

A Multi-disciplinary Approach to Modeling the Impacts of Land Use Change on
Vernal Pool-breeding Amphibians

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ABSTRACT¹:

A multi-disciplinary approach is developed to integrate a spatially explicit parcel-level economic model of land use change with a landscape permeability model for wood frogs (*Rana sylvatica*). Significant drivers of residential land conversion are identified and future conversions predicted in a discrete choice framework for the current landscape and under three future scenarios.

Attributes of a parcel that may influence the likelihood of development may include the parcel's geophysical characteristics (e.g. steep slopes or hydric soils), proximity to amenities or disamenities (e.g. the coast or interstate exits), neighboring land uses, and zoning or other local regulations. By using parcel-level data, it is possible to model the decision-making process of individual landowners and to identify the significant drivers of land use change at a micro-scale.

The three future landscapes predicted by the economic model are then analyzed in a landscape permeability model for wood frogs to examine the degree of connectivity between vernal pools that are required for breeding. Landscape permeability models take into account the dispersal abilities of the animals and the 'cost' of dispersing across different land use types to assess the connectivity of different habitat elements. This multi-disciplinary approach furthers understanding of the anthropogenic forces that drive land use change and the effects of such change on a vernal pool indicator species, as well as providing a method to predict the effects of local regulations. The results suggest that permeability is best maintained through the use of multiple vernal pool buffer zones.

Key Words: discrete choice, landscape permeability, land use change, wood frogs

1. INTRODUCTION

Vernal pools are seasonally flooded pools that usually fill in the fall or winter, swell with spring rains and snowmelt, and, in most years, dry out by late summer. Because they dry periodically, these wetlands do not support populations of fish. As a result, numerous species of amphibians and invertebrates have adapted to make use of these fishless pools for breeding and, in some cases, non-breeding habitat. Because of their small size and ephemeral existence, vernal pools have received little regulatory oversight (Calhoun et al. 2003). Furthermore a recent Supreme Court decision, *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers*, 531 U.S. 159 (2001), denied the ability of the federal government to regulate isolated wetlands through application of the Migratory Bird Rule (Section 404 Clean Water Act [1977]).

According to Pough et al. (1998) habitat modification and destruction, largely through land use change, are the most direct negative effect of humans on amphibians. According to the U.S. Fish and Wildlife Service, nearly 60,000 acres of wetlands are lost annually (Dahl 2000). Due to their small size, seasonal drying, and lack of regulatory protection, vernal pools may be especially susceptible.

Given that vernal pools have been found to be critical habitat for some amphibians, an increasing amount of attention has been devoted recently to landscape composition and habitat loss and

¹ This work would not have been possible without the guidance and support of my graduate committee at the University of Maine: Dr. Kathleen Bell (Advisor), Dept. of Resource Economics and Policy; Dr. Kate Beard, Dept. of Spatial Information Science; Dr. Aram Calhoun, Dept. of Plant, Soils and Environmental Science; Dr. Cynthia Loftin, Dept. of Wildlife Ecology; and Dr. Steve Sader, Dept. of Forest Management.

fragmentation in and around vernal pools (Di Mauro and Hunter 2002, Calhoun et al. 2003, Homan et al. 2004, Baldwin et al. 2006). While federal regulation of vernal pools is limited, some U.S. states, including New Jersey (Freshwater Wetlands Protection Act 1989, N.J.A.C. 7:7A), Massachusetts (MWPAP; 310 CMR 10.00 1996) and Maine (Maine Natural Resources Protection Act 1996; 38 M.R.S.A. Ch. 3: §480-A et seq.), currently offer them some protection. Maine has recently added Significant Vernal Pools (SVPs) to its list of Significant Wildlife Habitats, a status that offers them greater regulatory oversight. Under recent revisions to the Maine Natural Resources Protection Act, a vernal pool is considered ‘significant’ if either (1) it is used by a state-listed threatened or endangered species, or (2) there is a notable abundance of spotted salamanders, blue spotted salamanders, wood frogs, or fairy shrimp present. Important tasks remain, however, including monitoring and assessment of effectiveness of the new regulations. This research will complement these tasks.

In Maine, habitat loss and fragmentation due to residential and commercial development may be a serious threat to many species of wildlife. The number of housing units is expected to grow by 14% statewide between 2000 and 2015 with growth rates in excess of 30% in many southern Maine towns (Maine State Planning Office 2003). A recent U.S. Forest Service report identified the fifteen watersheds in the U.S. with the largest acreage of private forestland predicted to shift from rural to either exurban or urban use by 2030. Three of these top fifteen watersheds are in Maine (Stein et al. 2005). As population growth and land conversion alter the landscape, the risks to vernal pools and the species that depend on them are likely to change. This study proposes a mechanism to characterize these relative risks and to explore the sensitivity of habitat loss and fragmentation to the spatial distribution and intensity of future residential development.

Previous research has investigated the impacts of land use change on vernal pools (Baldwin 2005, Baldwin et al. 2006) and on wetlands in general (Kolozsvary and Swihart 1999, Lehtinen et al. 1999). Other work has investigated the impacts of land use change on habitat for specific taxa (Van Apeldoorn et al. 1998, Carroll et al. 2003, Stephens et al. 2003) or biodiversity in general (Theobald 2003, Schumaker et al. 2004). Most of this work has been done by wetland ecologists, wildlife biologists, or landscape ecologists. Future land use changes in these cases are typically based on hypothetical scenarios or trend analyses, with little emphasis on land markets or human behavior. Bauer et al. (2004) developed a framework to maximize the benefits of residential development subject to a constraint of a ‘healthy’ amphibian metapopulation ecosystem and demonstrate the economic efficiency of such an approach. A major contribution of this research is its use of an economic model to identify the drivers of land use change and forecast future landscapes. These forecasted landscapes may then be examined in a landscape permeability framework to integrate both economics and ecology into one study.

Spatially explicit economic models of land use change extend from models of land use or land conversion decisions. Economic models of land conversions explain the likelihood of conversion as a function of the relative returns to land in different uses (Plantinga and Irwin 2006). Conversions are assumed to be more likely to occur when the relative returns change and it becomes more profitable to alter the use of one’s land. In equilibrium, economists expect to see lands used in their highest and best use (i.e., the use with the highest return). Spatially explicit models of land use change emphasize the spatial heterogeneity in these returns across the landscape (Bockstael 1996, Irwin and Geoghegan 2001, Bell and Irwin, 2002, Hite et al. 2003,

Irwin et al. 2003, Carrion-Flores and Irwin 2004, Newburn and Berck 2006). Using parcel-level data, these models capture the decision-making process of each individual landowner. Such models provide more detailed information on the spatial distribution and configuration of land use change than the hypothetical scenarios typically used to examine habitat alteration or loss. For example, build-out analyses typically assume all developable lands will be built on, ignoring the variation in likelihood of development.

A second, notable advantage of parcel-scale modeling is the ability to incorporate regulatory constraints, such as minimum lot size or development restrictions, directly into the model. This enables the researcher to incorporate highly localized information and allows for forecasts to incorporate changes in these constraints. This research models the effects on landscape permeability of Maine's new Significant Vernal Pool protections under three scenarios, a development scenario, a baseline scenario, and a conservation scenario. By modeling both the human behavior that drives land markets and the population responses to the resulting landscape changes, this research, it is hoped, will represent a significant interdisciplinary contribution to the understanding of the impacts of land conversion on amphibian vernal pool indicator species.

2. ECONOMIC LAND USE MODEL

Overview

Researchers from various disciplines have devoted increasing attention in recent years to land use change. Many have used cellular automata, a class of mathematical models in which the researcher imposes rules that are used to determine the state of each cell, based on the states of neighboring cells. Examples include Wolfram (1986), Batty et al. (1989), Clarke et al. (1997), and Wu and Webster (1998). Others have used remotely sensed data on land use/cover change to estimate empirical models of some type of land use change, often incorporating socio-economic drivers (e.g. LaGro and DeGloria 1992; Mertens and Lambin 1997; Berger and Bolte 2004). While these models provide important information regarding the process of land use change, economic models may offer additional insights by identifying and explaining the drivers of land use change.

Spatially explicit economic models of land use show the cumulative effects of the individual choices of many landowners and have often been used to identify significant drivers of land conversion (Bockstael 1996, Kline and Alig 1999, Irwin and Geoghegan 2001, Bell and Irwin 2002, Irwin et al. 2003, Turner et al. 1996, Wear and Bolstad 1998, Carrion-Flores and Irwin 2004, Newburn and Berck 2006). Such models are also frequently used to predict future landscape changes resulting from specific land use regulations. For example, Kline and Alig (1999) assessed the effectiveness of Oregon's land use planning program at slowing conversion of forest and farmland, and other studies have predicted the future impacts of various aspects of Maryland's Smart Growth legislation (Bell and Irwin 2002, Irwin and Bockstael 2002, Irwin et al. 2003). This study will build upon this body of work by using an economic model of land use change and then analyzing the likely response of an amphibian population to the resulting landscape.

