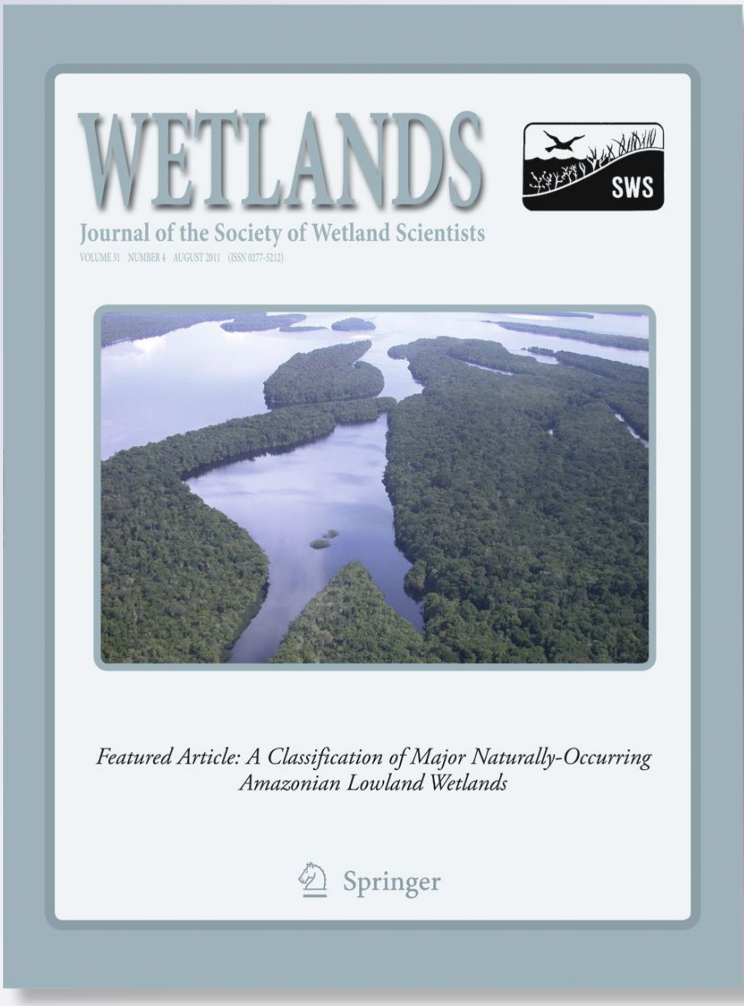
Incorporating Economic Models into Seasonal Pool Conservation Planning

Robert C. Freeman, Kathleen P. Bell, Aram J. K. Calhoun & Cynthia S. Loftin

Wetlands
Official Scholarly Journal of the Society of Wetland Scientists

ISSN 0277-5212
Volume 32
Number 3

Wetlands (2012) 32:509-520
DOI 10.1007/s13157-012-0284-x



Springer

Wetlands (2012) 32:509–520
DOI 10.1007/s13157-012-0284-x

ARTICLE

Incorporating Economic Models into Seasonal Pool Conservation Planning

Robert C. Freeman · Kathleen P. Bell · Aram J. K. Calhoun · Cynthia S. Loftin

Received: 6 March 2011 / Accepted: 30 January 2012 / Published online: 25 February 2012

Abstract Massachusetts, New Jersey, Connecticut, and Maine have adopted regulatory zones around seasonal (vernal) pools to conserve terrestrial habitat for pool-breeding amphibians. Most amphibians require access to distinct seasonal habitats in both terrestrial and aquatic ecosystems because of their complex life histories. These habitat requirements make them particularly vulnerable to land uses that destroy habitat or limit connectivity (or permeability) among habitats. Regulatory efforts focusing on breeding pools without consideration of terrestrial habitat needs will not ensure the persistence of pool-breeding amphibians. We used GIS to combine a discrete-choice, parcel-scale economic model of land conversion with a landscape permeability model based on known habitat requirements of wood frogs (*Lithobates sylvaticus*) in Maine (USA) to examine permeability among habitat elements for alternative future scenarios. The economic model predicts future landscapes under different subdivision open space and vernal pool regulatory requirements. Our model showed that even "no build" permit zones extending 76 m (250 ft) outward from the pool edge were insufficient to assure permeability among required habitat elements. Furthermore, effectiveness of permit zones may be inconsistent due to interactions with other growth management policies, highlighting the need for local and state planning for the long-term persistence of pool-breeding amphibians in developing landscapes.

Keywords Futures analysis · Habitat connectivity · Land use planning · Landscape permeability · *Lithobates sylvaticus* · Wood frog

Electronic supplementary material The online version of this article (doi:10.1007/s13157-012-0284-x) contains supplementary material, which is available to authorized users.

R. C. Freeman (✉)
Ecology and Environmental Science Program,
School of Economics, University of Maine,
5782 Winslow Hall,
Orono, ME 04469, USA
e-mail: Robert.Freeman@umit.maine.edu

K. P. Bell
School of Economics, University of Maine,
5782 Winslow Hall,
Orono, ME 04469, USA
e-mail: Kpbell@maine.edu

A. J. K. Calhoun
Department of Wildlife Ecology, University of Maine,
5755 Nutting Hall,
Orono, ME 04469, USA
e-mail: Calhoun@maine.edu

C. S. Loftin
U.S . Geological Survey, Maine Cooperative Fish and Wildlife
Research Unit, University of Maine,
Orono, ME 04469, USA
e-mail: Cynthia.Loftin@maine.edu

Introduction

Due the their complex life histories requiring access to distinct seasonal habitats, pool-breeding amphibian populations are vulnerable to habitat loss and fragmentation caused by urbanization and land use change (Cushman 2006; Hamer and McDonnell 2008). Most previous work examining the effects of land use change on pool-breeding amphibians has been conducted by ecologists (Lehtinen et al. 1999; Compton et al. 2007; Harper et al. 2008; Baldwin and deMaynadier 2009). Future land use changes are typically based on hypothetical scenarios or trend analyses, with little emphasis on land markets or human behavior (although see Bauer et al. 2010). Such predictions, while not lacking in rationale, fail to address the human decisions that drive land-use change as well as the institutional and regulatory constraints on these decisions. Integration of economic models of land markets and ecological models of the responses of amphibian populations to changing landscapes could better inform policymakers as to the likely effectiveness of conservation and growth-management policies.

