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Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations

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Abstract. Recent declines in amphibian populations have raised concern among conservation biologists, with habitat loss and degradation due to human activities among the leading causes. The most common policies used to protect the habitat of pond-breeding amphibians are wetland regulations that safeguard the wetland itself. However, many amphibians spend much of their adult lives foraging and over-wintering in upland habitats and exist as metapopulations with dispersal among ponds. With no consideration of lands in the dispersal matrix, wetland policies may be ineffective at protecting amphibians or other wetland species that disperse across the landscape. This paper examined the adequacy and cost effectiveness of alternative conservation policies and their corresponding land use patterns on the long-term persistence of pond-breeding amphibians in exurban landscapes. We used computer simulations to compare outcomes of wetland buffer policies and broader landscape-wide conservation policies across a variety of landscape scenarios, and we conducted sensitivity analyses on the model's species parameters in order to generalize our results to other wetland species. Results showed that, in the majority of human-dominated landscapes, some amount of dispersal matrix protection is necessary for long-term species persistence. However, in landscapes with extremely low-intensity land use (e.g., low-density residential housing) and high pond density, wetland buffer policies may be all that is required. It is not always more cost effective to protect core habitat over the dispersal matrix, a common conservation practice. Conservation costs that result from forgone residential, commercial, or agricultural activities can vary substantially but increase in a nonlinear manner regardless of land use zoning. There appears to be a threshold around an average habitat patch occupancy level of 80%, after which opportunity costs rise dramatically.

Key words: *Ambystoma*; amphibian; connectivity; conservation; cost effectiveness; dispersal; ecological-economic model; landscape; metapopulation; policy analysis; Richmond, Rhode Island, USA.

INTRODUCTION

Recent declines in amphibian populations have raised concern among conservation biologists (Green 2003), with habitat loss and degradation due to human activities hypothesized to be among the leading causes (Alford and Richards 1999). Residential and commercial development, agriculture, and forestry practices can all lower occupancy probabilities of amphibians in core habitat of breeding ponds (Guerry and Hunter 2002, Rothermel and Semlitsch 2002, Woodford and Meyer 2003, Homan et al. 2004, Weyrauch and Grubb 2004, Semlitsch et al. 2008). Roads, in particular, have detrimental impacts on amphibian populations (Fahrig et al. 1995, Vos and Chardon 1998, Trombulak and Frissell 2000, Hels and Buchwald 2001). In addition to the direct concern for amphibian populations, amphibians are good indicators of healthy wetland and riparian

ecosystems and may act as umbrella species whereby protection of amphibians leads to the protection of other wetland species (Vitt et al. 1990, Hecnar and M'Closkey 1996, Welsh and Droege 2001).

The most common policies used to protect pond-breeding amphibians in the United States are state and federal wetland regulations that safeguard the wetland itself and, in some cases, a small buffer of terrestrial habitat surrounding the wetland. However, many pond-breeding amphibians spend much of their adult lives foraging and overwintering in upland habitats, areas not directly protected by current regulations (Semlitsch 1998, 2007, Semlitsch and Bodie 1998, 2003, Harper et al. 2008). The discrepancy between wetland species habitat use and the habitat protection afforded by current wetland regulations prompted ecologists to advocate for additional protection of large buffers of critical upland terrestrial habitat for amphibians (Semlitsch 1998, Calhoun and Klemens 2002, Semlitsch and Bodie 2003, Calhoun et al. 2005).

Wetland conservation policies thus focus on the protection of local populations at individual ponds.

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However, human activities endanger long-term species persistence not only by reducing and degrading core habitat, but also by impeding dispersal among habitat patches (Gill 1978, Sjogren-Gulve 1994, Pope et al. 2000, Semlitsch 2007). For example, pond-breeding amphibians disperse across the landscape from one pond to another, which often occurs during the juvenile stage of the amphibian life cycle when some portion of juveniles leave their natal pond and establish themselves as adult breeders in other ponds. In this way, many amphibian species are thought to exist as metapopulations for which connectivity among ponds is critical to long-term survival (Marsh and Trenham 2001, Green 2003, Harper et al. 2008). Metapopulations consist of local subpopulations distributed throughout a patchy environment, with each subpopulation occupying its own habitat patch and exchanging individuals through dispersal (Hanski 1999). Without considering lands critical to dispersal between ponds (i.e., dispersal matrix lands), wetland policies may be ineffective at protecting amphibians and other wetland species (Harper et al. 2008). Additional or alternative conservation policies that protect portions of the dispersal matrix may be required in some human-dominated landscapes.

Conservation plans often focus on ecological benefits with little or no consideration for costs. However, incorporating economic costs into conservation planning can lead to greater ecological benefits for a limited conservation budget (Ando et al. 1998, Newburn et al. 2005, Polasky et al. 2005, Drecshler et al. 2006, Naidoo et al. 2006). Including economic considerations early in the planning process can avoid later changes to the conservation plan. For example, a recent decision by the U.S. Fish and Wildlife Service excluded >74 000 ha from its critical habitat designation for the California tiger salamander (*Ambystoma californiense*), almost half of the original proposal of 155 000 ha, because of the high opportunity costs associated with forgone residential and commercial development (U.S. Fish and Wildlife Service 2005). Could earlier consideration of economic costs have averted this shift in habitat designation?

This study combines metapopulation modeling with land use values to illustrate how economic considerations might aid conservation planning across a landscape. We combined principles of economics and ecology within a single framework to examine the adequacy and cost effectiveness of alternative conservation policies and their corresponding land use patterns on the long-term persistence of pond-breeding amphibians. We extended the metapopulation model of Hanski (1994) to incorporate core habitat degradation and dispersal barriers due to human land use. Our approach considered the roles of habitat patches and dispersal matrix while examining the opportunity costs of restricting land use as prescribed by a variety of conservation policies. We applied our model to a landscape based on an exurban community at the

rural–urban fringe. Many exurban communities in the United States are experiencing heavy development pressure and are considering implementation of a variety of land use conservation policies. We compared land use scenario outcomes that result under wetland buffer policies and landscape-wide conservation policies. We extended our analysis to multiple hypothetical landscapes representative of a range of exurban communities in order to generalize our results.

This study illustrates the application of a spatially realistic metapopulation model to wetland species and adds to the growing body of research that incorporates economics in conservation planning. The modeling approach used here can assist policy makers in finding ways to reduce the costs associated with achieving chosen levels of species protection or to increase species protection without increasing costs to landowners. While this study focuses on conservation of pond-breeding amphibians, the approach can be generalized to other species that exist as metapopulations.

METHODS

In this study, we assess ecological and economic outcomes of a variety of land use conservation policies in order to determine the appropriateness of wetland buffer policies for the protection of wetland species. A conservation policy describes where and how much land conservation occurs and, in doing so, restricts development. The term “development” used throughout this study refers to human-dominated land uses, including residential, commercial, industrial, and agricultural land use. A corresponding opportunity cost arises from restrictions on development. We used a spatially realistic metapopulation model to assess the long-term persistence of wetland species that resulted across a variety of conservation policies and exurban landscapes.

Amphibian metapopulation model

Previous researchers defined two measures of long-term metapopulation persistence: metapopulation capacity and metapopulation size (Hanski 1994, Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001). Both measures are derived from an occupancy-based metapopulation model in which the probability that a particular habitat patch is occupied is based upon local colonization and extinction rates. Colonization and extinction rates are, in turn, based upon the size and quality of habitat patches, the spatial arrangement of the habitat patch network, and dispersal barriers. Both metapopulation capacity and metapopulation size ignore the current occupancy configuration. Rather, they reflect the long-term steady-state equilibrium that is based solely on landscape structural elements and parameters of the focal species (Hanski and Ovaskainen 2003). These measures are analogous to the carrying capacity in traditional ecological models, such as the logistic growth model, whereby a larger carrying capacity is indicative of a larger equilibrium

population. Populations in landscapes with a larger metapopulation capacity or metapopulation size have a greater probability of long-term persistence. Habitat patch destruction, habitat patch deterioration, and dispersal barriers resulting from human-induced land use change all lower the metapopulation capacity and metapopulation size of a landscape.

Both metapopulation capacity and metapopulation size are based on a particular landscape's structure, which consists of habitat patch "effective areas" and inter-patch (dispersal matrix) "connectivity." Habitat patch effective area is based not only on patch size, but also on natural habitat quality and the quantity and type of development within the patch. More and greater intensity of development reduce effective area. Amphibian habitat patches are defined as the wetland itself (larval habitat) and a terrestrial upland buffer (foraging and overwintering habitat) but not dispersal matrix lands. Thus, in the amphibian case, development of habitat patches refers to development of the terrestrial buffer. Assuming a linear functional form, the effective area of habitat patch i , g_i , may be written as

$$g_i = \begin{cases} H_i A_i - \omega_{Ai} Q_{Ai} & \text{when } H_i A_i > \omega_{Ai} Q_{Ai} \\ 0 & \text{otherwise} \end{cases} \quad (1)$$

where A_i and H_i are the size and quality of habitat patch i , Q_{Ai} is the quantity of development that occurs in habitat patch i , and ω_{Ai} is a species-specific land use intensity parameter that indicates the marginal effect of development on effective area for a particular species. The marginal effect of development on effective area depends on the type of development and the target species (Wiens 1997). For example, amphibians are more likely to forage in areas of low-density development where some forest cover remains rather than in areas of high-intensity commercial development covered with parking lots. Because exurban communities tend to be a mix of land uses, different land use intensity parameters are required for each type of development that occurs within the landscape.

