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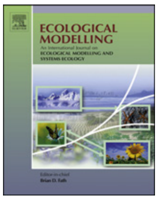

Evaluating expert opinion and spatial scale in an amphibian model

Noah D. Charney*

Organismic and Evolutionary Biology, University of Massachusetts Amherst, 221 Morrill Science Center South, Amherst, MA 01003-9297, United States

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ABSTRACT

When ecological models are used to guide conservation decisions, these models should be based upon substantial data and should be applied at appropriate spatial scales. Yet, ecologists are usually faced with scarce data and must often make subjective choices about scale. To handle limited data, the use of expert panels to parameterize models has become common. However, few studies evaluate the success of expert panels in improving models. In this study, I examine a recent resistant kernel model designed to prioritize amphibian breeding habitat for conservation. I compare the predictive ability of the model as originally parameterized by an expert panel to the predictive ability of simpler models. I optimize parameter values for spatial scale and landscape resistance using 896 ponds from 5 studies of spotted salamanders (*Ambystoma maculatum*) and wood frogs (*Lithobates sylvaticus*) in Massachusetts and Rhode Island. In predicting amphibian distributions, models examined in this study that relied upon expert-derived resistance values performed worse than null models with uninformative resistance values. The failure of the resistant kernel model offers support for the use of simple models in the face of complex ecological problems. The best scale for measuring upland habitat in these models was in the range of 1000–3000 m, an order of magnitude larger than the salamander migration scale previously proposed for wetland buffer zones.

1. Introduction

A major challenge in ecology is modeling complex problems with scant data. To deal with data scarcity, ecologists may aim for simpler models, develop new statistical frameworks (e.g. Ovaskainen and Soininen, 2011), or elicit expert opinion (Kuhnert et al., 2010). Expert opinion is increasingly used to parameterize models in the absence of data and as Bayesian priors to supplement sparse data (Yamada et al., 2003; Martin et al., 2005; Denham and Mengersen, 2007; Griffiths et al., 2007; Mac Nally, 2007; O'Neill et al., 2008; Low Choy et al., 2009; O'Leary et al., 2009; Murray et al., 2009; James et al., 2010). Yet, when lacking data, expert opinion does not necessarily offer an improvement (Cox, 2000; Pearce et al., 2001; Seoane et al., 2005). While this approach is growing in popularity, few studies in ecology have rigorously tested the success of expert panels in assigning meaningful values. If, when, and how expert opinion should be used in ecology remains an open debate.

In this study, I examine two types of parameters that are often assigned based upon expert opinion or scant data. One type of parameter includes those that match land cover classes with some aspect of habitat quality. When predicting species distributions across diverse landscapes, there is often little choice but to rely upon expert advice about what represents suitable habitat and what represents barriers to movement (Johnson and Gillingham, 2004). The second parameter type I examine is that of spatial scale. Selecting an appropriate spatial scale is a core modeling decision, but there is seldom much data on which to base this choice (Holland et al., 2004).

Identifying appropriate spatial scales is a fundamental problem in both ecology and conservation biology (Levin, 1992; Noss, 1992; Laurance, 2000). For conservation, it is important for the scales at which conservation initiatives can be implemented to match the scales at which organisms can respond (Warren et al., 2008). In constructing models, it is well understood that input data must be sampled with the appropriate extent and resolution to reflect the scales of landscape patchiness and habitat selection (Wiens, 2002; Hoffman and Wiens, 2004; Guisan and Thuiller, 2005; Nams et al., 2006). Some types of models also include explicit spatial parameters related to the focal organism that are assigned separately from the implied scale of the input data (e.g. Compton et al., 2007). Predicting the presence of amphibians at breeding ponds based upon upland habitat characteristics is a classic problem where researchers must decide on explicit spatial parameters. In evaluating each pond, researchers could include upland habitat characteristics within a radius described by population processes such as migration, or researchers could look at larger radii described by metapopulation processes such as dispersal (Semlitsch, 2008).

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* Tel.: +1 413 545 1781; fax: +1 413 545 3243.
E-mail address: noah@alumni.amherst.edu

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There is little data available to guide researchers in making such a choice between the scales of population and metapopulation processes.

Vernal pools are widely distributed, abundant, are the sole habitat of many organisms of conservation concern, and have long been used by researchers as a model system to understand basic ecological principles (Blaustein and Schwartz, 2001; Zedler, 2003; Meester et al., 2005). Obligate vernal pool amphibians often dominate these wetlands, migrating to the surrounding uplands during the drier seasons. National and local wetland protection laws typically ignore the terrestrial life stages of semi-aquatic organisms, but recent efforts have begun to reshape these laws to include terrestrial buffer zones encompassing upland habitat (Calhoun et al., 2003; Burne and Griffin, 2005).