In 2007 the state of Maine (USA) enacted legislation to create a regulated 76 m (250 ft) regulatory zone (hereafter called "permit zones")[1] around a subset of seasonal (vernal) pools called "Significant Vernal Pools" (SVPs). SVPs are defined largely by biological criteria: (a) egg mass abundance of three amphibian indicator species: wood frogs (*Lithobates sylvaticus* LeConte); spotted salamanders (*Ambystoma maculatum* Shaw); blue spotted salamanders (*Ambystoma laterale* Hallowell); or (b) the presence of either fairy shrimp (*Eubranchipus* spp.) or specific state-listed species associated with vernal pools (Mahaney and Klemens 2008). To date, roughly 20–25% of all documented vernal pools in Maine meet the criteria for SVPs (P. deMaynadier, Maine Department of Inland Fisheries and Wildlife, pers. comm.). There is concern, however, that conservation focused on breeding pools and narrow adjacent circular buffers, as opposed to contiguous terrestrial non-breeding habitat, may not protect connectivity among the full suite of habitats required by pool-breeding amphibians (Baldwin et al. 2006; Windmiller and Calhoun 2008; Bauer et al. 2010).

Patterns of distribution and abundance of pool-breeding amphibian populations may be driven in part by landscape connectivity among different habitat elements and across scales (Baldwin et al. 2006; Hamer and McDonnell 2008; Windmiller and Calhoun 2008). In this paper we examine landscape permeability at three scales defined by the life history of our focal species, the wood frog, and its documented needs in central and southern Maine. Amphibian habitat requirements are likely to vary regionally (Semlitsch et al. 2009), so it is important to use local information to the extent possible to inform local policy-making. The scales we examine include permeability between breeding pools, permeability between breeding and summer habitat, and permeability between clusters of pools. Permeability between breeding pools may be important for emerging juveniles and for adults traveling between pools or en route to summer refugia. Permeability between breeding and summer habitat is critical to adults, who typically undertake annual post-breeding migrations from breeding pools to upland or wetland forests for the summer (Vasconcelos and Calhoun 2004; Baldwin et al. 2006; Blomquist and Hunter 2010) and who exhibit strong breeding site fidelity (Berven and Grudzien 1990; Vasconcelos and Calhoun 2004, although see Petranka and Holbrook 2006). We define summer habitat as forested wetlands based on recent wood frog studies in our region (Baldwin et al. 2006; Blomquist and Hunter 2010). Permeability among clusters of pools (loosely defined as pools within the maximum reported travel distance of adults in our region (340 m) (Baldwin et al. 2006)) may be most important for dispersing juveniles who are largely responsible for genetic exchange (Berven and Grudzien 1990; Gibbs and Reed 2008) and who exhibit strong preferences for forested habitat (Popescu and Hunter 2011). Clusters also may be important because individual pools within a cluster may have fewer egg masses owing to distribution of reproductive effort within the cluster, in which case fewer pools (or no pools) may meet criteria for Significance, even though the cluster as a whole may be highly productive (Gibbs and Reed 2008). In such cases, protection of permeability within and among clusters may be important for enabling recolonization after pools are extirpated.

Two additional spatial considerations complicate conservation planning for amphibians with complex life cycles. The first is that the degree of clustering of vernal pools may vary geographically (Petranka et al. 2004). If several Significant pools are close enough that their permit zones overlap, permeability between these pools may be well-protected. However if pools are less closely clustered, their permit zones may not overlap, allowing greater possibility of development in the intervening matrix that could reduce or eliminate functional connectivity. The second is that different jurisdictions (e.g., neighboring towns or counties) may have different conservation and growth management policies that may conflict with one another. Both of these factors may alter the effectiveness of terrestrial permit zones, especially in an urbanizing landscape.

We employed an economic model to predict alternative future landscapes under different conservation and growth management policies and assessed the resulting functional connectivity in a landscape permeability model for the wood frog. We chose wood frogs as a focal species as they breed primarily in vernal pools and use additional post-breeding habitats for summering and hibernating (e.g., forested wetlands and well-drained uplands in our study region), requiring greater complexity in conservation planning (Semlitsch 2000; Baldwin et al. 2006).

Economic Models of Land Conversion

Economists frequently use parcel-scale models of land conversion to identify potential drivers of conversion and to describe future landscapes resulting from different policies

[1] We use the term "permit zone" because Maine's law does not prohibit development within this zone. Rather, it requires a permit for any development or disturbance within the zone. In our modeling, however, we have treated this permit zone as a no-development zone to provide a conservative estimate of the law's potential effects.

or scenarios (Bockstael 1996; Lewis and Plantinga 2007; Lewis et al. 2009). These partial-equilibrium models typically assume that each landowner attempts to maximize net returns (returns less conversion costs) from the use of her land. A key contribution of this line of research has been integration of economic models of land use change with ecological models of the environmental responses to such change (e.g., Lewis and Plantinga 2007; Wu and Irwin 2008). In contrast to build-out analyses, which assume all buildable parcels are developed, economic models of land conversion explicitly account for the spatial heterogeneity in returns to development. This information provides insight as to the likely responses of landowners to policies that affect use of their land and to future land patterns that may be observed prior to build-out.

The probability of conversion typically is modeled as the probability that the net returns from one particular land use exceed those of all other uses. Since not all factors influencing returns will be observable to the researcher, the probability typically is specified as a latent regression model in which what is observed (i.e., whether or not a parcel is converted) is modeled as a function of parcel attributes and a stochastic component (Bockstael 1996). Depending on the assumed form of the random component, logit and probit specifications are common.

A typical assumption in parcel-level economic models is that when a parcel changes land uses, the entire parcel is converted to the new use (Bockstael 1996; Irwin et al. 2003; Lewis and Plantinga 2007). In many jurisdictions, however, a percentage of each subdivided parcel is required to be set aside as open space. Although this open space is within a residential subdivision, it may represent viable habitat for selected wildlife species, particularly those with relatively limited mobility. Subdivision open space requirements, which vary widely, may influence the effectiveness of terrestrial permit zones intended to protect amphibian breeding habitat (Freeman and Bell 2011). Thus the amount, location and configuration of open space within subdivisions may be important considerations for land managers and planners attempting to balance demands for residential growth while providing effective measures to conserve wildlife populations in the developed landscape.

Models of Landscape Permeability

Landscape permeability models typically begin with raster land use maps, where each grid cell is assigned a "cost" or "friction" value that represents the cost to the animal of traveling across that cell on the landscape. Typically core habitat areas are identified with the goal of estimating permeability of the landscape between the core areas. Landscape permeability models have been developed for the common toad (*Bufo bufo*) and Alpine newt (*Triturus alpestris*) in Geneva, Switzerland (Ray et al. 2002); grizzly bears (*Ursus arctos*) in Washington and British Columbia (Singleton et al. 2004); the common toad in France (Joly et al. 2003); and invasive eastern gray squirrels (*Sciurus carolinensis*) in British Columbia (Gonzales and Gergel 2007), among many others. These models are relatively robust to the cost values assigned to different land-use types as long as the relative values between types remain consistent (Schadt et al. 2002; Compton et al. 2007).