Connectivity measures the ability of the species to disperse across the landscape and is based on the distance between habitat patches and the amount and type of land use that exists in this dispersal matrix. An exponential form of connectivity, f_{in} , is commonly used (Fleishman et al. 2002, Moilanen and Nieminen 2002):

$$f_{in} = [1 - B_{in}] \exp(-\alpha d_{in}) \quad (2)$$

where α is a species-specific parameter that reflects the dispersal ability of the focal species ($1/\alpha$ is the mean dispersal distance), d_{in} is the distance between habitat patches i and n , and B_{in} is a barrier function that measures the permeability of the dispersal matrix among patches (Moilanen and Hanski 1998). The greater the barrier between two patches, the smaller the contribution of those patches toward long-term persistence of the metapopulation. Because the connectivity between two

habitat patches can include multiple land uses, the dispersal matrix is divided into multiple dispersal matrix units, each one homogeneous in the type of development that can occur. Assuming a linear functional form, the barrier function between patches i and n may be written as

$$B_{in} = \begin{cases} \sum_{j=1}^J \left(\frac{d_{jin} \omega_{Zj} Q_{Zj}}{d_{in} Z_j} \right) & \text{when } \frac{\omega_{Zj} Q_{Zj}}{Z_j} < 1 \text{ for all } j \\ 1 & \text{otherwise} \end{cases} \quad (3)$$

where Z_j is the size of dispersal matrix unit j , d_{jin} is the distance between patches i and n that falls within dispersal matrix unit j , Q_{Zj} is the quantity of development that occurs in dispersal matrix unit j , and ω_{Zj} is the species-specific land use intensity parameter that indicates the marginal effect of development on connectivity. As in the case for effective area, different types of development will have different effects on species dispersal. For example, some species of amphibians will not cross agricultural fields while others will (Guerry and Hunter 2002, Weyrauch and Grubb 2004). In addition, the same type of development may affect species differently in habitat patches vs. dispersal matrix; thus, there is an additional set of land use intensity parameters for dispersal matrix.

Metapopulation capacity and metapopulation size are based on an $N \times N$ landscape structure matrix with elements consisting of habitat patch effective areas and inter-patch connectivity for an N -patch network (Hanski 1994, Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001). Each element, m_{in} , gives the contribution that habitat patch n makes to the colonization of habitat patch i when patch i is empty, multiplied by the expected lifetime (i.e., probability of local extinction) of patch i when it is occupied (Ovaskainen and Hanski 2003):

$$m_{in} = g_i^{\zeta_{ex}} + \zeta_{im} g_n^{\zeta_{em}} f_{in} \quad (4)$$

where ζ_{im} and ζ_{em} are species-specific immigration and emigration rate parameters that scale effective area to reflect the probability of immigrants reaching patch i and the probability of emigrants leaving patch i , respectively (Moilanen and Hanski 1998). The variable ζ_{ex} represents a species-specific parameter that relates increases in effective area to decreases in the probability of local extinction (Hanski 1992). In general, a larger effective area produces more emigrants, attracts more immigrants, and supports a larger local population that is less likely to go extinct. However, these relationships are not typically linear and the three species-specific "scaling" parameters adjust the effective area to account for this nonlinearity. For example, a doubling of habitat patch area does not necessarily double the probability that immigrants will find and colonize an empty patch. The processes of local extinction and colonization, which rely on immigration and emigration, are what

drive the long-term probability of metapopulation persistence.

Both metapopulation capacity and metapopulation size are measures of a landscape's ability to support a viable metapopulation over the long term. Metapopulation capacity may be considered an approximation of the quantity of species habitat in the landscape that accounts for the quantity and quality of core habitat patches, the spatial configuration of the habitat patch network, and dispersal barriers. Metapopulation capacity, K_M , is the leading eigenvalue of the landscape structure matrix described here (Hanski and Ovaskainen 2000). Thus, the metapopulation capacity provides a one-dimensional summary measure of the N -dimensional system (Hanski and Ovaskainen 2003). A species is predicted to persist in a landscape if the metapopulation capacity of that landscape is greater than the species' extinction threshold:

$$K_M > \delta \quad (5)$$

where $\delta = e/c$ and c and e are species-specific colonization and extinction rate parameters, respectively. Parameter e measures the natural ability of the species to persist as a local population, while parameter c measures the natural ability of the species to colonize empty habitat patches (Ovaskainen and Hanski 2002).

Metapopulation size measures the average probability of habitat patch occupancy or, alternatively, the weighted fraction of occupied patches at equilibrium (Ovaskainen and Hanski 2001). Metapopulation size, S_M , is also derived from the landscape structure matrix and is related to metapopulation capacity (Ovaskainen and Hanski 2003):

$$S_M = 1 - \frac{\delta}{K_M}. \quad (6)$$

Values of metapopulation size range between 0 and 1, reflecting the rarity or commonness of the species in the given patch network (values closer to 0 correspond to rare species and values closer to 1 correspond to common species).

Because metapopulation size measures the mean probability of habitat patch occupancy, it can also be interpreted as an approximation of the mean probability of long-term metapopulation persistence for the network of habitat patches in the landscape. Metapopulation size provides an easier and more meaningful interpretation for conservation policy analysis, especially for those people unfamiliar with particular species, who would be unable to assess a quantity of habitat measure. Thus, metapopulation size was used as the measure of long-term metapopulation persistence in all policy analyses.

Baseline landscape definition

This study focused on exurban landscapes at the rural-urban fringe, which contain a mix of residential, commercial, and agricultural land uses but also sub-

stantial amounts of undeveloped land. Because of increases in development pressure, many exurban communities are considering implementation of conservation policies that maintain ecosystem health and natural amenities. Richmond, Rhode Island, USA, is one such community. Richmond experienced dramatic growth during the 1990s, with the number of housing units increasing by 40% from 1875 to 2620 (U.S. Census Bureau 2000). A "buildout" analysis estimated the potential for an additional 10 000 single-family housing units under existing zoning and subdivision regulations (MPS 2004). In 2005, the community was considering implementing new land use regulations that would reduce the intensity of new residential development. We modeled our baseline landscape after Richmond in order to provide specific results of a real-world case study. However, we also performed extensive analyses on alternative hypothetical landscapes, varying the types of land use, the density of wetlands, and the definition of habitat patches, to allow for presentation of a broader set of results.

In 2005, Richmond consisted of ~ 100 km² of predominantly mixed-deciduous forest interspersed with a mosaic of residential development, commercial centers, and agricultural land. The town was divided into more than 30 zoning districts of varying sizes and land use types. For tractability, we pooled several of the smaller districts into larger districts. The resulting baseline landscape consisted of 16 "neighborhood" land units, each one zoned for one and only one of five different land use types (Table 1, Fig. 1). The baseline landscape contained 34.6% low-density residential housing, 48.5% medium-density residential housing, <0.5% high-density residential housing, 5.1% commercial and industrial land, and 11.4% agricultural land (Table 1). To establish a set of existing (2005) conditions, we acquired parcel-level tax assessor data from the town of Richmond that included information on whether the parcel was developed (24%), protected (33%), or vacant (undeveloped and unprotected; 43%).

Using geographic information system (GIS) software (ESRI 2005) and data from Rhode Island's GIS, we implemented a ponds-as-patches approach to define habitat patches, where the patch includes the pond and a buffer of terrestrial upland habitat (Gill 1978, Sjogren-Gulve 1994, Carlson and Edenhamn 2000, Pope et al. 2000). This approach is particularly appropriate for pond-breeding caudates and anurans that remain in the upland adjacent to the site throughout the nonbreeding season (Vasconcelos and Calhoun 2004, Gamble et al. 2007) because this allowed us to clearly delineate habitat patches. Potential seasonal ponds were previously identified and delineated using 1:12 000-scale panchromatic aerial photographs (Skidds and Golet 2005). We considered at least 334 potential seasonal ponds as viable amphibian breeding habitat, many of which are located in close proximity to neighboring ponds. Because Petranka et al. (2004) suggested that local

TABLE 1. Landscape conditions in 16 neighborhood land units in Richmond, Rhode Island, USA, in 2005.