The migration distance of pond-breeding amphibians has been suggested as a possible scale for effective terrestrial buffer zones for wetlands. Semlitsch (1998) proposed a 164-m buffer that would encompass 95% of a pond-breeding salamander population, based upon direct movement studies. However, this distance ignores metapopulation processes. Is this really the best scale for conservation? If 164 m is a natural scale for salamander conservation, then we should arrive at this same scale by asking the question in a different way. What scale is best for predicting current amphibian distributions in a network of vernal pools? If population processes are most important in maintaining salamanders on the landscape, then a model's predictive ability should be best when upland habitat is measured within approximately 164 m of each pond. The role of metapopulations in structuring communities of amphibians and other organisms has been debated in the literature (Marsh and Trenham, 2001; Freckleton and Watkinson, 2002; Smith and Green, 2005). Resolving this debate informs whether conservation must focus on large areas with interconnected ponds or whether single-pond efforts may be effective.

Measuring landscape features at multiple scales simultaneously is a common modeling strategy (Saab, 1999; Wang et al., 2001; Guerry and Hunter, 2002; Homan et al., 2004; Herrmann et al., 2005; Baldwin et al., 2006a; Cunningham et al., 2007; Clark et al., 2008). In a recent resistant kernel model of pond-breeding salamander habitat in Massachusetts, Compton et al. (2007) segregated habitat connectivity measures at population, metapopulation, and regional levels. The intent of this model is to prioritize areas for conservation, but the question remains as to which of these scales is most important in this task. When constructing such models, the landscape is often evaluated with kernels of a few discrete sizes that are selected a priori based upon direct movement studies, of which there are few. For instance, the local scale parameter in the Compton et al. resistant kernel model was based upon one season of radio telemetry at a Rhode Island golf course and one season of radio telemetry in Vermont. It is not clear that the scales arrived at from such direct movement studies are really the scales at which the models will best perform, and the predictive ability of a resistant kernel model has never been tested. Herrmann et al. (2005) conducted an analysis over 7 scales between 100 m and 2000 m, and found that the distributions of several amphibians are well predicted by scales up to 1000 m, much further than the expected seasonal migration distance. However, that study only incorporated 61 ponds, and thus had limited statistical power.

In this paper, I examine a resistant kernel model as a representative case of a sophisticated predictive model built with little field data (Compton et al., 2007). This model originally relied upon an expert panel to score land cover types and incorporated explicit spatial scale parameters. I combine data from previous studies of spotted salamanders (*A. maculatum*) and wood frogs (*L. sylvaticus*) to conduct a statistically powerful analysis with 896 ponds to determine the scale at which these amphibians respond to habitat fragmentation. I then use a subset of these data to optimize the land cover values in the resistant kernel model and evaluate the success of the expert panel parameterization compared to a null model.

2. Methods

2.1. Data sets

For this study, I aimed to include as many vernal pool amphibian studies as I could locate. The studies needed to include pond locations and detection/non-detection of spotted salamanders and wood frogs. I identified and contacted 16 primary investigators of vernal pool research in the eastern United States, including authors of at least seven data sets from published literature. Authors of two of the recently published papers were unable to locate their data. Through this effort, I was able to obtain nine separate data sets. After discarding data sets that did not have an effective sample size (defined as the smallest of the two outcomes, detection or non-detection) of at least 30 sites, and discarding data sets with spatial overlap, I was left with only five data sets. These included: one in Rhode Island with 151 ponds (Egan and Paton, 2008), one in suburban Boston with 105 ponds (Clark et al., 2008), one in the Quabbin Reservation in central Massachusetts with 171 ponds (D. Clark, Massachusetts Department of Conservation and Recreation, unpublished data), one in the Connecticut River Watershed in central Massachusetts with 103 ponds (Charney, 2011), and one in the Housatonic River Watershed in western Massachusetts with 366 ponds (Charney, 2011). All of these areas except the Quabbin Reservation contain a mix of many land uses including residential, industrial, forests, and fields. The Quabbin Reservation is composed almost entirely of forests, timber cuts, and a large reservoir. Aspects of survey methodology such as timing, intensity, and frequency of visits, differed substantially between studies. All relied upon diurnal visual and auditory surveys for some combination of egg masses, spermatophores, larvae, and adults of the target amphibians in the sampled ponds. While there is potential for high observation errors that may be correlated with pond characteristics, detection rates within a region are unlikely to be affected by characteristics of distant upland habitats (Grant et al., 2005). Thus, these errors should be neutral with respect to my questions of landscape connectivity. I handle differences in detection rates between data sets by treating each region separately in the analyses.

2.2. Simple scale analysis

For all of the data sets I conducted scale analyses using a simple model of percent forest cover within fixed radii circular buffers centered on the focal ponds (Fig. 1). Forest cover serves as necessary overwintering habitat for both spotted salamanders and wood frogs in the region (Windmiller, 1996; Porej et al., 2004; Regosin et al., 2005). I measured the percent canopy cover using the 2001 National Land Cover Data canopy density layer (www.epa.gov/mrlc). I conducted a single analysis for each species with all of the data sets combined, as well as separate analyses on each data set alone. In all models, detection of breeding amphibians was used as the binary response variable, with forest cover as the predictor variable in a logistic regression using the "glm" function in the "stats" package of R Statistical Software (R development core team, 2009). In the combined model, a categorical variable distinguishing the data sets was included as a covariate. This variable was included to account for differences between regions, observers, or methods that would cause the overall detection rate to differ between data sets. When the data sets were analyzed