Theoretical Model

In parcel-level economic models of land use change, each landowner is assumed to allocate his or her land to the use that maximizes the discounted present value of all future expected returns from the land. Thus, if a farmer is able to convert his or her land to a residential use and receive a price that exceeds the discounted present value of all future expected returns from farming, the farmer would be expected to do so.

A typical binary discrete choice formulation of an individual landowner's decision is presented in Bockstael (1996), where the landowner of parcel j , which is currently in undeveloped state u , selects the land use of parcel j in period t that maximizes net expected returns. Thus the conversion rule is that parcel j , which is currently in state u , will be converted to state r in time t if

$$W_{jrt|u} - C_{jrt|u} \geq W_{jut|u} - C_{jut|u}, \quad (1)$$

where $W_{jrt|u}$ represents the present value of all future expected returns to parcel j in state r at time t , and $C_{jrt|u}$ represents the cost of converting parcel j from state u to state r in period t . If this condition is not met, then the parcel remains undeveloped. Both the stream of future returns and the conversion costs are assumed to be influenced by a number of spatially heterogeneous variables.

Since not all factors influencing W and C may be observed, this equation may be rewritten in terms of probabilities, as follows:

$$\begin{aligned} P_{jrt|u} &= \Pr(V_{jrt|u} - \eta_{jrt|u} \geq V_{jut|u} - \eta_{jut|u}) \\ &= \Pr(V_{jrt|u} - V_{jut|u} \geq \eta_{jrt|u} - \eta_{jut|u}), \end{aligned} \quad (2)$$

where $P_{jrt|u}$ represents the probability of undeveloped parcel j being converted to use r in time period t , and V and η represent the systematic and random factors, respectively, that affect W and C . This equation provides the basis for the empirical model described in the subsequent section.

Empirical Model

It is hypothesized that the net expected returns of each parcel in both its undeveloped and developed state are a function of various parcel-specific attributes. (For the purposes of this paper, 'developed' land refers to land in residential use, as this study focuses only on residential conversion.) Such attributes may include proximity to certain amenities (major roads, schools, employment centers, public sewer and water, bodies of water, etc.), natural resource features that are likely to influence the cost of development (hydric soils, steep slopes, etc.), regulatory constraints (zoning, minimum lot size, open space requirements, etc.), and spatial externalities (i.e. neighboring land uses). For the sake of simplicity, let \mathbf{X}_{jt} represent the vector of parcel-specific attributes for parcel j in time period t , and let $\boldsymbol{\beta}$ represent the vector of parameters indicating the marginal effects of these variables on the probability of development. The conversion rule given in (2), then, may be rewritten as:

$$P_{jrt|u} = \Pr\{\eta_{jrt|u} < f(\mathbf{X}_{jt}; \boldsymbol{\beta})\}, \quad (3)$$

where $\eta_{jt} = \eta_{jrt|u} - \eta_{jut|u}$.

Numerous modeling approaches may be employed to estimate the expression given in (3). As this study is only concerned with conversion of undeveloped land to residential use, a binary

logit model is employed. Logit models assume that the error term (η in equation [3]) has a logistic distribution (for further explanation, see Griffiths et al. 1993, p. 760) and that the set of options from which the decision-maker chooses has the property of independence of irrelevant alternatives (for further explanation, see Freeman 1993, p. 135). This model assumes that each landowner of an undeveloped parcel decides whether or not to convert his or her land to residential use during the ten year time period under consideration. While this approach omits other possibilities, such as converting land to commercial or industrial use, such conversions are relatively rare. Between 1995 and 2005, 93% of all new construction in Falmouth was residential (unpubl. data), and local planning officials seem most concerned with residential growth.

The binary logit model assumes that the logarithm of the odds of an event occurring (in this case, a parcel being converted to residential use) is a linear function of the explanatory variables. (Natural logarithms are commonly used, although base-10 logarithms could be used as well, with the only result being a different intercept α .) Thus, for k explanatory variables, the model is:

$$\ln\left[\frac{P_j}{1 - P_j}\right] = \ln O_j = \alpha + \beta_1 x_{j1} + \beta_2 x_{j2} + \dots + \beta_k x_{jk} \quad (4)$$

where O_j is simply the conditional odds of conversion, given the explanatory variables.

Exponentiating both sides of the equation yields:

$$O_j = e^\alpha e^{\beta_1(x_{j1})} e^{\beta_2(x_{j2})} \dots e^{\beta_k(x_{jk})} \quad (5)$$

Maximum likelihood estimation is used, which finds estimates for alpha and the betas that maximize the conditional distribution function for the set of sample values for the dependent variable. The resulting parameter estimates are those values that maximize the probability of observing the sample data.

3. LANDSCAPE PERMEABILITY MODELS

Landscape Complementation

Dunning et al. (1992) coined the term “landscape complementation” to describe a situation in which organisms require different habitat types for different reasons, suggesting the importance of distance between habitat requirements and, as pointed out by Taylor et al. (1993), the connectivity of the landscape in between required patches, often called the matrix. Animal assemblages living under such conditions may be threatened by loss of any required patch type or by a loss of connectivity between required patch types (Reh and Seitz 1990). Vernal pool-breeding amphibians have complex life cycles that require access not only to vernal pools for breeding but also to other aquatic and terrestrial non-breeding habitat (Semlitsch 2000), thereby exemplifying landscape complementation. Wood frogs in particular migrate from breeding pools to upland forests and forested wetlands for the non-breeding part of their life cycle (Hunter et al. 1999), thus the fragmentation of the matrix in between their habitat requirements could pose a serious threat to wood frog populations.

Many researchers have emphasized the negative effects of fragmentation and the importance of landscape permeability for amphibians. Kolozsvary and Swihart (1999) found that several species of amphibians displayed significant responses to fragmentation induced by agriculture. Lehtinen et al. (1999) found amphibian species abundance to be positively correlated with site

isolation and negatively correlated with measures of fragmentation such as road density and proportions of neighboring agricultural and urban land. Pope et al. (2000) found strong positive effects on pond occupancy of the amount of nearby summer habitat for northern leopard frogs, *Rana pipiens*. Carr and Fahrig (2001) found negative effects of nearby road density, particularly for more vagile species. Wood frogs in particular have been found to be positively associated with forest area (de Maynadier and Hunter 1998, Guerry and Hunter 2002, Regosin et al. 2003), with juvenile migration success also dependent on proximity between breeding ponds and nearby forest (Rothermel 2004). In light of the complex life cycles and habitat requirements of vernal pool-breeding amphibians, several researchers have recently suggested a shift from a core-habitat conservation model to one that incorporates the multiple habitat requirements and connectivity between them (Calhoun et al. 2003, Rothermel 2004, Baldwin 2005, Baldwin et al. 2006).

Landscape Permeability Models

Landscape permeability models are typically based on raster land use maps, for which each grid cell is classified according to its habitat quality to the species of interest. Each cell is assigned a “cost” to an individual of traveling across that cell. For example, for wood frogs, the cost of traveling across a forested cell would be very low, as forest is their preferred habitat, while the cost of traveling across a major road or heavily developed area would be very high. Cost-distance functions in GIS may be used to estimate the total cost to an individual of dispersing from one habitat type to another, with the dispersal capabilities of the species determining the maximum possible cost. In this manner, landscape permeability models assess the degree of connectivity of a landscape.

Schippers et al. (1996) used such an approach to simulate dispersal of European badgers (*Meles meles*) with a random-walk model to identify permeability of a landscape in the Netherlands. Ray et al. (2002) constructed a permeability model for the common toad (*Bufo bufo*) and Alpine newt (*Triturus alpestris*) in Geneva, Switzerland using a cost distance function in GIS. Singleton et al. (2002) used a similar approach to identify permeability for large carnivores in Washington and for grizzly bears (*Ursus arctos*) in Washington and southwestern British Columbia (2004). Joly et al. (2003) constructed a permeability model for the common toad (*Bufo bufo*) in France. Hope et al. (2006) also use a least cost approach to identify permeability for three focal species, an old-growth woodland lichen (*Alectoria sarmentosa* subsp. *Sarmentosa*), a woodland/open-ground mosaic butterfly (*Boloria euphrosyne*), and an obligate open-ground butterfly (*Coenonympha tullia*) in Scotland. These studies demonstrate the utility of landscape permeability models in assessing connectivity in a heterogeneous landscape. This research will build upon previous work by assessing the permeability of a future landscape resulting from an economic model of human-induced land use change.