Land unit	Developed (ha)	Protected (ha)	Vacant (ha)	Zoning	No. patches	Land value (US\$/ha)
1	90	198	96	R-3	11	46 120
2	519	533	659	R-2	31	66 164
3	255	79	447	R-2	13	65 655
4	110	752	261	R-3	29	43 889
5	510	418	963	R-2	39	70 966
6	124	778	452	R-3	26	46 942
7	13	77	421	AGR	11	29 166
8	49	207	111	R-3	7	47 091
9	34	5	66	R-2	1	56 435
10	68	305	263	AGR	9	27 331
11	323	0	128	COM	13	178 655
12	12	4	22	R-1	1	108 371
13	58	0	3	COM	4	131 520
14	23	0	30	R-3	2	43 121
15	105	20	82	R-3	10	58 028
16	112	3	286	R-2	7	68 145
Town total	2405	3381	4290		214	

Notes: Land unit numbers correspond to numbers in Fig. 1. Zoning abbreviations are: R-1, high-density residential land (0.4-ha minimum lot sizes); R-2, medium-density residential land (0.8-ha minimum lot sizes); R-3, low-density residential land (1.2-ha minimum lot sizes); COM, commercial and industrial land; AGR, agricultural land.

amphibian populations less than 100 m apart are not demographically independent and should not be treated as subpopulations, we designated ponds within 100 m of each other as a single local population resulting in 214 distinct pond clusters. For each pond cluster, we defined 165-m buffer zones, measured from the pond center, of core terrestrial upland habitat as recommended by Semlitsch (1998) in order to encompass 95% of local populations for ambystomatid salamanders. We calculated habitat patch sizes and distances between each habitat patch pair as well as the portion of those distances that fell into each of the 16 dispersal matrix units. For pond-breeding amphibians, habitat patch quality is largely driven by the hydroperiod of the pond (Egan and Paton 2004), which varies over time as a result of stochastic weather events. Because the model used in this study is deterministic, habitat patch quality was assumed to be constant across the landscape ($H_i = 1$ for all i). Because the habitat patches are small relative to the size of the economically defined neighborhood land units, we assumed entire habitat patches had the land use zoning of the neighborhood land unit into which its centroid fell. The town is surrounded on three sides by rivers thought to be impermeable to amphibians. Although there is some opportunity for dispersal into and out of the northeast corner of the town, we assumed that this group of local populations was a separate metapopulation.

Land values

Because the model assumed development was evenly distributed throughout each land unit, a representative land value for each neighborhood land unit was needed. To determine these land values, we used LIMDEP

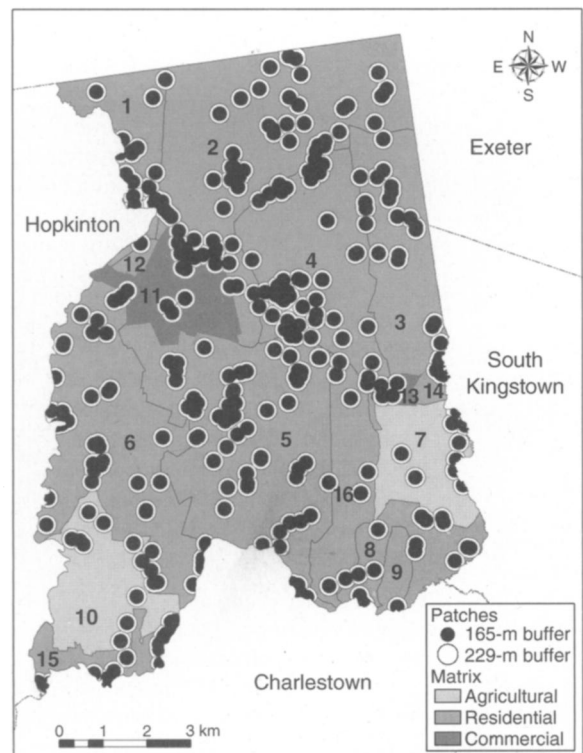


FIG. 1. Map of baseline landscape in Richmond, Rhode Island, USA, containing 16 neighborhood land units delineated by thin solid lines and shaded according to primary land use type. Numbers correspond to neighborhood land units described in Table 1. Dark areas are zoned for agricultural and industrial land use; light areas are zoned for residential land use; remaining areas are zoned for residential land use. There are 214 habitat patches and 16 dispersal matrix units. Dark circles are 165-m wetland buffers, and white circles are 229-m wetland buffers.

TABLE 2. *Ambystoma* salamander parameter values used in calculations of metapopulation size.

Parameter	Description	Value (range)
α	inverse dispersal distance	2.5
δ	extinction threshold	0.555
ζ_{ex}	patch area scaling for extinction	0.429
ζ_{im}	patch area scaling for immigration	0.0
ζ_{em}	patch area scaling for emigration	0.5
ω_{A1}	effective-area land use intensity for high-density residential	0.92 (0.69–0.99)
ω_{A2}	effective-area land use intensity for medium-density residential	0.87 (0.53–0.96)
ω_{A3}	effective-area land use intensity for low-density residential	0.71 (0.03–0.89)
ω_{A4}	effective-area land use intensity for commercial/industrial	0.98 (0.93–1.0)
ω_{A5}	effective-area land use intensity for agriculture	0.87 (0.69–0.96)
ω_{Z1}	dispersal barrier land use intensity for high-density residential	0.95 (0.78–0.99)
ω_{Z2}	dispersal barrier land use intensity for medium-density residential	0.88 (0.78–0.96)
ω_{Z3}	dispersal barrier land use intensity for low-density residential	0.73 (0.53–0.89)
ω_{Z4}	dispersal barrier land use intensity for commercial/industrial	0.99 (0.93–1.0)
ω_{Z5}	dispersal barrier land use intensity for agriculture	0.88 (0.78–0.96)

version 8.0 (Greene 2002) to perform multivariate ordinary least-squares regressions using Richmond tax assessor data. Land values ranged from a little more than US\$27 300 per ha for a 2-ha lot in agricultural districts to more than US\$178 600 per ha for a 0.4-ha lot in the central business district (Table 1). Habitat patches and dispersal matrix units were assigned the land values of the corresponding neighborhood land unit.

Species parameters

We selected a family of pond-breeding salamanders (Ambystomatidae) for our analyses because (1) they are particularly vulnerable to human-induced changes to their environment, (2) they are among the most abundant pond-breeding amphibians in Rhode Island (Egan and Paton 2004) and throughout much of the northeastern United States (DeGraaf and Rudis 1983), (3) it was difficult to get a complete set of parameters for a single species, and (4) the behaviors (e.g., habitat use, migration, and dispersal ability) are thought to be similar among the species. Among ambystomatids, both spotted salamanders (*A. maculatum*) and marbled salamanders (*A. opacum*) breed in Richmond. We focused on one particular family of amphibians in order to provide a specific case study. However, we also conducted substantial parameter sensitivity analysis and conservation policy analysis across alternative landscapes to allow for a broader interpretation of results.

Direct estimation of all required species parameters (Table 2) was beyond the scope of this study, and most were derived from existing ecology literature. Ecologists are just beginning to understand amphibian dispersal capabilities among ponds (Semlitsch 2007). Adult ambystomatid salamanders show high site fidelity to breeding ponds and the majority of dispersers are juveniles that disperse from the natal pond and establish breeding site fidelity in later years (Gamble et al. 2007). Gamble et al. (2006) quantified marbled salamander juvenile dispersal into non-natal ponds at distances up to 1230 m, with a mean dispersal distance of 269 m and

91% of dispersal events occurring between 100 and 400 m. Using the upper bound of this range, we set the inverse dispersal distance parameter (α) equal to $1 \div 0.4 = 2.5$.

The extinction threshold (δ) is calculated by dividing the species' extinction rate, e , by the species' colonization rate, c . Using five years of spotted salamander data collected in earlier studies (Mitchell 2005, Skidds and Golet 2005), we calculated the colonization rate as the ratio of the number of actual colonization events (years the species was absent one year, but present the next year) to the total number of potential colonization events (years the species was absent one year and a subsequent year of data was available) and the extinction rate as the ratio of the number of actual extinction events (years the species was present one year, but absent the next year) to the total number of potential extinction events (years the species was present and a subsequent year of data was available).

The patch area scaling parameter (ζ) consists of three components: ζ_{ex} , ζ_{im} , and ζ_{em} . Empirical studies have shown individual scaling parameters to vary widely, ranging from a minimum of 0.05 to a maximum of 2.30, with larger values corresponding to larger body sizes (Ovaskainen 2002). The sum of the three parameters ($\zeta = \zeta_{\text{ex}} + \zeta_{\text{im}} + \zeta_{\text{em}}$) generally falls between 1.0 and 2.0 for a "typical" metapopulation (Ovaskainen 2002). A single amphibian study estimated $\zeta_{\text{ex}} = 0.429$, $\zeta_{\text{im}} = 0.0$, and $\zeta_{\text{em}} = 0.5$ for a tree frog (*Hyla arborea*) metapopulation (Vos et al. 2000). Setting the immigration scaling parameter equal to zero may be reasonable because estimates of the extinction scaling parameter often include the immigration scaling parameter (Ovaskainen 2002). Since these tree frog parameters were the only data available for any species of amphibian, they were used in this study.