We integrate the two modeling approaches discussed above to demonstrate the importance of considering human behavior in land markets, the different landscape patterns resulting from different incentives created by various conservation and growth management policies, and their impacts on the effectiveness of vernal pool protection regulations. We also use this approach to examine the degree to which policies may have heterogeneous effects, owing to spatial factors such as differing degrees of clustering of vernal pools and differences in policies in different jurisdictions. The specific objectives of this study are to: (1) assess the effectiveness of regulatory vernal pool permit zones for maintaining landscape permeability for wood frogs at three different scales: (i) permeability between breeding pools; (ii) permeability between breeding and summer habitat; and (iii) permeability between clusters of pools; (2) assess the degree to which open space requirements in subdivisions may alter the effectiveness of vernal pool permit zones; and, (3) assess sensitivity of vernal pool permit zone effectiveness to pool arrangement (i.e., clustering).

Methods

Study Area

We conducted our analyses on data from the town of Falmouth in southern Maine, USA (see map in Fig. 1 of Electronic Supplementary Material), because both mapped vernal pool data and parcel-level tax assessment and zoning data were available in a Geographic Information System (GIS). Spruce-fir and mixed forest comprise roughly 56% of the town's land area, while roughly 10% is wetland. Although largely rural with limited agricultural lands interspersed in a primarily forested landscape, Falmouth has a rapidly urbanizing coastal village area adjacent to a major employment center (Portland) and thus is representative of many communities at the rural-urban interface experiencing rapid residential development.

Spatial Data Sources

Falmouth town officials provided GIS parcel, zoning, natural resource, and infrastructure maps that could be linked to tax assessment data. The town also provided a map of potential vernal pools, based on a 2002 remote sensing inventory (Oscarson and Calhoun 2002). The inventory identified 143 potential vernal pools (3.14 pools per km^2), numbers which are typical of other towns in our region (D. Morgan, University of Maine, pers. comm.), and reported rates of commission and omission errors of 9% and 30%, respectively. We acquired spatial data for soil type (http://soildatamart.nrcs.usda.gov/), National Wetlands Inventory (NWI) wetlands (1:24,000), and an orthophoto (1 ft.) and digital elevation model (10 m) from the Maine Office of GIS (MEGIS 2007). We included small landscape features, such as roads and buildings, as vector GIS layers provided by the town. Due to a temporal mismatch between available parcel data and land cover data, we used the 1993 land cover map (30 m pixel resolution) from the Maine Gap Analysis (Hepinstall et al. 1999) as a proxy for 1996 land cover and the 2004 Maine Land Cover Dataset (5 m pixel resolution) (Smith et al. 2006) as a proxy for 2005 land cover.

Alternative Future Landscapes

Our alternative future landscapes all assume construction of 1,600 new houses, based on the projected household growth rate extrapolated to roughly the year 2035 in our focal town (MESPO 2003). Thus the future landscapes each represent the same amount of development but simulate different development patterns that are likely to result from the different open space and vernal pool protection policies. In addition to the baseline (2005) landscape, we examined nine alternative future landscapes representing different scenarios. We modeled three vernal pool permit zone scenarios: (1) the absence of any permit zones; (2) a 76 m (i.e., Maine's 250 ft SVP regulated zone) permit zone around half of pools, with the protected pools randomly chosen; and, (3) a 76 m permit zone around all pools. For each of the three permit zone scenarios, we predicted landscapes under assumptions of 0%, 25%, and 50% open space in subdivisions. Our resulting nine future landscape scenarios examine the effectiveness of vernal pool permit zones, open space requirements, and the interaction between the two, at protecting landscape permeability for wood frogs.

The economic model used to predict location of development in the future scenarios is estimated with a binary discrete-choice model of conversion of undeveloped parcels to residential use. We estimated the model using a Bayesian Gibbs Sampler (LeSage 2000) to account for spatial error autocorrelation arising from omitted explanatory variables (Anselin 2002). For instance, it is likely that we did not observe certain relevant explanatory variables, and these variables, if spatially correlated, could introduce spatial correlation into the error term. Following LeSage (2000) and Fleming (2004), we employ a spatial error probit model. We begin with a model in latent form:

$$y* = X\beta + \varepsilon, \tag{1}$$

$$\varepsilon = \lambda W\varepsilon + u, \quad u \sim N(0, \sigma^2) \tag{2}$$

where y* is an unobserved continuous latent variable,[2] X is a matrix of explanatory variables, β is a vector of parameters, ε and u are disturbance terms, λ is a spatial autoregressive parameter, and W is spatial weight matrix. We do not observe the latent dependent variable, y*. Rather, we observe y_i, a binary indicator variable that takes the value of 0 if the parcel was not developed and 1 if the parcel was developed. Using the latent regression model framework, the probability that $y_i=1$ is assumed equal to the probability that $y_i^*\geq 0$. Each error term in (1) is determined by an i.i.d. stochastic component and a deterministic component related to neighboring error terms. The spatial error specification in (1) and (2) may be rearranged as:

$$y* = X\beta + (I - \lambda W)^{-1}u. \tag{3}$$

This specification emphasizes that the error term for each parcel-specific observation, y^*_i, is a function not only of X_i, but also of all neighboring error terms in the system. We tried constructing weights matrices based on both contiguity and nearest neighbors, varying the number of neighbors from one to five. The contiguity rule produced models with slightly greater pseudo-R-squares, and we used that form for the weights matrix.

We used LeSage's Matlab code for Bayesian Gibbs sampling estimation of probit models and convergence diagnostics (available at www.spatial-econometrics.com). Gibbs sampling is based on the idea that a probability density function for the parameters may be estimated from a large sample of parameter values in the posterior distribution. Further details on the Gibbs sampling method are provided and alternative estimation procedures reviewed in Fleming (2004). We estimated the parcel-level model during 1996–2005, focusing only on conversion to residential use, as >90% of new development was residential during the study period (Falmouth Planning Department, unpubl. data). Explanatory variables were chosen based on economic theory, and descriptive statistics are shown in Table 1 of the Electronic Supplementary Material (pseudo-R^2=0.57; cross-validation prediction error=0.24).