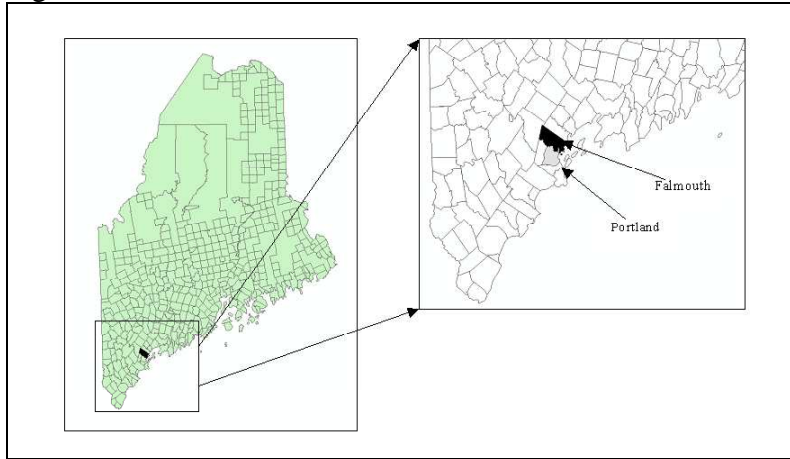
4. DESCRIPTION OF DATA

Study Area

The study area consists of the town of Falmouth, in rapidly growing southern Maine (see Figure 4-1). Falmouth was chosen because of the existence of both parcel-level GIS data and mapped vernal pools. It would be preferable to have a larger study area, for instance several contiguous towns or a watershed, as fauna obviously do not limit their movements by political boundaries.

The extremely sparse availability of mapped vernal pools, however, limited the focus to one town. Given the limited dispersal abilities of amphibians, however, the town-level is still a reasonable scale at which to study landscape permeability.

Figure 4-1: Location of Falmouth, Maine



Falmouth is a rapidly suburbanizing, high-income, coastal community adjacent to Portland, Maine’s largest city. As Table 4-1 shows, Falmouth saw tremendous growth in both housing units (21.4%) and population (35.5%) in the 1990s, much higher than the state averages of 18.1% and 3.8% respectively. Its median family income is nearly double that of the state, and it has seen significant job growth (12.7%) as well, also higher than the state average (3.9%). Falmouth’s population growth has slowed considerably since 2000 to 2.9% and was below the state average of 3.9% between 2000 and 2005.

Table 4-1: Demographic Data for Falmouth and Maine

	Year/Period	Falmouth	Maine
Housing Units ¹	1990	3,322	83,588
	2000	4,169	98,746
	% change '90-'00	25.5	18.1
Population ²	1990	7,610	1,227,928
	2000	10,310	1,274,923
	% change '90-'00	35.5	3.8
	2005	10,610	1,318,220
	% change '00-'05	2.9	3.4
Number of Jobs ³	1990	3,270	517,415
	1997	3,685	537,766
	% change '90-'97	12.7	3.9
Median Family Income ²	1999	\$87,304	\$45,179

¹ Source: Maine State Planning Office

² Source: U.S. Census Bureau

³ 1990 Source: U.S. Census Bureau

1997 Source: Maine Department of Labor

Residential Conversion Model Data

Falmouth town officials provided several geodatabases of GIS files, including parcel maps, locations of building footprints, zoning maps, location of public facilities, vernal pools and other natural resources. A copy of the tax assessor's database, which could be joined to the parcel map, was also provided. Tax Assessors' databases offer parcel-scale information about the lands in a town. Such databases contain valuable information about the use of the land, the value of the land, land attributes, and structural attributes. Information on subdivisions and year built, for example, allowed for creation of a spatial database representing the land use history in spatial form. Several other variables were acquired from other sources or generated using GIS (ArcGIS v. 9.2, ESRI Inc., USA). Explanatory variables describe the costs of development, the proximity of the parcel to amenities or disamenities, the availability of public services, relevant zoning and growth management policies, and spatial externalities from the surrounding landscape. Names, brief descriptions, and descriptive statistics for the explanatory variables are shown in Table 4-2.

GIS layers for soil type, hydrologic features, and other geographic features were downloaded from the Maine Office of GIS (MEGIS). A slope map was calculated from the digital elevation model (DEM) available from MEGIS. The Maine GAP Analysis Project provided a 30-meter land cover map from 1993, which was used as a proxy for 1995 land cover. Digital orthophotos from 2003, and a 2004 5-meter land cover map of Maine (MELCD), both downloaded from the Maine Office of GIS, were used as a proxy for 2005 land cover. These data layers also provided valuable information about the landscape of the study area and allow for validation of the tax assessment database information.

The costs of converting an undeveloped parcel to a residential use are estimated using attributes of the landscape that suggest higher or lower development costs. A soil map, acquired from the Maine Office of GIS, was used to create several variables, including the percentage of each parcel that has poorly draining hydric soils (HYDRIC_SHARE), the percentage of each parcel that contains prime farmland soils (AG_SHARE), and the percentage of each parcel containing steep slopes (>15%) (STEEP_SHARE). Hydric soils and steep slopes are expected to increase development costs, while prime farmlands soils suggest greater returns to farming and, therefore, higher opportunity cost of conversion to residential use. Thus negative coefficients are expected for all three of these variables. Parcels that contain areas identified by the Maine Department of Inland Fisheries and Wildlife (MDIFW) as Significant Wildlife Habitat are subject to additional development restrictions that may also increase development costs. A map of all locations of Significant Wildlife Habitat was provided by MDIFW, and the percentage of each parcel that is so designated was also calculated (SWH_SHARE). The zoning ordinance includes a Highland Lake Overlay Zone, which adds restrictions and additional requirements for any development within the zone. Such requirements would likely increase the cost of development, so a dummy variable, with an expected negative sign, was included and coded 1 for parcels within the overlay zone and 0 otherwise (HLK_OVERLAY).

Table 4-2. Explanatory variables used in Logit Model of Residential Land Conversion: Falmouth, Maine (1996-2005)

VARIABLE	DESCRIPTION	MEAN	STD. DEV.
Proxies for cost of development			
HYD_SHARE	Percentage of parcel containing hydric soil (ranges from 1 – 100)	18.845	31.299
AG_SHARE	Percentage of parcel containing prime agricultural soil (ranges from 1 – 100)	5.762	18.674
STEEP_SHARE	Percentage of parcel with steep slope (> 15%) (ranges from 1 – 100)	11.133	22.894
SWH_SHARE	Percentage of parcel in Significant Wildlife Habitat (ranges from 1 – 100)	5.748	21.151
HLK_OVERLAY	Within Highland Lake Overlay Zone (0/1 indicator variable)	0.070	0.255
Measures of proximity to amenities or disamenities			
LOGDCOA	Natural log of distance (in feet) to coast	8.547	1.692
LOGDPORT	Natural log of distance (in feet) to centroid of Portland, Maine	10.075	0.353
LOGDMJRD	Natural log of distance (in feet) to a major road	7.451	1.097
LOGDTPK	Natural log of distance (in feet) to Maine Turnpike Exit	9.446	0.649
LOGDI95EX	Natural log of distance (in feet) to I-95 Exit	9.374	0.727
LOGDVMU	Natural log of distance (in feet) to Village Mixed Use Zone	8.998	1.131
LOGDHLK	Natural log of distance (in feet) to Highland Lake	9.729	1.299
Local regulations and availability of public services			
SEWER1500	Within 1500 feet of existing sewer main (0/1 indicator variable)	0.403	0.491
WATER_1500	Within 1500 feet of existing water main (0/1 indicator variable)	0.795	0.404
MINLOTSIZE	Minimum allowable lot size (in square feet) under current zoning	49630.662	27913.298
DEV_LOTS	Maximum number of developable lots under current zoning	7.884	15.932
Landscape measures/spatial externalities			
DEV100	Percentage of neighborhood within 100 meters that is highly developed urban land (ranges from 1 – 100)	24.430	28.973
DEV1_500	Percentage of neighborhood between 100 and 500 meters that is highly developed urban land (ranges from 1 – 100)	16.513	16.756
FOR100	Percentage of neighborhood within 100 meters that is forested (ranges from 1 – 100)	41.207	28.033
FOR1_500	Percentage of neighborhood between 100 and 500 meters that is forested (ranges from 1 – 100)	44.661	21.598
AG100	Percentage of neighborhood within 100 meters that is agricultural or open land (ranges from 1 – 100)	27.048	25.377
AG1_500	Percentage of neighborhood between 100 and 500 meters that is agricultural or open land (ranges from 1 – 100)	24.253	17.544

Proximity variables measure the distance from the centroid of each parcel to amenities or disamenities, including the coast (LOGDCOA), the nearest major employment center, Portland (LOGDPORT), major state highways or interstates (LOGDMJRD), the Maine Turnpike and I-95 exits in town (LOGDTPK and LOGDI95EX), Highland Lake (LOGDHLK) and the Village Mixed Use Zone which serves as Falmouth's downtown (LOGDVMU). Proximity to the coast, Portland, Highland Lake and the Village Mixed Use Zone are all expected to make a parcel more attractive for residential development. Since these are measured as distances, however, a negative sign is expected for their coefficients, indicating that a greater distance from amenities corresponds to a smaller probability of development. Major roads and Interstate exits could be amenities, by allowing for easier commuting, or disamenities, by increasing noise and traffic congestion. Thus the expected signs of these variables are unclear. Linear, quadratic, and log-transformed versions of the proximity variables were all tried in the model, with the log-transformation providing the best fit.