The land use intensity parameters (ω_{A_j} and ω_{Z_j}) were derived from Compton et al. (2007), who convened a panel of amphibian experts to estimate ambystomatid salamander dispersal and migration "resistance" values for 24 land cover types. Dispersal refers to movement

from one pond to another while migration refers to movement from wetland to upland habitat. Thus, dispersal resistance corresponds to ω_Z while migration resistance corresponds to ω_A . We used their low-density residential, high-density residential, urban, and nursery land cover types to correspond with our medium-density residential, high-density residential, commercial/industrial, and agricultural land uses, respectively. Compton et al. (2007) did not have a land cover type that corresponded with our low-density residential land use (1.2-ha minimum lot sizes), so we assumed that the resistance would be half the resistance of their low-density residential land cover. Their resistance values ranged from 1 to 40, with 1 corresponding to no resistance and 40 corresponding to a full barrier. We converted their values to a 0–1 range, such that 0 corresponded with no resistance and 1 corresponded to a full barrier. As in the Compton et al. (2007) study, we assumed forest land offered no resistance (a land use intensity of 0 in our study).

Species parameter sensitivity analysis

In order to determine which species parameters had the greatest influence on model output and to broaden our analysis beyond a single family of salamanders, we varied the parameters one at a time $\pm 50\%$ and calculated the percentage of change in metapopulation size from the original value. We also calculated a sensitivity index (SI) that gives the percentage of difference in metapopulation size when varying the parameter from its minimum value to its maximum value (Hamby 1994):

$$SI = \frac{S_{Mmax} - S_{Mmin}}{S_{Mmax}} \quad (7)$$

In addition, we varied the land use intensity parameters one at a time from the minimum to the maximum “expert” values and calculated the percentage of change in metapopulation size and the sensitivity index. We repeated the parameter sensitivity analysis for several landscape structures and conservation policies.

Conservation policy analysis

We analyzed a series of 25 potential conservation policies that varied the levels of protection in habitat patches, dispersal matrix, or the entire landscape between 0% and 100%. Each conservation policy consisted of a pair of protection levels: percentage of habitat patch protection and percentage of dispersal matrix protection. Policies that provided zero protection (0%) of dispersal matrix were representative of wetland buffer policies. Policies that provided the same level of protection in habitat patches and dispersal matrix were representative of landscape-wide conservation policies. For each policy alternative, we calculated metapopulation size (S_M ; Eq. 6) and the opportunity cost (OC) associated with forgone development:

$$OC = \sum_{i=1}^N R_{Ai}P_{Ai} + \sum_{j=1}^J R_{Zj}P_{Zj} \quad (8)$$

where P_{Ai} and P_{Zj} are the quantities of protected land in habitat patch i and dispersal matrix unit j that result from implementation of the conservation policy, R_{Ai} and R_{Zj} are per hectare land values in habitat patch i and dispersal matrix unit j , N is the number of habitat patches, and J is the number of dispersal matrix units. Policy analysis assessed the ecological benefits and economic costs associated with the final landscape that resulted at full buildout for each policy alternative. “Full buildout” is a planning term that refers to the land use state at which no additional development can legally take place given the set of land use restrictions. Because the model is static, we assumed all protected land was forested at full buildout. All calculations were performed using MATLAB 7.4 (MathWorks 2007).

Landscape structure analysis

To broaden our analysis beyond the Richmond baseline landscape, we conducted conservation policy analysis on several hypothetical landscapes that varied across three main factors. First, Richmond had a large portion of land area zoned for low-density residential land use. Several studies have shown that the landscape composition affects the probability of successful migration between pond and upland (deMaynadier and Hunter 1999, Faccio 2003, Montith and Paton 2006, Rittenhouse and Semlitsch 2006) and dispersal among habitat patches (Joly et al. 2001, Ricketts 2001, Ray et al. 2002, Compton et al. 2007, McDonough and Paton 2007). If more land were zoned for more intense land uses, metapopulation size would decrease while opportunity cost would increase for each policy alternative. To assess the implications of different land use intensities, we defined five homogeneous landscapes, one for each land use type in Richmond (Table 1). We used an area-weighted mean of land values from the neighborhood land units of the corresponding land use type in the calculation of opportunity costs.

Second, the baseline Richmond landscape contained a relatively high density of ponds, 3.30 ponds/km² compared to a density of 2.02 ponds/km² throughout the larger watershed. Gibbs' (1993) study area in Maine, USA, had a pond density of 0.59 ponds/km², Semlitsch and Bodie's (1998) study area in South Carolina, USA, had a pond density of 0.48 ponds/km², while four additional study areas in Maine had pond densities of 0.77 ponds/km², 1.48 ponds/km², 1.49 ponds/km², and 2.72 ponds/km² (R. Freeman, *personal communication*). In landscapes with lower pond density, dispersal matrix lands would be even more important for metapopulation persistence on both ecological and economic grounds. To examine the conservation implications of habitat patch density, we conducted policy analysis for additional hypothetical landscapes with pond densities lower than the baseline. We defined two additional sets

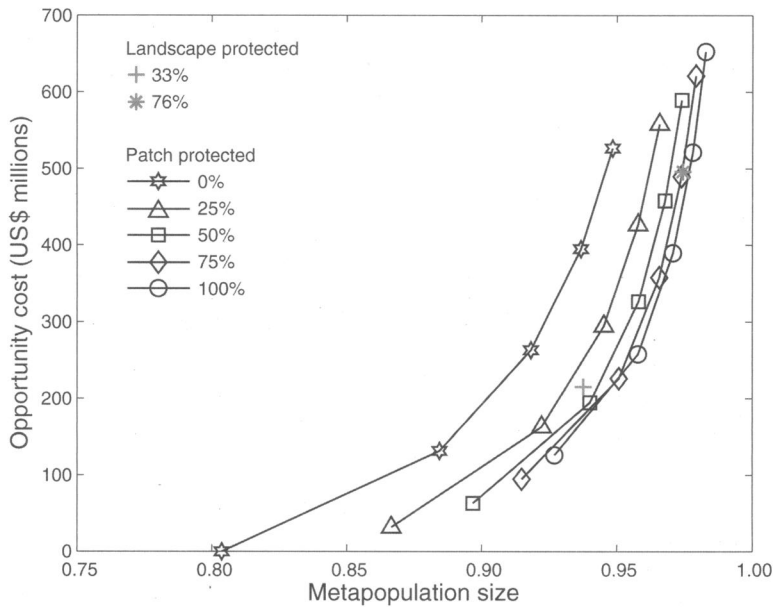


FIG. 2. Opportunity costs of forgone development and salamander metapopulation size for five series of conservation policies and two additional landscape-wide conservation policies all applied to the Richmond baseline landscape. For each of the five policy series, each individual point corresponds to a pair of protection levels: percentage of patch protected and percentage of matrix protected. For each series of data points, the bottom point corresponds to “0% matrix protected,” the next point corresponds to “25% matrix protected,” and so on.

of landscapes by randomly selecting 50 and 100 habitat patches from the baseline set of 214 patches, resulting in landscapes with densities of 0.5 ponds/km² and 1.0 ponds/km², respectively. In order to maintain the same total area for all landscapes in our comparison, we added the land area from the nonselected habitat patches back into the land area of the respective dispersal matrix unit. Thus, the hypothetical landscapes defined here had fewer habitat patches and more dispersal matrix, but the same total land area as the baseline landscape.

Third, there is emerging evidence that the salamander migration distances used by Semlitsch (1998) in recommending the 165-m wetland buffer may have been too low (Faccio 2003, McDonough and Paton 2007, Semlitsch 2007). For example, McDonough and Paton (2007) found that adult female spotted salamanders migrated twice as far (214 ± 25 m) as male spotted salamanders (102 ± 15 m) across a forested landscape fragmented by a golf course. Thus, use of a mean migration distance for the species as a whole may preclude protection of female salamanders. To examine the implications of potentially incorrect habitat patch definition, we conducted conservation policy analysis on additional hypothetical landscapes with habitat patches containing 229-m buffers based on the recommendation of Calhoun et al. (2002, 2005). This larger habitat patch definition would encompass the 218-m mean maximum migration distance for a group of salamanders reported by Semlitsch and Bodie (2003) and may protect 95% of local populations of ambystomatids (Faccio 2003). In

total, we conducted conservation policy analysis for 36 different landscapes (one actual and 35 hypothetical), allowing for comparison of results across land use type, habitat patch density, and habitat patch size.