The parameter estimates from the parcel-level model enabled predictions of future conversion probabilities for each parcel in the study area. Varying open space and vernal pool permit zone scenarios meant that a parcel could have different numbers of developable lots in different scenarios.

[2] For further explanation of latent regression models see Greene (2008), chapter 23.

For this reason, a different number of parcels is required to accommodate 1,600 houses in each scenario, and we assumed the parcels with the greatest conversion probabilities would be developed.

To simulate the placement of houses and open space within each subdivision, we used a second spatial probit model (descriptive statistics available in Table 2 of the Electronic Supplementary Material) of house location at the cell-level (10 m cell size) in our study area over the same time period, conditional on the parcel being developed (pseudo-R^2=0.22; cross-validation prediction error=0.42). We acknowledge the likely endogeneity in this approach. Developers are likely to consider suitable housing sites when choosing a parcel for purchase or development, so our conditional approach is not optimal. We simply use it here as an initial investigation into the importance of the location of houses and open space within subdivisions. Predicted probabilities from this model enabled creation of a cell-scale housing suitability surface, from which we could estimate where houses and open space most likely would be placed if a parcel were to be developed. In the scenarios without open space requirements, we assumed each parcel would be built at its maximum density under existing zoning, so that the entire parcel, less unbuildable areas, was converted to residential use.

Implementation of the Landscape Permeability Model

Cost coefficients for the various land use types were developed through a process similar to that used by Clevenger et al. (2002), including a combination of a literature review and several iterative rounds of input and feedback among local wetlands ecologists and herpetologists (Table 1). We executed the model with the "cost-weighted distance" function in ArcGIS (v. 9.2) (ESRI 2006), which identifies the area around each source pool (or cluster of pools) with accessible habitat (hereafter referred to as cost-distance bands), given the travel cost of the surrounding cells and a maximum travel distance (340 m, maximum adult wood frog migration distance (Baldwin et al. 2006)). The width of the resulting cost-distance bands is half of the maximum travel distance from a pool, so that two overlapping bands create connected habitat features treated as one "patch" (Fig. 1). We performed two cost-distance calculations at the pool-to-summer habitat scale, representing habitat around vernal pools and around forested wetlands potentially accessed post-breeding, and we used the ArcGIS function "corridor" to identify overlap between these two cost-distance layers. We defined patches as the areas of overlap, which indicate functional connectivity between breeding and summer habitat (Fig. 2). We defined

Table 1 Cost values used in landscape permeability model

Maine Land Cover Dataset (MELCD) description (ref. #) (Smith et al. 2006)	Reclassified Description	Cost/ Friction Value
Deciduous forest (Blomquist and Hunter 2010) Evergreen forest (Bockstael 1996)	Forest/ Wetlands	1
Mixed forest (Clevenger et al. 2002)		
Light partial cut [<50% canopy removed] (Irwin et al. 2003)		
Wetland forest (Cushman 2006)		
Wetlands (ESRI 2006)		
Heavy partial cut [>50% canopy removed] (Joly et al. 2003) Regenerating forest [seedling to sapling] (Lehtinen et al. 1999)	Recently cut forest	3
Recent clearcut [>90% canopy removed] (Hepinstall et al. 1999) Scrub/shrub (Compton et al. 2007)	Clearcut/ scrub/ shrub	5
Pasture/hay (Benedict and McMahon 2002) Grassland/herbaceous (Berven and Grudzien 1990)	Field	7
Unconsolidated shore (Gonzales and Gergel 2007)	Uncons. Shore	7
Developed open space [<20% imperv.] (Baldwin and deMaynadier 2009) Cultivated crops (Bauer et al. 2010)	Lawn/crops	9
Low intensity developed [21–49% impervious] (Baldwin et al. 2006)	Devel. – low	11
Bare land (Greene 2008)	Bare Land	15
Med. intensity developed [50–79% impervious] (Baddeley and Turner 2005)	Devel. – med.	15
High intensity developed [>80% impervious] (Arendt 1996) Roads/runways (Fleming 2004)	Devel. – high	20
Other vector layers overlaid onto MELCD		
Minor road	Neighborhood/ connector road	15
Major road	Highway/major artery across or through town	20
Interstates	I-95 or Turnpike	100

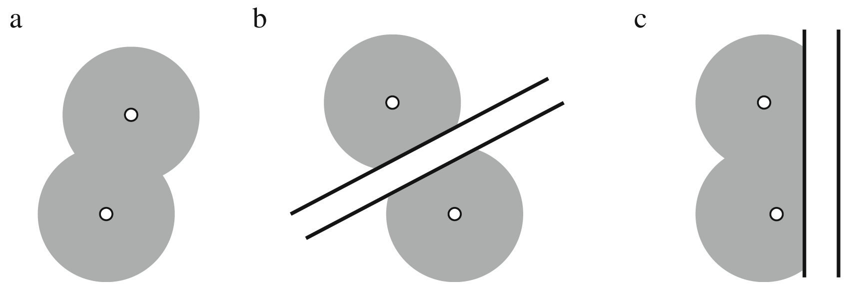


Fig. 1 Examples of patches for pool-to-pool connectivity metrics: **a** one unfragmented patch connecting two pools; **b** two patches fragmented (e.g. by a road), resulting in an increase in number of patches and a decrease in mean patch area; **c** one unfragmented patch with reduction in available habitat (e.g. due to a road), resulting in no change in number of patches and a decrease in mean patch area

clusters at the cluster-to-cluster scale as pools accessible within our maximum adult migration distance (340 m) of one another. We used Fragstats to calculate patch (i.e., cost-distance band) metrics, including mean patch area and number of patches resulting from each permit zone scenario (McGarigal et al. 2002).