GIS zoning maps were used to identify zoning regulations that were applicable to each parcel. Notably, these maps isolate lands that can be developed and the intensity at which they may be developed and, therefore, assist with sample definition. Only parcels that were either undeveloped or were large enough to be subdivided into at least four lots under 1995 zoning were included, resulting in 1,435 developable parcels in the data set. The locations of all new residences built between 1996 and 2005 were included and considered the "developed" parcels (n=843). Minimum allowable lot size was determined for each parcel based on the zoning ordinance. Parcel size was divided by minimum lot size (both measured in square feet) to determine the maximum number of developable lots for each parcel (DEV_LOTS). Assuming larger subdivisions are preferred by developers, this coefficient would be expected to have a positive sign. Town policies support connection to public sewer and water infrastructure if a parcel is within 1500 feet of existing lines. Thus 1500-foot buffers were created around the existing sewer and water lines. Two dummy variables (SEWER1500 and WATER1500) were then created for each parcel and coded as 1 if the parcel is within the appropriate buffer and 0 otherwise. All else equal, parcels would be expected to be more likely to be developed if they are within these buffers.

Concentric buffers were created around each parcel in rings measuring 100 meters, and 100-500 meters. The Maine Gap Land Cover map and the 2004 Maine Land Cover Dataset were reclassified into four general land cover types, agricultural/open field, forested, developed, and wetland. The Gap land cover was used for the empirical model of 1996-2005 conversions, and the 2004 land cover map (MELCD) was used for predictive purposes. The percentage of land within each buffer area was calculated for each land cover type. Since all land falls into one of these four cover types, wetlands were omitted from the model in order to serve as a baseline. Expected signs for these variables are unclear, as each land type could either attract or repel development.

Landscape Permeability Model Data

In 2002 a consulting firm, Woodlot Alternatives, was hired by the Town of Falmouth to produce a preliminary map of vernal pools from aerial photography and limited field verification. With the help of the Maine Audubon Society and the Falmouth Conservation Commission, volunteer

citizen-scientists performed further field verification and catalogued the location and size of 143 vernal pools in Falmouth between 2003 and 2005. A GIS layer of these vernal pools was also provided and used as core breeding habitat for wood frogs in the landscape permeability model and to simulate future vernal pool conservation efforts in the predictive models.

The 2004 Maine Land Cover Dataset was reclassified from 27 cover types to 6 general types, forest, recently cut forest, field/lawn, bare ground, water, and developed land/road. The complete reclassification table is included in the Appendix. Certain important landscape components were not detected in the MELCD, including some roads and existing buildings. These features existed in vector format in the Town of Falmouth databases and were converted from vector to raster format (Feature to Raster command in Arc Toolbox) and then combined with the reclassified land cover map (Raster Calculator in Arc Toolbox) to produce a map of general habitat types. Each habitat type was assigned a cost coefficient based on current knowledge of habitat use by the focal species (Heatwole 1961, Bellis 1965, Berven and Grudzien 1990, deMaynadier and Hunter 1998, Baldwin et al. 2006, Patrick et al. 2006). Interstates, buildings, and Highland Lake were considered absolute barriers to travel and were assigned cost values that exceed the dispersal capability of the focal species. Costs, excluding barriers, ranged from 1 to 20 and are shown in Table 4-3.

Table 4-3: Cost coefficients for each habitat type*

Forest	1
Recently cut forest	5
Field, lawn, or minor road	10
Bare ground	15
Major arterial road	20
Barriers	1000

* Based on: Heatwole 1961, Bellis 1965, Berven and Grudzien 1990, deMaynadier and Hunter 1998, Baldwin et al. 2006, Patrick et al. 2006)

To produce cost rasters for the three predicted future scenarios, it was necessary to determine which parcels would be developed, how many houses would be placed on each parcel, and where those houses would be located. The economic model identified the parcels that are most likely to be developed, and the variable DEV_LOTS determined the number of houses that could be located on each parcel, assuming developers subdivide land at its maximum allowable density. Points (one per house) were randomly placed in each parcel using Hawth's Tools "Generate Random Points" tool (<http://www.spatial ecology.com/htools/>) in ArcGIS 9.2. A random sample of 25 houses built in the study town in the last ten years showed that the average house footprint was 2,313 square feet (~215 m²), and the average yard size was 22,230 square feet (~2,065 m²) (unpubl. data). Thus, around each point, two square polygons were created to represent the average house and yard footprint. After converting these to raster format, the cells representing new houses were reclassified as barriers in the landscape, and the cells representing new yards were reclassified as field/lawn and assigned a cost value of ten in the new landscape. New roads are not included in the model at this time.

The maximum dispersal distance used in the permeability model was 430 meters (from Patrick et al. 2006). This is a fairly conservative assumption in that it is one of the higher dispersal

distances reported for adult wood frogs (Bellis 1965, Baldwin 2006). While most wood frogs do not disperse such great distances, it is clear that some, particularly juveniles are able to do so (Berven and Grudzien 1990). Nonetheless it should be noted that use of a shorter dispersal distance in the models would result in less permeable landscapes than those reported here.

5. RESULTS AND DISCUSSION

Model of residential conversion

For the logit model of residential land conversion, overall model significance was assessed with a likelihood ratio chi-squared test ($\alpha = 0.05$, with appropriate degrees of freedom) (Hosmer and Lemeshow 1989). Model selection began by including all explanatory variables in the model and proceeding in a stepwise fashion with backward elimination, again based on a likelihood ratio chi-squared test ($\alpha = 0.05$, $df=1$), and by comparison of the Akaike Information Criterion (AIC). Significance of individual parameter estimates was assessed with a Wald statistic test ($\alpha = 0.05$). Results of the final model are shown in Table 5-1.

Table 5-1: Results from logit model of residential conversion, 1996-2005

VARIABLE	COEFFICIENT	STD. ERROR	P-VALUE	MARGINAL EFFECTS	MARG. EFF. STD. ERROR	MARG. EFF. P-VAL.
INTERCEPT	-0.607	2.587	0.815	-0.124	0.529	0.815
SEWER1500	0.991	0.190	0.000	0.208	0.040	0.000
MINLOTSIZE	1.74E-05	4.01E-06	0.000	0.000	0.000	0.000
AG500	0.022	0.005	0.000	0.005	9.40E-04	0.000
DEV100	-0.014	0.006	0.021	-0.003	0.001	0.021
DEV1_500	0.028	0.011	0.009	0.006	0.002	0.009
LOGDPORT	-1.51	0.302	0.000	-0.309	0.061	0.000
LOGDMJRD	0.429	0.084	0.000	0.088	0.017	0.000
LOGDCOAS	0.528	0.089	0.000	0.108	0.018	0.000
LOGDVMU	0.589	0.116	0.000	0.120	0.023	0.000
N = 1,435						
Log Likelihood = -775.28						
Restricted log likelihood = -912.47						
AIC = 1.094						

The estimated coefficients indicate the change in the log odds of development given a one-unit change in the predictor. Since this interpretation is not readily intuitive, marginal effects are a convenient alternative. Marginal effects represent, for continuous explanatory variables, the change in the probability of development for a one-unit change in the explanatory variable, evaluated at the mean of the explanatory variable. For dummy variables, a one-unit change is the difference between the condition being true and false. Thus for SEWER1500, the marginal effect of 0.208 represents the increase in the probability of development for a parcel that is within 1500 feet of the sewer lines over an otherwise identical parcel that is not within this distance. For MINLOTSIZE, which is measured in square feet, a one-unit change is very small (e.g. from 40,000 to 40,001), so the marginal effect is essentially zero. The positive sign, however, indicates that, other things equal, larger lot sizes are preferred.