RESULTS

Baseline conservation policy analysis

Using the results of conservation policy analysis based on the baseline landscape of Richmond (214 habitat patches, 165-m wetland buffers, and heterogeneous land use; Fig. 1), both metapopulation size and opportunity cost increased as the level of protection increased (Fig. 2). However, while the rate of increase in metapopulation size was similar for increases of habitat patch protection and protection of dispersal matrix, the rate of increase in opportunity costs was greater for increases of dispersal matrix protection. That is, protection of habitat patch area was more cost effective in terms of increasing metapopulation size in the baseline landscape. For example, consider a scenario starting at no protection (Fig. 2). Protecting 50% of each habitat patch achieved a larger metapopulation size with a lower associated opportunity cost than protecting 25% of dispersal matrix.

This result is further highlighted by a scenario starting at a 25% landscape-wide level of protection, which corresponded to a salamander metapopulation size of 0.922 and an associated opportunity cost of US\$163 million (Fig. 2). Protecting the remaining habitat patch area while allowing the remaining dispersal matrix to be

TABLE 3. Sensitivity of *Ambystoma* metapopulation size (S_M) to one-at-a-time changes in species parameters for the Richmond baseline landscape with 33% landscape-wide protection.

Parameter	Brief description	Change in S_M due to increase or minimum (%)	Change in S_M due to decrease or maximum (%)	Sensitivity index
A) Changes due to 50% increase/decrease				
α	dispersal distance	4.3	7.7	0.1151
δ	extinction threshold	3.3	3.3	0.0645
ζ^\dagger	patch area scaling	12.3	4.4	0.1604
ω_A^\dagger	patch land use intensity	1.7	4.3	0.0599
ω_Z^\dagger	matrix land use intensity	2.2	6.5	0.0855
B) Changes due to expert minimum/maximum				
ω_{A1}	high-density residential	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω_{A2}	medium-density residential	0.3	0.7	0.0032
ω_{A3}	low-density residential	2.4	1.3	0.0368
ω_{A4}	commercial or industrial	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω_{A5}	agricultural	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω_{Z1}	high-density residential	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω_{Z2}	medium-density residential	0.1	$\ll 0.1$	0.0016
ω_{Z3}	low-density residential	1.3	1.6	0.0287
ω_{Z4}	commercial or industrial	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω_{Z5}	agricultural	$\ll 0.1$	$\ll 0.1$	$\ll 0.0001$
ω^\dagger	combined land use intensity	3.4	3.5	0.06

Notes: Values in panel (A) show 50% changes to parameter values. Values in panel (B) are expert minimum and maximum parameter values. Full parameter descriptions are provided in Table 2.

\dagger Groups of parameters varied simultaneously: $\zeta = (\zeta_{\text{sex}}, \zeta_{\text{sem}}, \zeta_{\text{sim}})$; $\omega_A = (\omega_{A1}, \omega_{A2}, \omega_{A3}, \omega_{A4}, \omega_{A5})$, $\omega_Z = (\omega_{Z1}, \omega_{Z2}, \omega_{Z3}, \omega_{Z4}, \omega_{Z5})$; $\omega = (\omega_{A1}, \omega_{A2}, \omega_{A3}, \omega_{A4}, \omega_{A5}, \omega_{Z1}, \omega_{Z2}, \omega_{Z3}, \omega_{Z4}, \omega_{Z5})$.

developed (100% habitat patch protection and 25% dispersal matrix protection) resulted in a corresponding metapopulation size of 0.958 and an associated opportunity cost of \$258 million, an additional opportunity cost of \$95 million. In comparison, protecting the remaining dispersal matrix while allowing the remaining habitat patch area to be developed (25% habitat patch protection and 100% dispersal matrix protection) resulted in a corresponding metapopulation size of 0.966 and an associated opportunity cost of \$558 million, an additional opportunity cost of \$395 million. Thus, additional protection of habitat patch area was again more cost effective in terms of increasing metapopulation size in the baseline landscape.

In 2005, Richmond was 76% forested (33% of the landscape was protected forest and 43% of the landscape was undeveloped and unprotected forest). With 76% landscape-wide protection, metapopulation size was 0.974, indicating that, on average, 97% of the habitat patches in the network would be occupied (or, alternatively, there was a 97% probability that each patch was occupied). This result coincides with the actual preponderance of ambystomatid salamanders in Richmond. The opportunity cost corresponding to 76% landscape-wide protection was \$496 million, which can be segregated into two components. The first component represents the value of the existing (2005) protected land, \$215 million, an opportunity cost previously incurred by the town. Thus the town had already invested substantially in conservation measures. The second component represents the value of the existing (2005) undeveloped and unprotected land, \$281 million, an opportunity cost that would need to be incurred if

this land were formally protected. A laissez-faire policy of no further protection would result in 33% landscape-wide protection in the Richmond baseline landscape at full buildout. No additional opportunity cost would be incurred and the resulting salamander metapopulation size would be 0.938. That is, because a large portion of the study area was zoned for low-density residential housing and 33% of the landscape was already protected, >93% of the salamander habitat patches would be occupied over the long term. Thus, it appears that ambystomatid salamanders were well protected by prior conservation decisions in Richmond.

Species parameter sensitivity analysis

All species parameter changes resulted in expected changes to metapopulation size (Table 3, Fig. 3). Increases in inverse dispersal distance (α), which correspond to decreases in the dispersal ability of the species, resulted in decreases in metapopulation size. Habitat patch occupancy is less likely to occur if the species has greater difficulty in reaching other habitat patches. Increases in the extinction threshold (δ) also resulted in decreases in metapopulation size. Higher relative rates of local extinction to colonization will result in lower overall occupancy levels. Increases in the patch area scaling parameter (ζ) resulted in increases in metapopulation size. Larger values of the scaling parameter indicate a higher probability of immigrants colonizing an empty patch and a lower probability of an occupied patch going extinct, both of which act to increase overall patch occupancy. Increases in the land use intensity parameters (ω_A and ω_Z) resulted in decreases in metapopulation size. More intense land

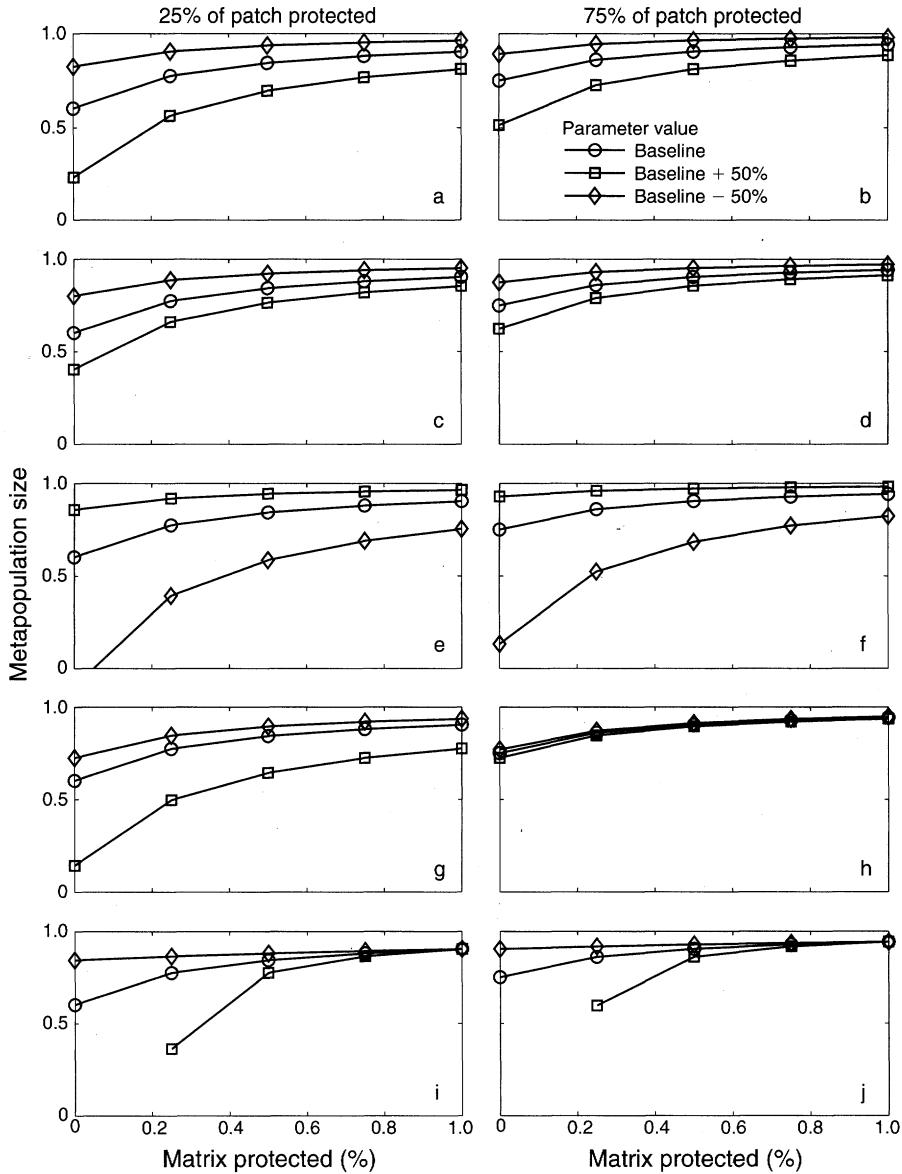


FIG. 3. Species parameter sensitivity analysis showing the effect of varying parameters one at a time $\pm 50\%$ of the baseline value (Table 2) for a landscape with 50 patches, 165-m buffers, and heterogeneous land use: (a, b) inverse dispersal distance, α ; (c, d) extinction threshold, δ ; (e, f) patch-area scaling, ζ ; (g, h) combined effective area land use intensity, ω_A ; and (i, j) combined dispersal barrier land use intensity, ω_Z . Baseline values are listed in Table 2. In the left-hand panels, 25% of each habitat patch is protected; in the right-hand panels, 75% of each habitat patch is protected. The metapopulation size for 0% matrix protected in both (i) and (j) is zero; the connecting line segment is not shown because we did not establish the exact matrix protection level at which metapopulation size falls to zero.

uses reduce effective area, which increases the probability of local extinction and impede dispersal among habitat patches, which decreases the probability of colonization.