We assessed permeability of our alternative future landscapes at three scales based on wood frog life history: (1) permeability among breeding pools; (2) permeability between breeding pools and preferred summer habitat (forested wetlands); and, (3) permeability among clusters of breeding pools. We defined functional connectivity between breeding pools and between breeding and summer habitat based on adult migration distance, as these scales are important primarily to migrating adults. We used a maximum adult migration distance of 340 m, the maximum migration recorded for adult wood frogs in our region (Baldwin et al. 2006). We used the mean dispersal distance of ~1,200 m (Berven and Grudzien 1990) for assessing permeability between clusters of pools. Smith and Green (2005) suggest that dispersal distances may exceed 10 km, so our figure is likely to be conservative. We used region-specific travel distances because amphibian habitat requirements are likely to vary regionally (Semlitsch et al. 2009). We explored different migration and dispersal distances in our sensitivity analysis to examine changes in effectiveness of permit zones

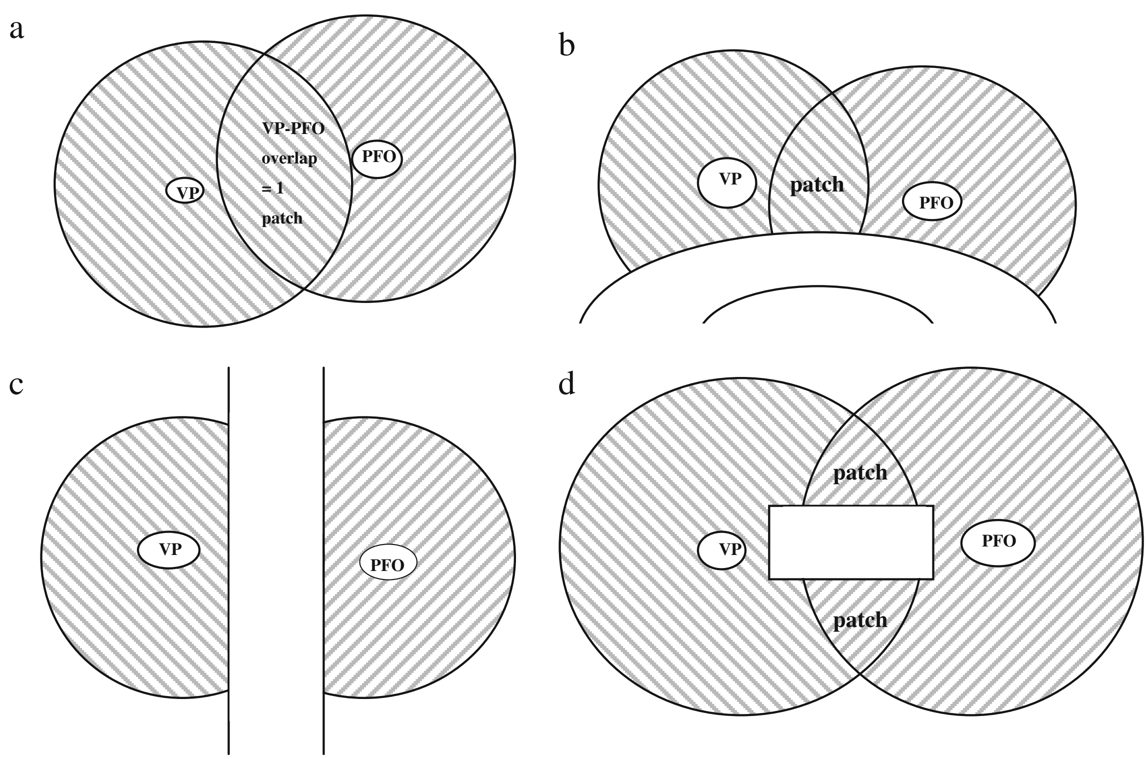


Fig. 2 Examples of patches for pool (VP)-to-summer habitat (palustrine forested wetland [PFO]) connectivity: **a** one undisturbed patch; **b** one patch made smaller by development; **c** patch eliminated by development; **d** one patch cut into two patches (e.g. by a single house lot)

in maintaining functional connectivity among habitat elements at different life stages and to capture a range of potential migration and dispersal distances.

Sensitivity Analysis

Our sensitivity analysis simultaneously examined two assumptions of the landscape permeability model, the maximum migration/dispersal distance and the values of the land cover cost coefficients. We halved or doubled the maximum migration/dispersal distances, which is equivalent in a landscape permeability model based on a cost surface, to doubling and halving, respectively, the cost coefficients assigned to land cover types.

We hypothesized that our results may be sensitive to the degree of clustering in our breeding pools, because our dataset indicated significant clustering of vernal pools ($z=-7.49$, $p<0.01$). We tested the importance of the degree of pool clustering by fitting a homogeneous Matern Cluster process model (Matern 1986) to the vernal pools in undeveloped portions of our study town with the function "kppm" in R's Spatstat package (Baddeley and Turner 2005). We masked developed areas, because there are presently no functioning vernal pools in those areas. We created seven simulated vernal pool layers with various degrees of clustering, following a Matern Cluster process. For each simulation, we varied the parameters controlling the intensity of cluster centers and the number of pools per cluster to produce different degrees of clustering, while forcing pool density to roughly equal the actual pool density (3.14/km^2) in undeveloped areas of our focal town. The simulations included a regular distribution (representing spatial repulsion, the opposite of clustering), a random distribution, and five distributions with increasing degrees of clustering. Nearest neighbor Z-scores from our simulated distributions ranged from +20.4 (regular pattern) to −10.1 (most clustered distribution). We then repeated our projections of future development and permeability analysis with the actual land cover in our study town for each simulated pool distribution. We assumed no open space requirement and protection of half of the pools, chosen at random, for these scenarios.

Results

Permeability Between Breeding Pools

The 2005 baseline landscape contains 57 patches (NP) with mean area (MN_AR)=111.8 ha (Table 2). Number of patches increased in all future scenarios, indicating that the original 57 patches were fragmented into smaller, disconnected patches, and permeability among breeding pools decreased. Protecting half of pools with permit zones consistently produced fewer fragmented patches (i.e., smaller increases in NP) and smaller reductions in patch size than scenarios without permit zones. Open space requirements of 0% or 25% and protection of half the pools with permit zones resulted in fragmentation of eight patches and reduction of mean patch area by 25–30 ha. Permit zones around all pools resulted in fewer fragmented patches and smaller reductions in patch size, indicating that vernal pool permit zones do offer some protection of connectivity among breeding pools.

Increasing requirements for open space in subdivisions generally improved pool-to-pool permeability. With one exception, incremental increases in open space increased patch size and decreased patch number in all permit zone scenarios (Table 2). The effect of increasing open space is greatest when no permit zones exist and least when all pools

Table 2 Pool-to-pool connectivity metrics on predicted future landscapes

Landscape/Scenario	No. Patches (NP)	Change in NP since 2005	Mean Patch Area [ha] (MN_AR)	Change in MN_AR since 2005
2005 - baseline	57	–	111.8	–
2035 - No Permit Zones				
No open space	73	+16	69.5	−42.4
25% open space	68	+11	77.8	−34.0
50% open space	63	+6	88.2	−23.6
2035 - Protection of 50% of pools				
No open space	65	+8	83.0	−28.8
25% open space	65	+8	86.2	−25.6
50% open space	61	+4	94.6	−17.3
2035 - Protection of all pools				
No open space	60	+3	93.9	−17.9
25% open space	59	+2	99.0	−12.8
50% open space	58	+1	101.6	−10.3

are protected, suggesting that to some extent, open space may substitute for direct protection of pool perimeters.