The neighborhood variables are measured as percentages, so, for instance, a one-unit change in AG500 indicates a one percentage-point increase in the amount of agricultural/open land within 500 meters of a parcel. The marginal effect indicates that this change would increase probability of development by 0.005. This result may suggest a preference on the part of homebuyers to live in a rural, scenic setting, near farms and fields, thus providing higher returns to residential land in such areas. Alternatively, as many suburban lawns are placed in this land use class as well, this may indicate that new houses tend to be located near existing ones. The negative coefficient for DEV100 suggests lower returns to residential conversion within 100 meters of developed land, such as major roads, shopping centers, or industry. The positive sign for DEV1_500, however, indicates a higher probability of development for parcels that are between 100 and 500 meters of developed land. These results may indicate that it is desirable to live some distance from developed land, while still being relatively close.

The variables indicating proximity to amenities and disamenities are measured as natural logarithms of distances, with distances in feet. The variable, LOGDPORT, for example, has a range from 9.08 to 10.76. Exponentiating these values returns the distances in feet, so a one-unit increase from 9.5 to 10.5 represents an increase in distance of 13,360 feet to 36,316 feet ($e^{9.5}=13,360$; $e^{10.5}=36,316$), a difference of 22,956 feet. The marginal effect, then, indicates that for an increase of 22,956 feet in distance to Portland, a parcel's probability of development would decrease by about 0.309. Similar interpretations of marginal effects for the remaining variables indicate that a parcel is more likely to be developed if it is closer to Portland but farther away from major roads, the coast, and the Village Mixed Use Zone.

Predicting Future Residential Conversion

For the 1,079 parcels that could still be developed as of 2005 (i.e. those that were undeveloped or had four or more developable lots), new explanatory variables were created to reflect 2005 land cover and zoning conditions. The parameter estimates from the economic model were then used to predict future land conversion. Predicted probabilities of development for each developable parcel are shown in Figure 5-1. Probability of development is highest for parcels near the lake in the western area of the study region and in the east-central area. They are generally lowest along the coast and in the west-central area.

To examine the impacts of different growth management policies, three scenarios were modeled. Under scenario 1, the development scenario, the town's current zoning is used, but there is no protection around vernal pools. The current zoning ordinance determines minimum lot sizes for each zone and requires 50% of the net buildable area of any subdivision to be set aside as open space. It is assumed that the parcels with the highest probability of development will be converted first. Under this scenario, 187 current parcels are developed into 843 house lots. Figure 5-2 shows which areas are developed under this scenario. The development occurs primarily around the lake in the western portion of town and in the east-central portion of town.

Figure 5-1: Predicted probability of future development

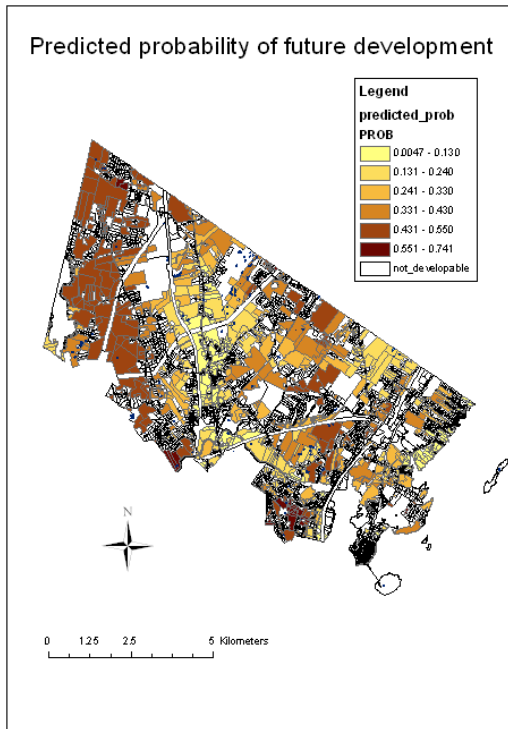
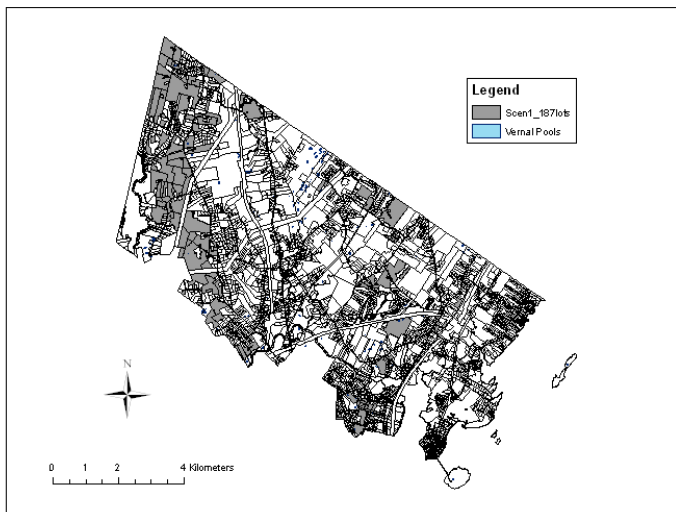


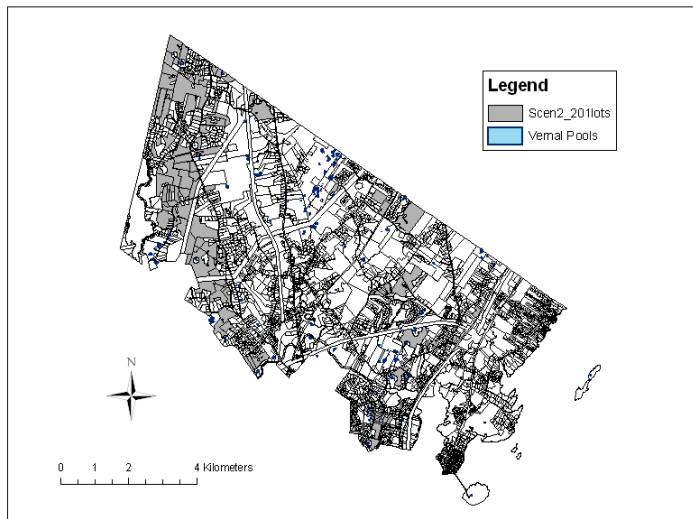
Figure 5-2: Parcels developed under development scenario (scenario 1)



Under scenario 2, the baseline scenario, the current zoning is used again, but a 250-foot buffer around vernal pools is protected from development. This is considered the baseline scenario, as it most closely reflects the existing zoning in the study town as well as the State's new vernal pool legislation. Under the baseline scenario, 201 current parcels are developed into 843 house lots. Figure 5-3 shows which parcels are developed under this scenario. The development occurs in essentially the same areas as in the development scenario. However an additional 14

lots are required to accommodate the new houses due to the removal from the net buildable area of a 250 foot buffer around each vernal pool.

Figure 5-3: Parcels developed under baseline scenario (scenario 2)