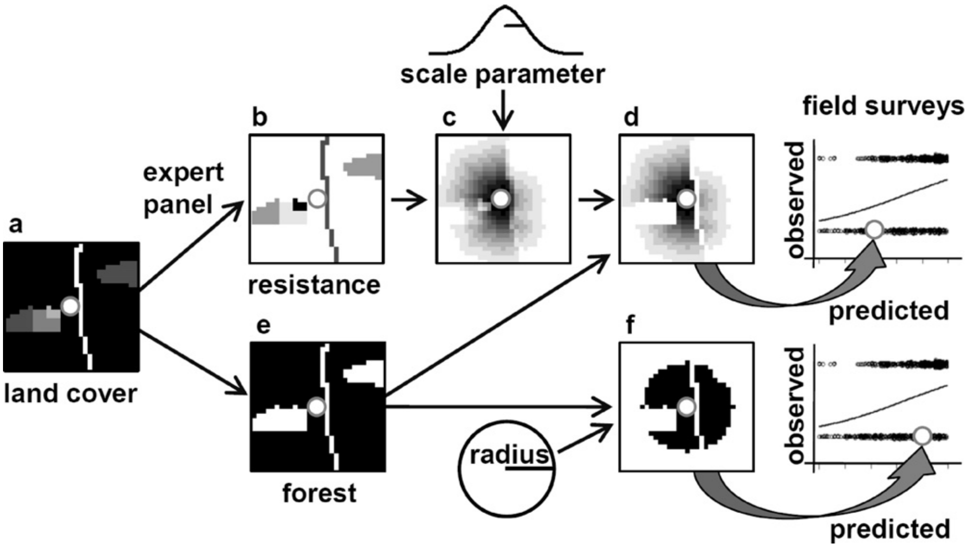

Fig. 1. Flow chart showing a simplified representation of two models used to score ponds based upon potential amphibian habitat in surrounding uplands. A hypothetical landscape is depicted centered upon a single focal pond. Both methods begin with a GIS map of land cover (a). In map (a), forests are represented by black. The top row shows the Compton et al. (2007) resistant kernel model which relies upon expert opinion to assign resistant values to each land cover type (b). A Gaussian scale parameter is then incorporated into the resistant kernel algorithm to calculate the least cost distance between the pond and each cell in the surrounding landscape (c). Cells that do not contain forest are set to zero (d) before summing the accessibility values across the landscape to generate a single local habitat score for each pond. The bottom row depicts a simple circular buffer model, which measures the amount of forest within a fixed distance of each pond (e and f). The predictive ability of each model was evaluated in the present study with logistic regression analysis. In this analysis, the pond scores produced by each model were used as the predictor variable, while the response was the outcome of field surveys for the presence of breeding amphibians at the focal ponds.

individually, I included latitude, longitude, and the interaction term between latitude and longitude as covariates to account for spatial autocorrelation. These spatial terms were used to reduce the chance that the scale analysis would be biased towards larger radii buffers that better capture simple coarse scale geographic patterns such as climatic gradients that might also be driving amphibian distributions. I varied the buffer radius at 50-m intervals between 50 m and 20,000 m, calculating the logistic regression likelihood at each step, for a total of 400 different buffer sizes in each model set. I generated a maximum likelihood estimate for the best scale parameter, and a support interval defined as the highest and lowest radii that produced models within two log-likelihood units of the maximum likelihood (Edwards, 1992).

To see if I would arrive at smaller optimal scales with GIS data sampled at finer resolutions, I also performed the analysis on 5-m resolution land cover data using the ponds from the four Massachusetts datasets. I generated 5-m resolution land cover data using the 0.5-m resolution forest cover layer from the Massachusetts Office of Geographic and Environmental Information (www.mass.gov/mgis). Rhode Island was excluded from this analysis because the finer resolution data layer only covers Massachusetts. I performed the scale analysis with buffer radii ranging from 10 m to 5000 m at 10 m intervals, for a total of 500 buffer sizes in each model set. Computational limitations guided my choice of land cover pixel size and maximum buffer radii.

For the simple scale analysis, I designed a mapping-error model to identify potential biases that could be introduced by a combination of noisy GIS data, pond location errors, and the fact that larger buffer circles sample from a greater number of cells. In this mapping-error model, I used the same GIS-based measures of forest cover as the predictor variable, but I used forest cover as measured on the ground during pond visits as the response. These data were available only for the Connecticut River watershed and Housatonic River watershed datasets. During field sampling in these regions, the percent forest canopy cover within 30 m of the edge of each pond was recorded. I converted this local forest cover into a binary variable (greater or less than 50%) to fit my logistic regression model. The expectation is that GIS-based forest cover measured in the smallest radii buffers should best predict local forest cover at the pond, and models should get monotonically worse as buffers increase. The best scale at which this mapping-error model performs represents the minimum reliable scale for prediction using the GIS data, independent of the amphibian distributions.