Permeability Between Breeding and Summer Habitat

In the absence of permit zones and open space, the number of patches connecting breeding and summer habitat changed very little relative to the baseline, however, small patches replaced large patches, decreasing mean patch area by 16.4 ha (Table 3). Results are similar when open space is included, with small decreases in patch number and size. While some patches are lost in all three no permit zone scenarios, more open space resulted in larger patches that were less fragmented, creating a more connected landscape between breeding and summering habitat (Table 3).

When half of the pools are protected, the reduction in number of patches for the 0%, 25%, and 50% open space scenarios is 3, 2, and 1 patches, respectively, while the reduction in patch size is 6.5, 4.8, and 3.7 ha, respectively. Patch sizes are consistently larger for increasing open space requirements than for the no permit zone scenarios. Protection of all pools in the 0% and 25% open space scenarios results in the largest patch sizes and greatest reductions in patch number of all future landscapes, likely because some patches that were fragmented in the no permit and half permit zone scenarios remain intact when all pools are protected.

Permeability Between Clusters of Pools

Our baseline landscape consists of 30 patches with a mean patch area of 800 ha (Table 4). Patches become fragmented and habitat is lost in all future scenarios. The greatest fragmentation and reduction in mean patch size occurred with no permit zones. Protecting half of pools produced smaller changes in both patch number and mean patch area than the absence of permit zones, and protecting all pools produced further improvements. Protecting all pools and requiring no open space produced results similar to no protection zones with 50% open space.

Sensitivity Analysis

Although varying the maximum migration/dispersal distance and cost coefficients in the landscape permeability model resulted in variation in the number of patches and mean patch area, the trends were consistent across the six future landscapes (3 biological scales X 2 migration/dispersal distances). The mean change in the metrics relative to the baseline for these six landscapes is presented in Table 5. Protecting half of pools produced a more connected landscape than was created with the absence of permit zones, and protecting all pools offered further improvements. In general, less patch fragmentation and larger patch sizes result from increasing the open space requirement.

Figure 3 graphs the relationship between the two landscape metrics and the degree of clustering at the pool-to-pool scale. There is a clear trend in the results, with greater clustering (indicated by lower Z-scores) corresponding to greater numbers of patches and smaller patch size, both indicative of greater fragmentation. The results of the clustering simulations are less compelling at the other scales; we do not present them here, however, we return to this issue in the Discussion.

Discussion

While breeding pool permit zones conserve a portion of amphibian breeding habitat, location of these protection

Table 3 Pool-to-summer habitat connectivity metrics on predicted future landscapes

Landscape/Scenario	No. Patches (NP)	Change in NP since 2005	Mn. Patch Area [ha] (MN_AR)	Change in MN_AR since 2005
2005 - baseline	35	–	68.6	–
2035 - No Permit Zones				
No open space	35	0	52.2	−16.4
25% open space	34	−1	55.8	−12.8
50% open space	33	−2	62.1	−6.5
2035 - Protection of 50% of pools				
No open space	32	−3	62.1	−6.5
25% open space	33	−2	63.8	−4.8
50% open space	34	−1	64.8	−3.7
2035 - Protection of all pools				
No open space	30	−5	69.0	0.4
25% open space	30	−5	71.5	2.9
50% open space	33	−2	67.2	−1.4

Table 4 Cluster-to-Cluster connectivity metrics on predicted future landscapes (max. dispersal=1200 m)

Landscape/Scenario	No. Patches (NP)	Change in NP since 2005	Mn. Patch Area [ha] (MN_AR)	Change in MN_AR since 2005
2005 - baseline	30	–	800.0	–
2035 - No Permit Zones				
No open space	37	+7	541.4	−258.5
25% open space	33	+3	632.3	−167.7
50% open space	32	+2	662.1	−137.9
2035 - Protection of 50% of pools				
No open space	34	+4	603.1	−196.8
25% open space	33	+3	645.4	−154.5
50% open space	31	+1	705.2	−94.8
2035 - Protection of all pools				
No open space	32	+2	649.1	−150.9
25% open space	31	+1	692.3	−107.6
50% open space	32	+2	677.3	−122.6

zones relative to other key habitat elements and human development patterns affects their conservation function. Vernal pool permit zones will provide greatest conservation benefit when the conservation, planning and development communities collaborate to identify appropriate areas for development that maximize landscape connectivity for species that use vernal pools.

Including permit zones around a larger percentage of breeding pools and requiring more open space in subdivisions create a greater number of larger patches that more effectively maintain functional connectivity at the pool-to-pool and cluster-to-cluster scales. At the pool-to-pool scale, permit zones protect local landscape connectivity, however, they allow fragmentation in areas travelled by wood frogs beyond the zone limits. Patterns in the results at the cluster-to-cluster scale are similar to those at the pool-to-pool scale, however the magnitude of change in the number of patches is smaller. It is important to note, however, that increases in the number of patches at the cluster-to-cluster scale indicate that an entire population may have been isolated from another population, thus decreasing the chance of recolonization after a local extinction. A relatively small number of such events could significantly affect the population as a whole, particularly in species such as the wood frog with a short life span and high fecundity (Harper et al. 2008). Furthermore, our study focuses on one relatively small town. This same pattern, if repeated over a larger area, could have serious consequences on the regional-scale probability of long-term survival. This suggests the benefit of landscape scale approaches to maintaining corridors between clusters of breeding pools, ideally by incorporating local knowledge and priorities and coordinating planning efforts across jurisdictional boundaries.