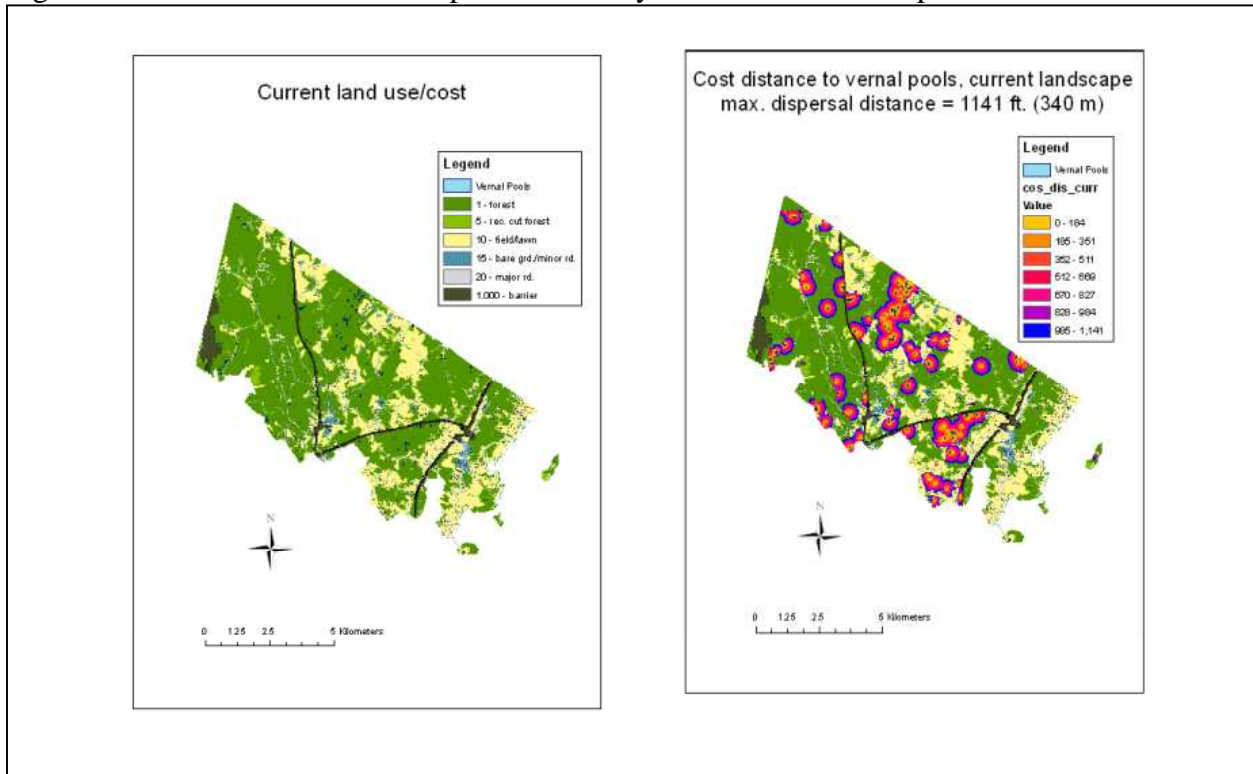
Under scenario 3, the conservation scenario, the current zoning is used again, but the vernal pool protections are expanded to more closely reflect the “Best Development Practices” described in Calhoun et al. (2005). Best Development Practices include allowing no development within the 250 foot buffer around each vernal pool, but also create an additional buffer of 320 meters (~755 feet) within which no more than 25% of the land may be disturbed. Under this scenario, the same lots are developed as in the baseline scenario, but houses may be clustered together on smaller lots to ensure that no more than 25% of the land within the outer buffer is disturbed. While this may, in some cases, violate the minimum lot sizes in the current zoning ordinance, the overall density of each subdivision remains unchanged.

Landscape Permeability Models

Landscape permeability was assessed for four different landscapes, the current landscape, the development scenario (scenario 1), the baseline scenario (scenario 2), and the conservation scenario (scenario 3). The land use raster and cost-distance raster for the current landscape and for future scenarios 1, 2, and 3 are shown in Figures 5-4, 5-5, 5-6, and 5-7 respectively.

The current land use/cost raster in Figure 5-4 shows that the majority of the current land cover in the study region is forest, with a significant amount of field/lawn as well. The majority of the field/lawn area, particularly in the central to eastern area, is suburban lawn or active recreation land, with what little agricultural land that exists concentrated in the northwest area. The cost-distance raster for the current landscape shows that most, though not all vernal pools are within the dispersal distance of other vernal pools and of areas of forest. The diminished dispersal ability across fields and lawns as compared to forests is clear, as are the limiting effects of barriers.

Figure 5-4: Land Use and Landscape Permeability for Current Landscape



Landscape permeability models assume that the focal species can travel up to its maximum dispersal distance in its preferred habitat, but that it cannot travel as far in lower quality (i.e. more “costly”) habitats. Thus the regions in the cost-distance rasters that indicate possible dispersal will be larger in higher quality habitat and smaller in lower quality or more fragmented habitat. One summary measure of the quality of different predicted landscapes, then, is the number of cells in the cost-distance raster of each landscape. The cost-distance raster for the current landscape contains 523,509 cells. At 5x5 meters per cell, this represents an area of $523,509 \times 25 = 13,087,725$ square meters (~3,234 acres) within which dispersal is possible. All three future scenarios involve some development within the potential dispersal area for the focal species, so the cost-distance rasters for the future scenarios will have fewer cells than the cost-distance raster for the current landscape does. A larger number of cells indicates a more permeable landscape (i.e. more cells within the potential dispersal area) for the focal species. The number of cells in the cost-distance raster for the current landscape and the three future landscapes is shown in Table 5-2.

Table 5-2: Comparison of potential wood frog dispersal for current and future landscapes

Landscape	Number of cells in potential dispersal area	Potential dispersal area	Potential dispersal area lost to development
Current	523,509	13,087,725 m ² ~3,234 ac.	--
Development Scenario	508,910	12,722,750 m ² ~3,144 ac.	364,975 m ² ~90 ac.
Baseline Scenario	515,052	12,876,300 m ² ~3,182 ac.	211,425 m ² ~52 ac.
Conservation Scenario	515,729	12,893,225 m ² ~3,186	194,500 m ² ~48 ac.

The most apparent difference between the cost-distance raster for the development scenario and that of the current landscape is the many new houses and yards in the forested western portion of the study region. As there are relatively few vernal pools in this region, permeability is not greatly affected. There are, however, many new houses located very close to vernal pools, and the number of cells within the potential dispersal area represented by the cost-distance raster has decreased to 508,910. This represents the loss of 14,599 cells, for a total of 364,975 square meters (~90 acres) lost relative to the current landscape.

