrangement and land cover than to the particular values of migration, dispersal, and resistance values.

Another issue omitted from the model is an analysis of key pools (or sets of pools) that act as critical links or “stepping stones” to connect two or more clusters of pools. If these key pools (or linkages to and from these pools) are destroyed or degraded, a large complex of interconnected pools could be split into two smaller complexes, with potential implications for metapopulations they support (Semlitsch & Bodie 1998). Identifying pools that contribute disproportionately to connectivity would require an iterative “take-one-out” analysis (e.g., Keitt et al. 1997; Urban & Keitt 2001). At the scale of this anal-

ysis, such an approach would be computationally infeasible; perhaps future investigation along these lines will provide valuable insights on critical pools or groups of pools.

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