2.3. Resistant kernel optimization

To evaluate the Compton et al. (2007) local-connectivity resistant kernel model, I examined three types of parameterizations: models with the resistance values assigned by an expert panel, null models with non-informative resistance values, and models where the resistance values were optimized to my data. For both wood frogs and spotted salamanders, I optimized the resistance values and scale parameter for the Compton et al. (2007) local-connectivity resistant kernel model using the three Massachusetts data sets containing urbanized areas. This model relies upon resistance values for movement of amphibians through each land cover type, ranging from one to infinity, with one being minimal resistance. For a focal pond, the model calculates the least cost distance between the pond and each cell in the surrounding landscape (Fig. 1). Accessibility values for each cell on the landscape are then assigned using a Gaussian function of least cost distance. The scale parameter sets the standard deviation of this Gaussian function. The accessibility values of all cells with suitable non-breeding habitat (forest) in the landscape are summed to create a single local habitat connectivity score for the focal pond. In the original parameterization, the authors set the scale parameter to 124 m, and assembled an expert panel of seven researchers to assign resistance values to 24 land cover types. I did not optimize the neighborhood level in the Compton et al. resistant kernel model because during initial tests the neighborhood model performed many orders of magnitude worse than the local model at predicting my data.

Land cover maps were generated at 30 m resolution from 2005 aerial photographs using the methods described by Compton et al.

(2007). I fixed the resistance of cells containing forest at one, and varied the resistance of 23 other cover types used by Compton et al. between one and 40, with 15 steps evenly spaced along a log scale. Thus, the resistance values examined for each cover type on each pass of the optimization procedure were: 1, 1.3, 1.7, 2.2, 2.9, 3.7, 4.8, 6.3, 8.2, 10.6, 13.8, 17.9, 23.3, 30.3, and 39.4. I also examined a null model where all resistances were fixed at one. This null model is nearly identical to the circular buffer model used in the simple scale analysis, except that forest is weighted based on distance from the center according to the Gaussian envelope. For the scale parameter, I examined the following 16 values evenly spaced along a log scale: 100 m, 130 m, 170 m, 220 m, 290 m, 370 m, 480 m, 630 m, 820 m, 1060 m, 1380 m, 1790 m, 2330 m, 3030 m, 3940 m, and 5120 m.

The Compton et al. (2007) resistant kernel model generates a habitat score for every pond, and I used these scores in a logistic regression to predict observations of breeding amphibians. The Housatonic River Watershed, Connecticut River Watershed, and Boston data sets were combined into a single statistical model by incorporating a categorical variable with three levels, one for each data set. Likelihood values were used to assess the fit of the model for each parameterization.

Due to the complexity of the resistant kernel model, I sought a simple optimization strategy that carried few assumptions and one that could easily be tracked, paused, and restarted throughout the procedure. I thus settled on a modified direct search of the likelihood space (Bolker, 2008), in which I iteratively optimized one parameter at a time with a "square wheel" procedure developed for R statistical software (Appendix A, R development core team, 2009). In this procedure, while all 15 step sizes were tried for a focal parameter, the other parameters were held fixed. The focal parameter was then fixed to the maximum likelihood value, and the next parameter was run. The procedure continued to rotate through all of the parameters repeatedly until the parameter values no longer changed.

While direct search methods carry few assumptions about the geometry of the likelihood space, examining univariate slices in a multiparameter optimization carries the potential for interactions between the variables to mislead the procedure (Bolker, 2008). In tests, I found that for a given scale parameter, the starting parameters had no effect on the output. This indicates that the procedure consistently settles on a single global optimum and is not misled by interactions among the land cover parameters. However, if I allowed the scale parameter to vary along with the other parameters, then the starting values influenced the outcome. This is not surprising, given that the scale parameter only has meaning relative to the resistance values; if I double both the scale parameter and the resistance values, I will end up with the exact same resistant kernel output. Therefore, I optimized the resistance values separately for each of the scale steps, and then constructed a likelihood curve for the scale parameter from these parameterizations.

For model comparison, I defined support intervals as plus or minus two log-likelihood units from the maximum likelihood estimate (Edwards, 1992). For each parameter, I calculated the influence as the difference in likelihood between the minimum and maximum likelihood estimates obtained by changing that variable. I also used the coefficient of variation in parameter estimates as a measure of parameter stability.

The number of parameters in a resistant kernel model is based on the number of land cover types mapped in the available GIS layers. This cannot be changed without either generating new GIS layers from scratch, or using expert opinion to collapse similar land cover types. I did not have the capacity to do either of these. Thus, the number of parameters remained fixed in all of the resistant kernel models and simple likelihoods were sufficient for model comparison.

3. Results

3.1. Simple scale analysis

For predicting spotted salamander distributions from forest cover in concentric circles, the likelihood curve for the combined data sets peaked at 1650 m (support interval: 1150–2150 m) for the 30-m resolution data. Using 5-m resolution data with the four combined Massachusetts data sets, the likelihood curve for spotted salamanders peaked at 2460 m (support interval: 1080–2870 m). With wood frogs as the response variable, the model using 30-m resolution data peaked at 1150 m (support interval: 800–1900 m) and the model using 5-m resolution data peaked at 1670 m (support interval: 710–5000 m).