Figure 5-5: Dispersal Cost and Landscape Permeability for Development Scenario

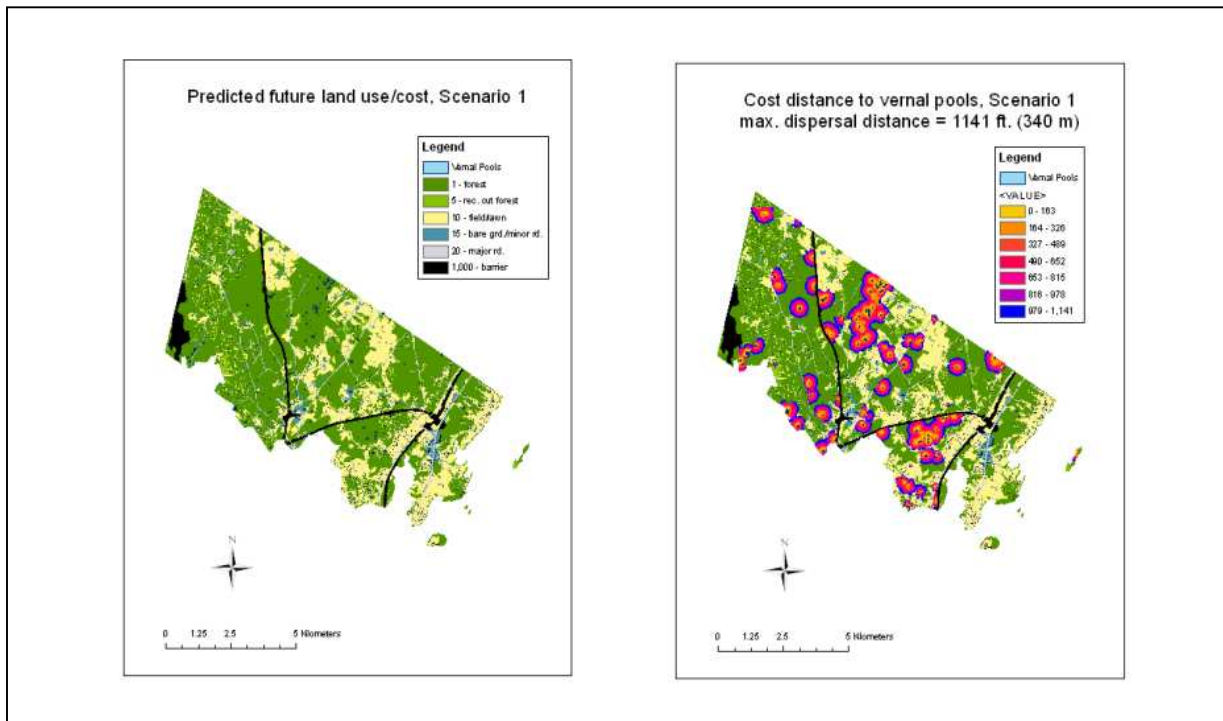


Figure 5-6: Dispersal Cost and Landscape Permeability for Baseline Scenario

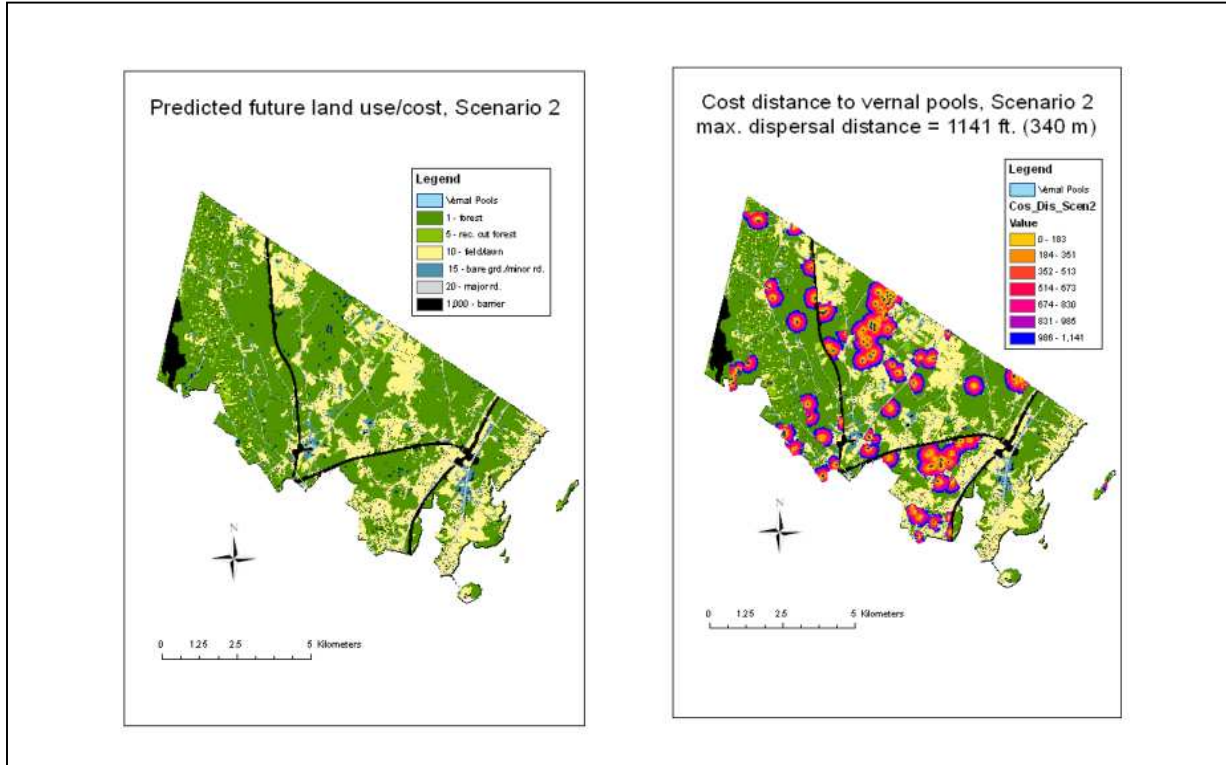
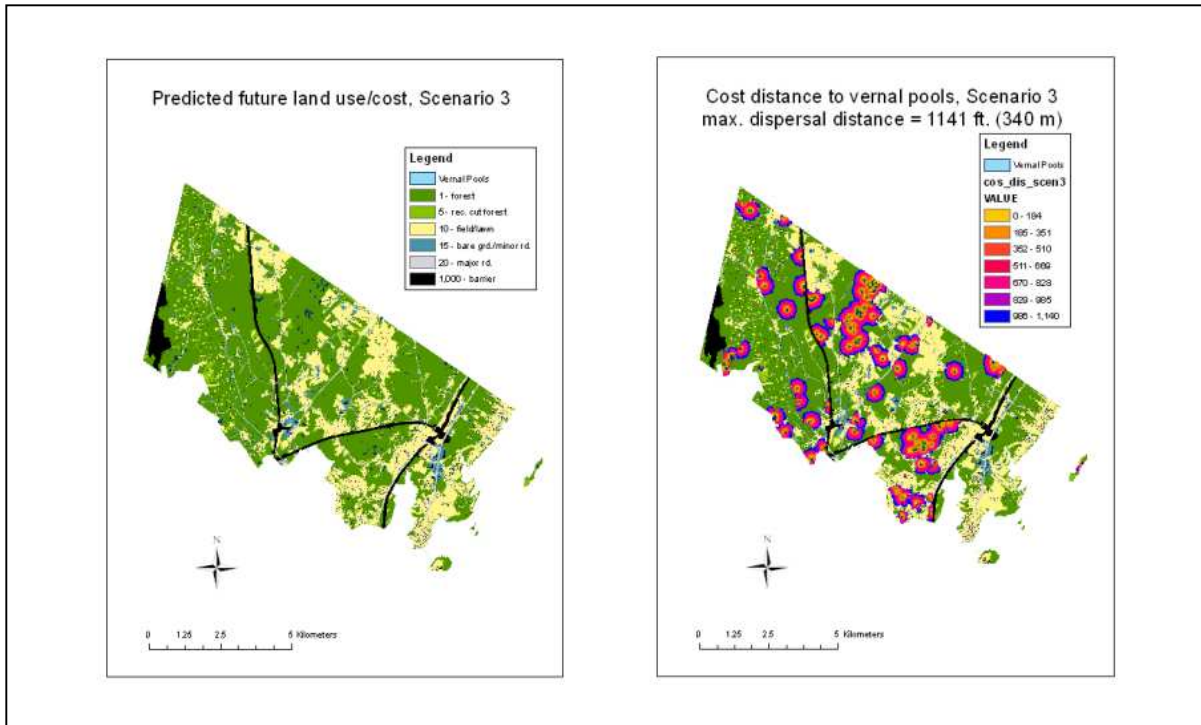


Figure 5-7: Dispersal Cost and Landscape Permeability for Conservation Scenario



While Table 5-2 provides some evidence of the beneficial effects of conservation measures on overall landscape permeability, focusing on one smaller area may provide even greater insights. The next four figures focus on the southeast portion of the study area, an area with a high probability of future development and a high concentration of vernal pools. Figure 5-8 shows permeability for the current landscape in the southeast portion of the study area. Permeability is currently relatively high between vernal pools and between vernal pools and upland forest. If a population were to go extinct due to stochastic forces, it seems relatively likely that dispersers from another pool would be able to recolonize, making the overall metapopulation relatively stable.

Under the development scenario (Figure 5-9) new houses are located in what are likely to be key travel corridors between many vernal pools. While successful travel between pools may still be possible, the landscape is clearly more fragmented, and such dispersal seems more difficult. A local extinction seems much less likely to be recolonized than in the current landscape.

Figure 5-10 shows that the baseline scenario, despite preserving more of the potential dispersal area overall, does relatively little to improve permeability between vernal pools over the development scenario. While no houses are located within 250 feet of a pool, many are located in corridors between pools, making dispersal difficult.

Under the conservation scenario in Figure 5-11, permeability is noticeably better than under either of the other two future scenarios. Despite the fact that this scenario resulted in only slightly more potential dispersal area overall, it does a much better job of maintaining connectivity in this region. The requirement that no more than 25% of land within 755 feet be disturbed resulted in this case in a more clustered pattern of housing, leaving important travel corridors undisturbed.

Conclusions

Several policy implications are suggested by this work. Significant drivers of residential conversion have been identified, many of which are distances from amenities or disamenities or the condition of the neighboring landscape. These are factors over which planning officials have little control, suggesting that the ability of policymakers to decide where development occurs may be somewhat limited. Significant drivers that are under the control of local officials are sewer service areas, minimum lot sizes, and other land and zoning regulations. Clearly public sewer service is a valuable amenity that increases returns to residential land, so extensions of such service areas should be viewed as important growth management decisions. The fact that larger minimum lot sizes appear to increase residential returns suggests that some sort of incentive is likely needed if a town or region wants to encourage higher-density development.