Parameter sensitivity analysis using the baseline landscape indicated that metapopulation size was not sensitive to one-at-a-time 50% changes in species parameters (Table 3). Metapopulation size was most responsive to a decrease in the patch area scaling parameter, an increase in the inverse dispersal distance

parameter, and an increase in the combined dispersal matrix land use intensity parameter. Sensitivity index values also indicated relatively higher sensitivity to these parameters. There was little change to metapopulation size when varying the land-use intensity parameters one at a time from the expert minimum to the expert maximum (Table 3). These results confirm that ambystomatid salamanders had a high probability of persistence in the baseline landscape, even if our estimates of the species parameters are relatively uncertain.

In contrast, parameter sensitivity analysis conducted for alternative landscapes did show a high sensitivity of metapopulation size to species parameters (Fig. 3). In general, metapopulation size was more sensitive to changes in species parameters in landscapes with lower levels of both habitat patch and dispersal matrix protection and in landscapes with lower patch density. Metapopulation size was particularly sensitive to parameter changes when less than 40% of the dispersal matrix was protected. This result was most dramatic when all the dispersal barrier land use intensity parameters (ω_Z) were jointly increased by 50% (Fig. 3i, j). In this case, because all land use intensity parameters were >1.0 , the landscape contained full barriers to dispersal, which resulted in metapopulation extinction. Metapopulation extinction also resulted for a 50% decrease in the patch area scaling parameter (ζ) in a landscape with 25% habitat patch protection and $<25\%$ dispersal matrix protection (Fig. 3e).

There are two ways to interpret these results. First, ambystomatid salamanders are particularly vulnerable to extinction in landscapes with low patch density and low levels of protection, if the true parameter values deviate from the baseline. Alternatively, other wetland species with parameter values that vary from the salamander baseline values may be even more vulnerable to extinction, particularly in landscapes with low levels of protection. Wetland species with shorter dispersal distances (larger α), less ability to migrate or disperse through areas dominated by human land use (larger ω), or lower rates of immigration and emigration (smaller ζ) are most vulnerable.

Alternative landscape conservation policy analysis

The economic and ecological outcomes of the set of conservation policies varied dramatically over different land use types and landscape structures (Figs. 4 and 5). In essence, the key parameters varied were the land use intensity parameters (ω_A and ω_Z ; Fig. 4). Four out of the five homogeneous landscapes required some level of protection in order to avoid species extinction. Only the low-density residential development landscape ($\omega_A = 0.71$ and $\omega_Z = 0.73$) resulted in a positive metapopulation size with no conservation. In the landscape with the most intense land use (commercial and industrial development, $\omega_A = 0.98$ and $\omega_Z = 0.99$), both habitat patch and dispersal matrix protection were required to avoid extinction. This result was also true for a landscape with 214 habitat patches (not shown in Fig. 4), indicating that even in a landscape with high patch density, dispersal matrix protection may be required for species that are vulnerable to a particular land use (i.e., ω_A and $\omega_Z \geq 0.95$). In fact, landscapes with moderate land use intensity (ω_A and $\omega_Z \geq 0.80$) required some dispersal matrix protection to achieve a metapopulation size >0.80 , a reasonable goal for maintaining a common species. Thus, wetland buffer policies would not be successful in many landscapes for many species.

The baseline landscape of Richmond was most similar to the low-density residential landscape, although the small mix of other higher valued land uses in Richmond's heterogeneous landscape result in higher opportunity costs than the purely homogeneous landscape. Similarly, the medium-density residential landscape and the agricultural landscape both have the same land use intensity impact ($\omega_A = 0.87$ and $\omega_Z = 0.88$), but the opportunity cost associated with conserving agricultural land was much less (in Richmond). Thus, land values can play a big role in deciding where to conserve.

The economic and ecological outcomes of the set of conservation policies also varied over different landscape structures (Fig. 5). In general, lower patch density and smaller habitat patches both resulted in dramatically lower metapopulation sizes. Opportunity costs changed slightly for some policies (and not at all for landscape-wide conservation policies), because total habitat patch area is small relative to total dispersal matrix area in all of the landscapes. In the medium-density residential landscape that might be considered typical of exurban communities, no protection resulted in metapopulation extinction for three of the six landscape structures and overall habitat occupancy of $<50\%$ for the other three landscape structures (Fig. 5). Because changes to habitat patch density and habitat patch size both alter the mean distance between patches (d_{in}), changes to landscape structure resulted in similar policy outcomes as changes in the inverse dispersal distance parameter (α) reported in the sensitivity analysis. For example, decreasing patch density has a similar effect on metapopulation size (Fig. 5) as increasing the inverse dispersal distance parameter (Fig. 3), because the species must on average travel farther to get from one habitat patch to another.

As in the case for the baseline landscape (Fig. 2), there was a nonlinear relationship between metapopulation size and opportunity cost for all 35 hypothetical landscapes, with costs rising dramatically for metapopulation sizes greater than 0.8 (Figs. 4 and 5). That is, the marginal cost of increasing metapopulation size increased with an apparent threshold around 80% habitat patch occupancy, which has implications for communities that desire higher ecological outcomes.

To examine cost effectiveness more closely, we compared the economic and ecological outcomes of two conservation policy alternatives across all 36 landscapes. The two policies are representative of what a community might consider for protecting wetland species: (1) a policy that protects 100% of the habitat patch but no dispersal matrix (a wetland buffer policy) and (2) a policy that protects 25% of habitat patches and 25% of dispersal matrix (a landscape-wide policy). In general (22 of the 36 landscapes), there was a trade-off between opportunity cost and metapopulation size for the two conservation policies. In these landscapes, the