Examining the data sets individually, clear likelihood peaks for spotted salamanders are seen between the 1000 m to 3000 m radii in the 30-m resolution models from the Connecticut River watershed, Housatonic River watershed, Quabbin Reservation and Boston area (Fig. 2). The Rhode Island data optimal radius was not reached until 9500 m. For wood frogs using the 30-m resolution data, the likelihood peaked at scale parameters between 700 m and 1500 m for the three Massachusetts datasets, however it peaked at 250 m for the Rhode Island dataset. In addition to the peak in likelihood at larger scales for spotted salamanders, local maxima are also seen at much smaller radii with the 5-m resolution data in the Connecticut River watershed and the Quabbin Reservation. Wood frogs showed small scale local maxima using the 5-m resolution land cover for all data sets except the Quabbin Reservation. For the mapping-error model predicting forest cover measured during pond visits, the likelihood peaked within the first 100 m and decreased rapidly and monotonically as the buffer radii increased for both land cover resolutions, as expected.

3.2. Resistant kernel optimization

In the resistant kernel model, when land cover resistances were allowed to vary, the best fit to the spotted salamander data was achieved when the scale parameter was set to 3030 m (support interval: 1380–3030 m; Fig. 3). For wood frogs, the best fit was achieved at 1060 m (support interval: 290–3030 m). When land cover resistance values were set to the expert panel values the maximum likelihood of the scale parameter for spotted salamanders and wood frogs were 2330 m (support interval: 1380–3030 m) and 480 m (support interval: 370–1060 m), respectively. In nearly all cases, the null model with all resistances set to one had a higher likelihood than the expert panel model.

The land cover types that influenced the model fit the most were vernal pool, non-forested wetland, minor street or road, and unpaved road (Table 1). Optimized resistance values varied across scales with a mean coefficient of variance for all parameters' optimal resistance values of 0.8 (Appendix B). There was very low correlation between mean optimized resistance values and the resistance values as judged by the expert panel (Pearson's $r = 0.3$).

4. Discussion

The most interesting finding of this study is not the comparison between the optimized and expert panel models, but the comparison between the expert panel models and the null models. In this analysis, the Compton et al. (2007) resistant kernel model demonstrated a surprising failure of expert opinion. Not only did the expert panel fail to improve the model, but experts made the model significantly worse than the null model. In considering spatial scale, few vernal pool studies include upland habitat at distances greater