Table 5 Mean percent change relative to baseline, across six future landscapes with differing migration/dispersal distances

Landscape/Scenario	Avg. % Change in NP since 2005	Avg. % Change in MN_AR since 2005
2035 - No Permit Zones		
No open space	17.5	−31.3
25% open space	8.3	−22.2
50% open space	8.1	−18.9
2035 - Protection of 50% of pools		
No open space	11.0	−22.5
25% open space	5.5	−15.6
50% open space	3.5	−11.2
2035 - Protection of all pools		
No open space	5.1	−14.8
25% open space	4.5	−12.9
50% open space	3.9	−11.4

Because patches were defined differently at the pool-to-summer habitat scale, that is, consisting only of areas of overlap between two types of cost-distance bands, interpretation of the metrics is somewhat ambiguous. More patches may indicate more functional connections between breeding and summer habitat, or it may indicate fragmentation of patches. In reality, there may be some combination of patch

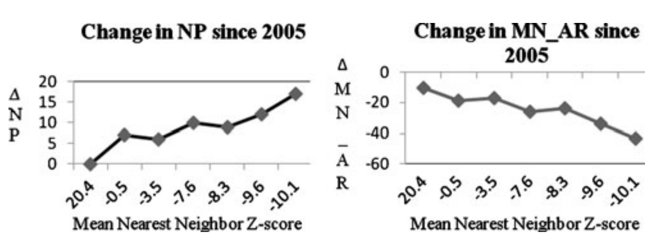


Fig. 3 Relationship between change in landscape metrics, number of patches (NP) and mean patch area (MN_AR), and degree of clustering of vernal pools

loss and fragmentation in all of the pool-to-summer habitat scenarios, so it may be necessary to focus on mean patch area at this scale. Decreases in patch size generally are less with greater percentages of open space and with permit zones around more pools, thus mirroring our results at the other scales. Nonetheless, the reductions in patch size do suggest some fragmentation occurring between breeding and summer habitat in most scenarios.

Our research demonstrates that effectiveness of a single conservation tool, such as regulated permit zones around vernal pools, varies spatially. Particularly in urbanizing areas, open space requirements for subdivisions complement permit zones around breeding pools by providing additional habitat for pool-breeding amphibians. Although we held other zoning and growth management policies (e.g., minimum lot size or maximum density requirements) constant in our model, they also are likely to alter permit zone effectiveness across jurisdictional boundaries, as they can vary widely across municipalities and regions. The degree of breeding pool clustering affects landscape permeability as well. Our results suggest that more clustered pools are subject to more fragmentation at the pool-to-pool scale. At the pool-to-summer habitat scale, our results were less compelling, we suspect, because it is not only the degree of pool clustering, but the proximity of pools to summer habitat that is important at this scale. At the cluster-to-cluster scale, a larger study area is likely needed to fully investigate the effects of pool clustering. Thus while we have demonstrated the effect of pool clustering on permit zone effectiveness, further research is needed to investigate the role of pool clustering across a larger landscape, as well as the influence of interjurisdictional policy differences in altering effectiveness of permit zones (Petranka et al. 2004).

A related issue to pool clustering is that of the location and pattern of significant vernal pools. In our 50% pool protection scenarios we randomly selected half of our pools for protection. If there are spatial patterns in the location of significant pools, this must be considered as well. For instance if more productive pools tend to be clustered close to one another, we might expect more potential for fragmentation at the pool-to-pool scale, as was the case in our clustering simulations. Significant pools appear to be randomly distributed in our region, however, additional research is needed in this area.

Given the benefit provided by large-area open space requirements, they may provide an alternative or additive approach for protecting vernal pools. In terms of the amount of land subject to regulation, however, vernal pool permit zones are a less restrictive policy than a large-area open space requirement. For most of our metrics, permeability was similar for the 50% open space/no permit zone scenario and the 0% open space/all pools protected scenario. The 50% open space scenario without permit zones sets aside ~782 ha of otherwise developable land in the form of subdivision open space, while the 76 m permit zone, if enforced around all vernal pools in town including those on parcels unlikely to be developed, involves ~154 ha of potentially otherwise developable land. Thus, while we acknowledge other benefits to open space and suggest that open space may enhance the effectiveness of permit zones, we do not suggest that it is an economically efficient substitute if the goal is realistic and consistent region-scale amphibian conservation. Further, vernal pool permit zones are implemented on a statewide basis, making their effects more predictable and consistent, as opposed to open space requirements which may vary from one town to the next.

We employed a static, simple, albeit realistic, method of locating houses and open space within subdivisions. The results differed substantially across housing patterns, even holding the amount of development and the vernal pool permit zone policy constant. Further economic research could improve our understanding of how developers decide where to build houses and where to locate open space within subdivisions; how returns to subdivision development may vary with levels and configurations of open space; and how communities adjust zoning policies over time in response to changing economic and ecological systems. A dynamic modeling approach could also examine the incremental effects of development, rather than our static, one-time period approach. Such improvements may help identify policies that could encourage housing and open space patterns that protect critical habitat and corridors of permeability. Our results show that the location and configuration of open space matters, particularly to less vagile species such as amphibians for which a relatively small area may serve as suitable habitat or may connect critical habitat requirements.

We suggest the need for a multi-scale approach to pool-breeding amphibian conservation that addresses the different scales at which key biological processes operate and that protects permeability between vital habitat elements at each scale. Pool-breeding amphibians have complex habitat requirements that encompass the needs of many other wildlife species (Mitchell et al. 2008), and thus progress toward vernal pool conservation can be an important component of a coarse filter, habitat-based strategy for wildlife conservation (deMaynadier 2011). Further we note that land use planning and conservation planning occur on the same landscape, however, they often are the responsibility of multiple stakeholders. Co-occurring policies may enhance or impair one another, and a multi-scale approach to conservation necessitates coordination among state regulatory agencies and local municipal planning activities. Although there is not a single solution to the complex issue of conservation planning for sensitive ecosystems, the emerging concepts of Conservation Zoning (Arendt 1996; Freeman and Bell 2011) and Green Infrastructure (Benedict and McMahon 2002; Tzoulas et al. 2007) involve proactive planning across scales to incorporate important ecological features into a linked network of open space, while accommodating residential growth. Similarly, we have combined an economic model of the behavior of people in land markets with a model of the wildlife responses to human decisions. In addition to highlighting the value of conservation planning at multiple scales, we stress the importance of an interdisciplinary approach at addressing natural resource policies that are economic, political, and ecological in nature.

Acknowledgments Thanks to S. Sader and K. Beard for insightful comments and guidance. P. deMaynadier provided thoughtful discussion that informed our development of the landscape permeability model. The manuscript was improved with reviews provided by B. Compton, D. Patrick, P. deMaynadier, and two anonymous reviewers. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. government. This material is based upon work supported by the National Science Foundation under award # EPS-0904155 and the Maine Agriculture and Forestry Experiment Station.