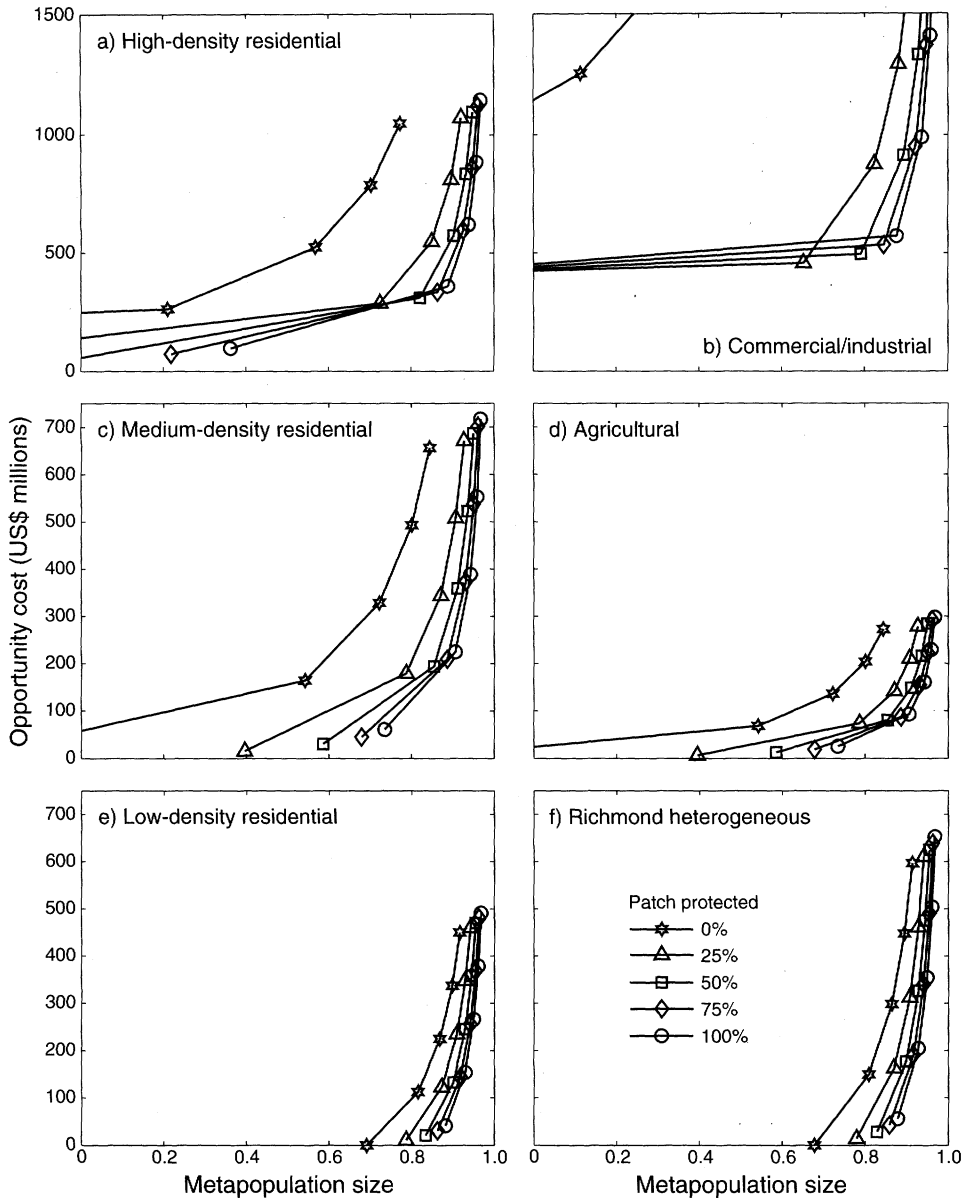


FIG. 4. Conservation policy outcomes for five homogeneous landscapes and one heterogeneous landscape (all consisting of 100 habitat patches with 165-m buffers), showing the impact of varying land use intensities. Land use intensity parameters are listed in Table 2. For each policy series, each individual point corresponds to a pair of protection levels: percentage of patch protected and percentage of matrix protected. For each series of data points, the bottom point corresponds to “0% matrix protected,” the next point corresponds to “25% matrix protected,” and so on. Note the different y-axis scales in panels (a) and (b) required to accommodate higher land values.

wetland buffer policy cost less than the landscape-wide policy, but also resulted in lower habitat patch occupancy. For the 10 low-density residential and heterogeneous landscapes with landscape structures not consisting of 214 habitat patches and 229-m buffers, the policy that protects 100% of the habitat patch resulted in a higher metapopulation size and a lower opportunity cost than the 25% landscape-wide protection policy (e.g., Fig. 2 and Fig. 4e, f). That is, in most low-intensity landscapes ($\omega_A, \omega_Z \leq 0.75$), it was more

cost effective to choose the wetland buffer policy. In contrast, in the four highest land use intensity landscapes with 214 habitat patches and 229-m buffers, the policy that provides 25% landscape-wide protection resulted in a higher metapopulation size and a lower opportunity cost than the policy that protects 100% of habitat patches (e.g., Fig. 5b). That is, in landscapes with shorter distances between patches, more total patch area, and high-intensity land use, a landscape-wide conservation policy was more cost effective. Thus, it is

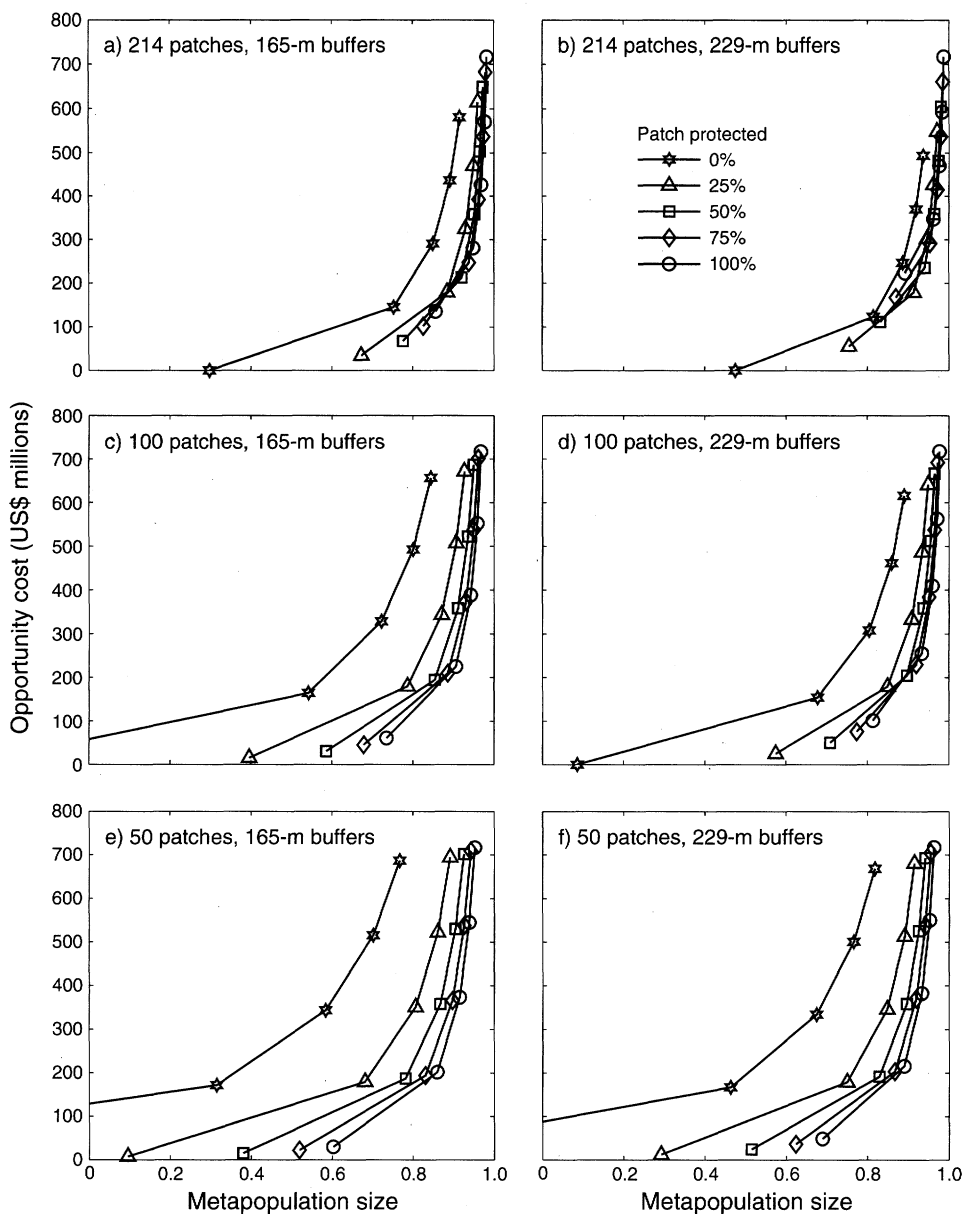


FIG. 5. Landscape structure analysis showing conservation policy outcomes for landscapes of varying habitat patch density and habitat patch size. All six landscapes are homogeneous, medium-density residential land use (land value = \$67 893/ha; $\omega_A = 0.87$; $\omega_Z = 0.88$). Abbreviations are: ω_A , combined effective-area land use intensity; ω_Z , combined dispersal barrier land use intensity. See Fig. 4 for an explanation of protection levels.

not always more cost effective to protect additional habitat patch.

To better assess the ability of wetland buffer policies to protect common species, we identified which of our 25 conservation policies would achieve metapopulation sizes of 0.80 and 0.90 at least cost for each of our 36 landscapes (Table 4). In general, wetland buffer policies were successful in maintaining common species at an 80% occupancy level in landscapes of low to medium land use intensity ($\omega_A, \omega_Z \leq 0.88$) and higher patch density (shorter distances between patches and larger patches).

To achieve a 90% habitat occupancy level in landscapes with medium land use intensity, some dispersal matrix protection is required. It was not necessary to protect 100% of the habitat patch for any landscapes with high patch density. Landscapes with low patch density required 75% or 100% habitat patch protection to achieve 90% habitat patch occupancy for all land use types. For landscapes with high land use intensity or low patch density, some investment in dispersal matrix protection is required to maintain a common species at or above 80% habitat patch occupancy.

TABLE 4. Least-cost conservation policy that achieves 80% and 90% long-term habitat occupancy in 36 landscapes.