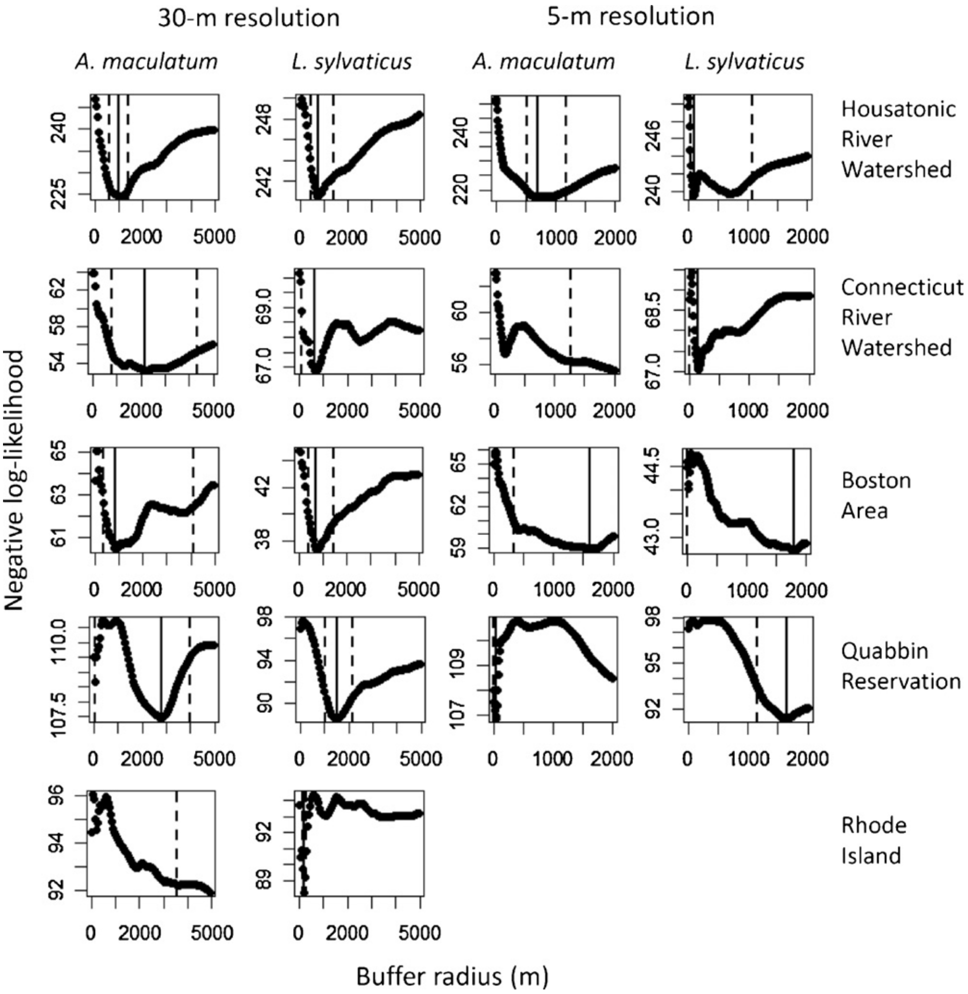

Fig. 2. Likelihood curves for buffer radius used to measure percent forest cover surrounding ponds. Better fitting models are lower on the *y*-axes. Percent forest sampled at two resolutions is used to predict detections of breeding spotted salamanders (*Ambystoma maculatum*) and wood frogs (*Lithobates sylvaticus*) at focal ponds in five study regions. Solid vertical lines indicate the maximum likelihood estimate. Dashed vertical lines indicate the support interval within two log-likelihood units of the maximum likelihood. For ease of viewing, I do not display the full extent of radii used in the model, but only the portions in which most features are expressed in all of the plots. In the 30-m resolution Rhode Island data, the maximum likelihood for *A. maculatum* occurred above the maximum displayed scale, at 12,550 m. In the 5-m resolution Connecticut River watershed data, the maximum likelihood for *A. maculatum* occurred at 4300 m.

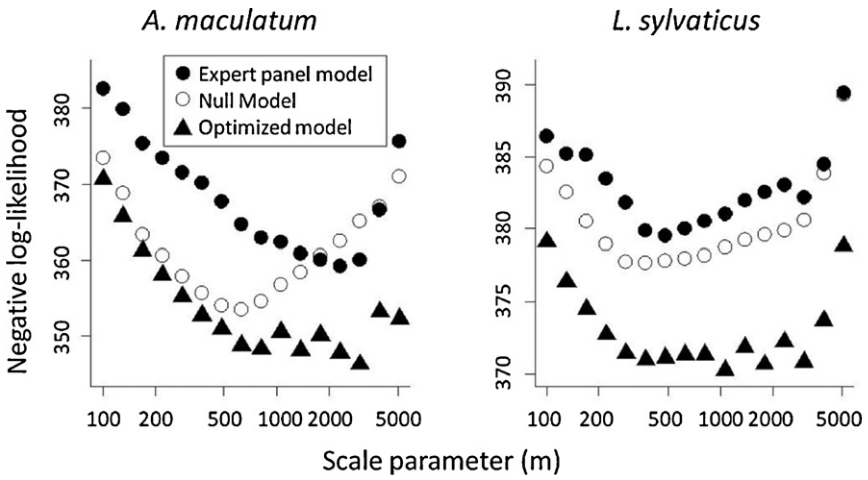

Fig. 3. Likelihood for 64 parameterizations of resistant kernel model in predicting spotted salamander (*Ambystoma maculatum*) and wood frog (*Lithobates sylvaticus*) distributions at ponds in Massachusetts. Better fitting models are lower on the *y*-axes. Landcover resistances are set to the optimized values, values determined by an expert panel, or set to one in the null model. At almost every scale, the null model performs better than the expert panel model.

Table 1
Resistance value ranks and influence of land cover types fit to amphibian breeding survey data averaged across 16 different values of the Compton et al. (2007) resistant kernel scale parameter, with standard deviations in parentheses.

Cover type	Compton rank[a]	*Ambystoma maculatum*		*Lithobates sylvaticus*	
		Influence[b]	Optimized rank[c]	Influence	Optimized rank
Vernal pool	1	12 (11)	3.5 (4.6)	6(7)	9.2 (6.6)
Nonforested wetland	5	10 (4)	14.3 (6.7)	3.4(1.4)	15.6 (1)
Minor street or road	12	9 (3)	8.9 (6.4)	4.8(1.4)	4.1 (4.9)
Unpaved road	8	6 (3)	2.1 (3)	3.7(1.2)	1.8 (3.3)
Powerline	6	4 (2)	4.8 (5.1)	2.5(0.8)	1(0)
Row crop	14	4 (3)	1(0)	2.5(0.6)	3.5 (4.6)
Stream: 1st order	3	3 (1.3)	1.8 (3.3)	2(1.2)	6 (5.9)
Major highway	21	3 (1.5)	9.6 (7)	1.1(1.3)	14.9 (1.2)
Pasture	13	2.3 (1)	1(0)	1.6(0.5)	4.1 (4.8)
Low-density residential	10	2 (1)	10 (8.2)	2.4(1)	1(0)
Old field	7	2 (1.2)	4.1 (6)	1.4(0.3)	2.1 (3)
Pond/lake	19	1.5 (1)	5.4 (7.9)	1.5(0.9)	18.5 (2)
Major road	18	1.3 (0.6)	14.7 (1.8)	0.7(0.4)	14.7 (2.2)
Stream: 4th order	22	1.2 (1.1)	19.9 (5.3)	1.3(0.7)	18.7 (2.7)
Stream: 2nd order	4	1.2 (1)	19 (7.3)	0.7(0.6)	14.3 (7.5)
Railroad	17	1 (0.5)	3.4 (6.5)	1(0.4)	2.4 (3.8)
Expressway	23	0.9 (1.2)	5.3 (7.1)	0.5(0.5)	2.1 (2.9)
Stream: 3rd order	15	0.9 (0.5)	19.6 (2.1)	0.6(0.3)	14.9 (5.1)
Urban	20	0.8 (0.6)	20.8 (1.4)	1(1)	17.9 (2.7)
High-density residential	15	0.6 (0.3)	21.8 (0.8)	0.6(0.2)	18.6 (5.2)
Orchard	9	0.5 (0.5)	11.9 (5.6)	0.2(0.2)	10.3 (9.1)
Nursery	10	0.2 (0.1)	20.8 (2.6)	0.22(0.16)	17.8 (2.1)
Salt marsh	23	0.03 (0.02)	20.7 (1.9)	0.02(0.03)	17.3 (1.9)
Forest	1	Fixed	1	Fixed	1
Missing data	1	Fixed	1	Fixed	1

[a] Focal land cover resistance rank, relative to all land covers as assigned by expert panel in Compton et al. (2007).