References

Anselin L (2002) Under the hood: issues in the specification and interpretation of spatial regression models. Agricultural Economics 17:247–267

Arendt R (1996) Conservation design for subdivisions: a practical guide for creating open space networks. Island Press, Washington

Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12: 1–42 URL: www.jstatsoft.org

Baldwin R, Calhoun AJK, deMaynadier PG (2006) Conservation planning for amphibian species with complex habitat requirements: a case study using movements and habitat selection of the wood frog *Rana sylvatica*. Journal of Herpetology 40:443–454

Baldwin RF, deMaynadier PG (2009) Assessing threats to pool-breeding amphibian habitat in an urbanizing landscape. Biological Conservation 142:1628–1638

Bauer DM, Paton PWC, Swallow SK (2010) Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations. Ecological Applications 20:798–815

Benedict MA, McMahon ET (2002) Green Infrastructure: smart conservation for the 21st century. Renewable Resources Journal 12–19

Berven KA, Grudzien TA (1990) Dispersal in the wood frog (Rana sylvatica): implications for genetic population structure. Evolution 44:2047–2056

Blomquist SM, Hunter ML Jr (2010) A multi-scale assessment of amphibian habitat selection: wood frog response to timber harvesting. Ecoscience 17:1–14

Bockstael NE (1996) Modeling economics and ecology: the importance of a spatial perspective. American Journal of Agricultural Economics 78:1168–1180

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conservation Biology 16:503–514

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conservation Biology 21:788–799

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128:231–240

deMaynadier P (2011) Vernal pools: milestones and misconceptions. IFW Insider: newsletter of the Maine Department of Inland Fisheries and Wildlife, Augusta, ME

ESRI (2006) ArcGIS v. 9.2 Environmental Systems Research Institute, Inc. Redlands, California, USA.

Fleming M (2004) A Review of techniques for estimating spatially dependent discrete choice models. In: Anselin L, Florax R (eds) Advances in spatial econometrics. Springer, Berlin

Freeman RC, Bell KP (2011) Conservation versus cluster subdivisions and implications for habitat connectivity. Landscape and Urban Planning 101:30–42

Gibbs JP, Reed JM (2008) Population and genetic linkages of vernal pool-associated amphibians. In: Calhoun A, deMaynadier PG (eds) Science and conservation of vernal pools in Northeastern North America. CRC Press, Boston

Gonzales EK, Gergel SE (2007) Testing assumptions of cost surface analysis—a tool for invasive species management. Landscape Ecology 22:1155–1168

Greene WG (2008) Econometric analysis 6/E. Prentice Hall, Upper Saddle River

Hamer AJ, McDonnell MJ (2008) Amphibian ecology and conservation in the urbanizing world. Biological Conservation 141:2432–3449

Harper EB, Rittenhouse TAG, Semlitsch RD (2008) Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. Conservation Biology 22:1205–1215

Hepinstall JA, Sader SA, Krohn WB, Boone RB, Bartlett RI (1999) Development and testing of a vegetation and land cover map of Maine. Tech. Bull. 173 Maine Agricultural and Forest Experiment Station, University of Maine, pp 104

Irwin EG, Bell KP, Geoghegan J (2003) Modeling and managing urban growth at the rural-urban fringe: a parcel-level model of residential land use change. Agricultural and Resource Economics Review 32:83–102

Joly P, Morand C, Cohas A (2003) Habitat fragmentation and amphibian conservation: building a tool for assessing landscape matrix connectivity. Comptes Rendus Biologies 236:S132–S139

Lehtinen RM, Galatowitsch SM, Tester JR (1999) Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19:1–12

LeSage JP (2000) Bayesian estimation of limited dependent variable spatial autoregressive models. Geographical Analysis 32:19–35

Lewis DJ, Plantinga AJ (2007) Policies for habitat fragmentation: combining econometrics with GIS-based landscape simulations. Land Economics 83:109–137

Lewis DJ, Provencher B, Butsic V (2009) The dynamic effects of open-space conservation policies on residential development density. Journal of Environmental Economics and Management 57:239–252

Mahaney WS, Klemens MW (2008) Vernal pool conservation policy: the federal, state, and local context. In: Calhoun A, deMaynadier PG (eds) Science and conservation of vernal pools in Northeastern North America. CRC Press, Boston

Matern B (1986) Spatial variation. Number 36 in lecture notes in statistics. Springer Verlag, New York

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html

MEGIS (2007) Data Catalog (http://megis.maine.gov/catalog/). Maine Office of GIS, Augusta, ME

MESPO (2003) Housing unit forecast by town to 2015. Maine State Planning Office, Augusta

Mitchell JC, Paton PWC, Raithel J (2008) The importance of vernal pools to reptiles, birds, and mammals. In: Calhoun A, deMaynadier PG (eds) Science and conservation of vernal pools in Northeastern North America. CRC Press, Boston

Oscarson DB, Calhoun AJK (2002) Developing vernal pool conservation plans at the local level using citizen-scientists. Wetlands 27:80–95

Petranka JW, Smith CK, Scott AF (2004) Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications 14:1065–1078

Petranka JW, Holbrook CT (2006) Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? Restoration Ecology 14:404–411

Popescu VD, Hunter ML Jr (2011) Clearcutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecological Applications 21:1283–1295

Ray N, Lehmann A, Joly P (2002) Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. Biodiversity and Conservation 11:2143–2165

Schadt S, Knauer F, Kaczensky P, Revilla E, Wiegand T, Trepl L (2002) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian Lynx. Ecological Applications 12:1469–1483

Semlitsch RD (2000) Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615–631

Semlitsch RD, Todd BD, Blomquist SM, Calhoun AJK, Gibbons JW, Gibbs JP, Graeter GJ, Harper EB, Hocking DJ, Hunter ML Jr, Patrick DA, Rittenhouse TAG, Rothermel BB (2009) Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. Bioscience 59:853–862

Singleton PH, Gaines WL, Lehmkuhl JF (2004) Landscape permeability for grizzly bear movements in Washington and southwestern British Columbia. Ursus 15:90–103

Smith MA, Green DM (2005) Disperal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128

Smith M, Palmer M, Brenner A (2006) Landcover development: state/federal collaboration improves data quality, saves money. Earth Imaging Journal 3:16–19

Tzoulas K, Kropela K, Venn S, Yli-Pelkonen V, Kazmierczak A, Niemela J, James P (2007) Promoting ecosystem and human health in urban areas using Green Infrastructure: a literature review. Landscape and Urban Planning 81:167–178

Vasconcelos D, Calhoun AJK (2004) Movements patterns of adult and juvenile *Rana sylvatica* (Le Conte) and *Ambystoma maculatum* (Shaw) in three restored seasonal pools in Maine. Journal of Herpetology 38:551–561

Windmiller B, Calhoun AJK (2008) Conserving vernal pool wildlife in urbanizing landscapes. In: Calhoun A, deMaynadier PG (eds) Science and conservation of vernal pools in Northeastern North America. CRC Press, Boston

Wu J, Irwin EG (2008) Optimal land development with endogenous environmental amenities. American Journal of Agricultural Economics 90:232–248