Habitat occupancy level by zone	214 patches		100 patches		50 patches	
	229-m buffers	165-m buffers	229-m buffers	165-m buffers	229-m buffers	165-m buffers
High-density residential						
80%	25:25	25:25	25:25	50:25	75:25	100:25
90%	50:25	50:25	75:25	50:50	75:50	100:50
Medium-density residential						
80%	50:0	75:0	100:0	50:25	50:25	75:25
90%	25:25	50:25	75:25	100:25	75:50	100:50
Low-density residential						
80%	0:0	0:0	25:0	50:0	50:0	100:0
90%	25:0	50:0	75:0	50:25	75:25	75:50
Commercial or industrial						
80%	25:25	25:25	50:25	75:25	75:25	100:25
90%	50:25	75:25	100:25	75:50	75:50	100:50
Agricultural						
80%	50:0	75:0	100:0	50:25	50:25	75:25
90%	25:25	50:25	75:25	100:25	75:50	100:50
Richmond heterogeneous						
80%	0:0	0:0	25:0	50:0	100:0	50:25
90%	25:0	75:0	100:0	75:25	100:25	75:50

Notes: Each of the 36 simulated landscapes consists of land developed in one of six land uses using one of six habitat patch definitions. Each entry contains a conservation policy pair of protection levels (percentage of patch protected : percentage of matrix protected). Wetland buffer policies are those that protect 0% of dispersal matrix.

DISCUSSION

Conservation implications of policy analyses

The goal of this study was to determine under what circumstances wetland buffer policies would be cost effective for protecting wetland species in an exurban landscape. Although we described our analysis in terms of ambystomatid salamanders, the analysis could be broadened to other wetland species by considering the results of parameter sensitivity analysis and conservation policy analysis across varying landscapes. We modeled the ecological benefits and economic costs that result at full buildout from the implementation of a set of conservation policies on one actual (baseline) and 35 hypothetical landscapes.

Because a large portion of the baseline landscape was low-density residential land that has relatively low impact on salamander migration and dispersal, existing (2005) and full-buildout conditions in Richmond were shown to support relatively large salamander metapopulations (97% and 93% occupied habitat patches, respectively). If the residents of Richmond wanted to maintain the salamander metapopulation size above a particular level, say 0.95, they could use the results displayed in Fig. 2 to assist in determining the most cost-effective conservation policy (pair of habitat patch and dispersal matrix protection levels) to meet their objective. Of course, they would need to consider the existing levels of development as some protection levels would not be possible. For example, policies protecting 100%

of all habitat patches would not be feasible given 24% of the town is already developed. However, a landscape with 75% of habitat patches protected and 25% of dispersal matrix protected might be feasible and would result in a salamander metapopulation size of 0.95. Thus, in Richmond, where 33% of dispersal matrix is already protected, a wetland buffer policy that protects 75% of habitat patch area would achieve an objective of 95% patch occupancy.

The most cost-effective conservation policy we modeled was a mixed policy that protected relatively more habitat patch area than dispersal matrix area. In the baseline landscape (Fig. 2), full protection of habitat patches with no protection of dispersal matrix resulted in a larger metapopulation size at lower cost than 25% landscape-wide protection. This result was also true for homogeneous low-density residential landscapes. In comparison, 25% landscape-wide protection resulted in higher metapopulation size at lower cost in landscapes with higher land use intensity and high patch density. In the remaining landscapes, a 25% landscape-wide protection policy resulted in larger metapopulation sizes than wetland buffer policies but with greater costs, indicating a trade-off between ecological benefits and economic costs. However, once some amount of dispersal matrix was protected, it was generally more cost effective to protect additional habitat patch area rather than additional dispersal matrix.

Wetland buffer policies are only cost effective in maintaining common species in landscapes of low land

use intensity or moderate land use intensity with high habitat patch density (Table 4). All other landscapes require some amount of dispersal matrix protection to achieve 80% habitat patch occupancy, a level of habitat patch occupancy that might be considered the minimum for a common species. Some communities may desire an even higher level of patch occupancy (90% or above) for a common species acting as an umbrella for other species or as an overall indicator of healthy ecosystems. Parameter sensitivity analysis confirmed that protection of dispersal matrix is important for other wetland species as well, particularly those that have shorter dispersal distances, are more sensitive to human-dominated land uses, or have lower intrinsic immigration and emigration rates.

Conservation often occurs over time, and it is worth noting that there exists some path dependence among conservation choices. For example, it is not always possible to make use of the least-cost conservation policy for achieving 90% patch occupancy if a community has previously implemented the least-cost policy for achieving 80% patch occupancy (e.g., Table 4, medium-density residential development, 100 patches, and 229-m buffers).

We found a nonlinear relationship between metapopulation size and opportunity cost in all landscapes investigated. Initially, conservation is relatively inexpensive, but it becomes increasingly expensive as greater ecological protection (higher salamander metapopulation sizes) is required. This trend of increasing marginal cost for species conservation has been found in other studies (Montgomery et al. 1994, Ando et al. 1998, Polasky et al. 2001, 2005). In our study, there appeared to be a threshold around a metapopulation size of 0.80 or an average 80% habitat patch occupancy over the long term (Figs. 4 and 5), which may be considered a minimum acceptable level of occupancy for a common species. The actual desired ecological outcome would be determined through a social or political process.

Assumptions, limitations of the model, and future research

In the metapopulation model used in this study, larger habitat patches resulted in higher metapopulation sizes (Fig. 5). However, metapopulation size will not actually be greater for larger patches if, in fact, the species does not use part of the patch because, for example, its maximum migration distance is shorter than the buffer size. The conservation policy analysis conducted here assumed that the wetland buffers would be set at an appropriate distance for the target species and that the species would use the entire habitat patch. In reality, however, wetland regulations would likely establish buffers to protect more than one species. Several recent amphibian studies examining species richness have shown that different species inhabit different types of ponds and surrounding landscapes (Laan and Verboom 1990, Lehtinen et al. 1999, Snodgrass et al. 2000, Oertli et al. 2002). The model used here could be enhanced to

measure metapopulation size based on patches defined according to individual species migratory movements while measuring opportunity costs on patches defined according to the wetland buffer established by regulations or that was defined according to the species with the largest migratory capability (Semlitsch 2007).

For this analysis, we assumed that habitat patch quality was homogeneous across patches. However, previous research has shown that local population sizes vary based on pond characteristics such as hydroperiod, acidity, and vegetation type (Egan and Paton 2004, Weyrauch and Grubb 2004), as well as the number of ponds in close proximity. The model could be extended to incorporate local patch characteristics in the definition of habitat patch effective area.

The analysis conducted here was based on a static model and landscapes that resulted in full buildout after implementation of a conservation policy. We assumed that all land would remain in the land use implied by its zoning designation in 2005, that protection would occur all at once, and that land values would not change as land was protected. In reality, towns do change their zoning laws and in many communities agricultural land is converted to residential housing. In addition, conservation quite often takes place over time. A dynamic version of this model that allows for changing land use zoning and changing land values is left for future work.

Some researchers have questioned the appropriateness of the metapopulation paradigm for amphibian species (Smith and Green 2005, Petranka and Holbrook 2006). One necessary condition of using metapopulation models for any species is that habitat patches are discrete and clearly defined (Hanski 1999). Applications of the metapopulation model used in this study might not be feasible for some wetland species. For example, some amphibians migrate >1 km from natal breeding ponds (Semlitsch 2007). If we were to define habitat patches with 1-km wetland buffers in our 214-patch landscape, the buffer of each pond would overlap with at least one other pond's buffer, creating one large odd-shaped habitat patch surrounded by dispersal matrix. Thus, a metapopulation structure might not be appropriate for wetland species with high migration capabilities in landscapes with high pond density. Despite this caveat, we feel that the metapopulation model was appropriate in all of our landscapes because salamanders, in general, have shorter migration distances than frogs or toads (Rittenhouse and Semlitsch 2007) and ambystomatid salamanders, in particular, have mean migration distances of <260 m (Semlitsch and Bodie 2003), enabling habitat patches to be clearly delineated in all of our landscapes.

Two other conservation policy implementation issues are worth noting. First, there are different policy implementation approaches. One approach would use funds from a local land trust or local property taxes to purchase conservation lands. In this case, the cost burden might be distributed among all residents of the

town. A different approach would be to change land use regulations, such that some level of conservation needs to occur for all new development (e.g., 1 ha protected for each hectare developed). In this case, the cost burden falls upon owners of undeveloped land. The total amount and distribution of cost can impact the political feasibility of any conservation effort. Second, because there is uncertainty associated with any simulation model and because the model focuses on full buildout, which in most communities would not occur for many years, it would be important to monitor the status of the species over time to avoid any unexpected metapopulation declines.

Conclusion

In summary, we applied an ecological-economic model utilizing a metapopulation framework to the conservation of wetland species. We showed that in most landscapes where a portion is engaged in intensive land use, some amount of dispersal matrix protection is necessary for long-term species persistence. Only under certain landscape conditions (low-intensity land uses and high pond density) are wetland buffer policies sufficient for species protection because of minimal barriers to species dispersal. Conservation costs that result from forgone residential, commercial, or agricultural activities can vary dramatically, but they increase in a nonlinear manner regardless of land use zoning. There appears to be an opportunity cost threshold around an average habitat patch occupancy level of 80%.

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