[b] Maximum change in log-likelihood exerted by focal land cover, averaged over all parameterizations, with standard deviations in parentheses. Because the number of parameters stays fixed in the models, change in log-likelihood is directly proportionate to change in log-likelihood.

[c] Focal land cover resistance rank, relative to all land covers in the best fitting parameterization optimized to my data.

than 1000 m. Yet, in most cases the models in this study performed best at even larger scales.

4.1. Simple scale analysis

The distributions of spotted salamanders in the datasets were best predicted by measuring land cover at distances between approximately 1000 m and 3000 m from breeding ponds. These scales are consistent with the findings of previous studies with similar methods (e.g. Herrmann et al., 2005; Egan and Paton, 2008), but are substantially larger than the scales of wetland protection laws, the "life zone" encompassing 95% of a salamander population, the scale parameter originally used to parameterize the local resistant kernel model, and the neighborhood scale of the Compton et al. resistant kernel model (Griffin, 1989; Semlitsch, 1998; Compton et al., 2007). One explanation for the difference is that the life zone scale reflects population-level processes, while this study may reflect larger scale metapopulation-level processes. Both the life zone concept and original local resistant kernel parameterization are based on annual salamander migration distances. Habitat characteristics within the migration distance of breeding ponds should influence adult survival and thus predict population growth parameters. The models in this study were not based on population size, but rather they were based on the presence of detectable populations which depends in part on colonization rates. The presence of salamanders at a focal pond may indicate that the pond is surrounded by a large enough area of good habitat to encompass a functioning metapopulation. Such a network of connected ponds allows recolonization events to compensate for extinction events ensuring the long term persistence of salamanders in the area. The scale at which landscape characteristics influence colonization ought to be determined by dispersal distance. Dispersal distances as calculated through individual movement studies and genetic analyses on pond breeding amphibians are closer to the range of the optimal scales found in this study (Semlitsch, 2008).

In most cases, wood frog detections were best predicted by measuring land cover at smaller radii than spotted salamanders. Dispersal studies do not suggest that wood frog dispersal distances are any smaller than spotted salamander dispersal distances (Semlitsch, 2008). In fact, because frogs are able to hop over obstacles and use con-specific vocalizations to locate ponds, one might expect wood frogs to be better at colonizing isolated ponds in a fragmented landscape than spotted salamanders (Smith and Green, 2005).

Perhaps the high vagility of wood frogs means that very few ponds in these landscapes are sufficiently isolated to prevent colonization. If ponds are so close to each other that they all receive many dispersing juveniles every year, then the distribution of breeding populations would not be explained by metapopulation processes (Marsh and Trenham, 2001; Smith and Green, 2005). Instead, the availability of upland habitat within the adult migration distance of ponds might be a better predictor of presence of a detectable breeding population. Indeed, compared to spotted salamanders, the scales that worked best for wood frogs are a bit closer to what we would expect their migration distance to be (Baldwin et al., 2006b). In addition, in the 5-m scale analysis wood frogs showed a more substantial small-scale peak than spotted salamanders for three of the four data sets examined.

4.2. Resistant kernel optimization

Despite the sophistication of the Compton et al. (2007) resistant kernel algorithm, when the expert panel resistances were used, the model was outperformed by my simple model that measures only percent forest area surrounding ponds. Compared to the resistant kernel model as originally parameterized, a higher likelihood was attained by the optimized simple circular buffer model in all three regions for both amphibian species. The likelihood of the resistant kernel null model parameterization was also higher than the expert panel parameterization at almost all scales. There are four scales for spotted salamanders at which the expert panel likelihood was greater, and these are explained by the fact that peaks of the likelihood curves occur at different scales in the two models. A smaller scale peak was expected in the null model because the resistances are minimized and therefore the effective kernel volume is larger for a given scale. The fact that the optimized model was many log-likelihood units greater than the other models demonstrates that, if parameterized correctly, the resistant kernel model can offer a much better fit to the data than the simple model. The expert panel parameterization, however, resulted in a worse fit.

The failure of the expert panel in the case of this study does not imply that expert opinion is never useful in ecological modeling. It is well understood that the methods used to elicit, combine, and employ expert opinion can dramatically impact the reliability of the expert-derived values (Ayyub, 2001). To parameterize the original model, Compton et al. (2007) elicited independent opinions from seven experts. For each land cover type, a trimmed mean of the resistance value was calculated by dropping the minimum and maximum assigned values before averaging. It is possible that a consensus-seeking elicitation technique, such as the Delphi method (Hsu and Sandford, 2007) would have produced a better set of resistance values. It is also possible that the task of assigning meaningful resistance values in such a complex model is too difficult. The values provided by the expert panel may be a very good reflection of the relative quality of each habitat type, however these values may be quite different from the non-intuitive resistance values that a resistant kernel model relies upon. I employed a very basic form of expert opinion in the simple circular models by equating forest with non-breeding habitat. Perhaps there is an ideal level of expert input that is intermediate between the complexity of a resistant kernel model and the simplicity of my circular model.

The optimization procedure produced parameter values substantially different from those of the expert panel. The relative optimized resistance values for land covers including row crops, pasture, and all types of roads were much lower than their expert panel values for both amphibian species. Other land covers, including non-forested wetlands, second order streams, and vernal pools had higher optimized resistances than expected. Inconsistencies in the land cover resistances may in part reflect the inability of a single parameter to capture the myriad types of direct and indirect impacts that land uses can have on the various amphibian life stages.

While the expert panel parameterization did not offer an improvement over the null model, I also have little trust in the parameter values obtained by the optimization procedure. Of particular concern are the high variances in the parameter values across scales, suggesting instability in the optimized values (Table 1). Due to sample size limitations and processor constraints, I did not include a hold-out dataset to test the optimized model against. To optimize the model for wood frogs alone took approximately 1300 core-hours. I did not have sufficient resources to perform both full optimizations as well as partial optimizations on subsetted data. Perhaps the sample size is too low to appropriately optimize this model. Yet, in light of my efforts to track down all useable data sets, I feel that a study of much greater magnitude is unlikely to occur soon. This is a large sample compared to other pond breeding amphibian studies. With 574 ponds, a presence/absence ratio of 0.99 and 0.98 and 23 land cover types, there are still more than 12 times as many samples as land cover types. For future study, it would be insightful to generate multiple GIS maps with variable levels of differentiation between land cover types. The models could then be run with varying numbers of input resistance values to determine how many are necessary.

The optimization procedure allows an objective way to compare the impact of multiple land cover types on amphibians using observed data, which may ultimately help steer conservation regulations. However, given the potential unreliability of the resistance estimates, the optimized values should be used very cautiously if at all. Even if the optimized values are correct within the model context, because resistance is a non-intuitive concept, it is not clear how to translate these values into a form that is useful for conservation. The resistant kernel approach is still new and there is still much work to be done on understanding how to appropriately parameterize and employ it.

Arguably, this study was an unfair test of a resistant kernel model. To begin, one might think that the neighborhood model developed by Compton et al. (2007) would be better suited to predicting population presence. Yet, I discarded the neighborhood model early on because it performed orders of magnitude worse than the local model. This implies that, while a metapopulation scale may be the best scale for prediction, the structure of the local resistant kernel model outperforms the structure of the neighborhood model. Part of this could be explained by the fact that the neighborhood model relies upon good knowledge of the distribution of ponds on the landscape, yet the available data on pond distributions is very incomplete. A second consideration is that the Compton et al. (2007) resistant kernel model was not intended to predict the results of recent detection/non-detection surveys for amphibians, but rather to assess potential long term future viability of the populations. Perhaps it would have been better to use older land cover data in predicting the current amphibian distributions to allow population time lags to take effect. However, the model need only gauge the quality of most ponds relative to each other. While human densities and land use activities have changed over the past century, the ponds that were in the most fragmented habitats in the recent past are likely to be the ponds in the most fragmented habitats today and in the future. For example, the density of roads within 1000 m of my focal ponds in 1830 (Hall et al., 2002) is a good predictor of the density of roads within 1000 m of the ponds in 2000 (www.MassGIS.gov). While the time lag effect may partially explain overall poor model performance, this does not explain the fact that the resistant kernel performed so much worse than the null model. The null model began with the same handicapped GIS data, but incorporated 24 fewer variables. If a resistant kernel model is to be relied upon for conservation planning, I would expect it to at least outperform the null model.

5. Conclusions

Echoing the sentiment of Ockham's razor, in the absence of data, simple models with few parameters may be preferable to complex models parameterized by expert opinion (Starfield, 1997). This study offers a cautionary lesson against the growing role of expert opinion in ecological models. In the case of amphibians, accurately predicting the influence of many different land use types on populations may be prohibitively complex given our current resources. While I have parameterized the resistance values for the data in this study, perhaps other researchers would arrive at substantially different values in other areas, or using other response variables such as genetic distance. Few studies have examined the relative impacts of the various land cover types on amphibians, which is why the expert panel was convened. However, numerous studies have demonstrated that spotted salamanders and wood frogs in this region need upland forest habitat. To identify target ponds for conservation I would recommend simple models based on this one known parameter, such as the simple circular buffer model used in the scale analysis in this paper, rather than opting for complexity.

To be effective, any model and any long-term conservation initiative requires application at the appropriate spatial scales.

The relative importance of population scale versus metapopulation scale influences may vary from species to species, and more work is needed to describe this balance. This study suggests that maintaining vernal pool assemblages is best done by coordinating conservation efforts over fairly large scales, up to 1–3 km radius areas. Pursuing conservation of amphibians through small scale actions such as wetland buffer zones might protect populations in the short term, but may not allow for colonization events that are important for species such as spotted salamanders in the long term.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.05.026.

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