Figure 5-8: Current landscape permeability in southeast Falmouth

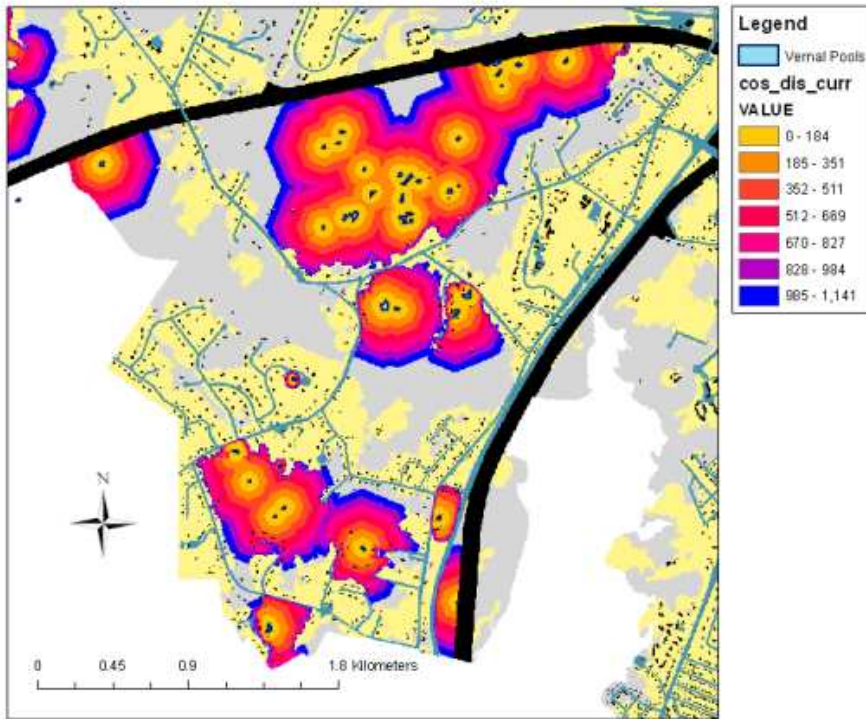


Figure 5-9: Landscape permeability in southeast Falmouth under development scenario

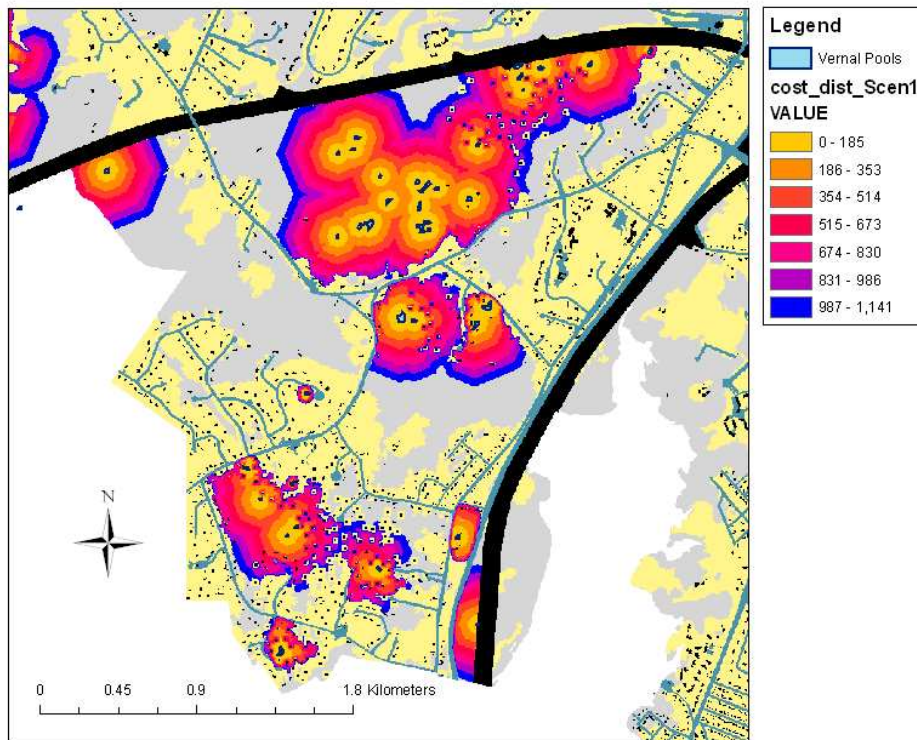


Figure 5-10: Landscape permeability in southeast Falmouth under baseline scenario

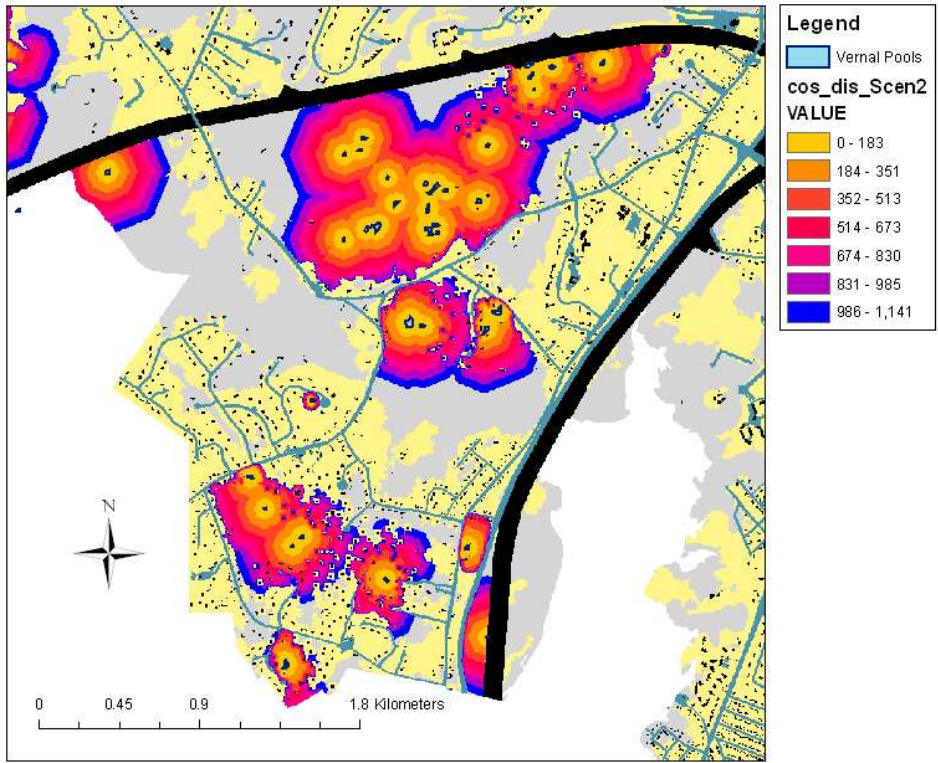
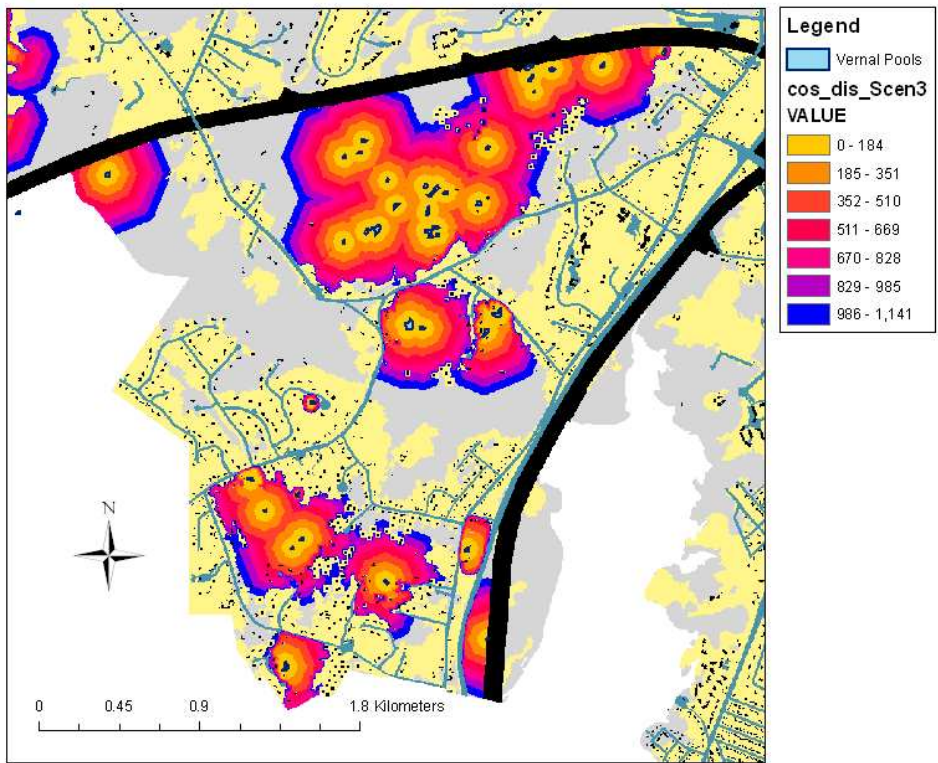


Figure 5-11: Landscape permeability in southeast Falmouth under conservation scenario



This work also identified the areas of the study town that are most likely to be developed in the near future. Some of the high-growth areas have very few vernal pools, while others have many. Clearly the areas with a high concentration of vernal pools and a high probability of development may be important considerations when deciding where to spend limited conservation resources. This result, while applied only to one town in this study, highlights the fact that an interdisciplinary approach, combining land use economics and landscape ecology, can provide important information for prioritizing conservation efforts that possibly neither discipline would have produced alone.

Another important conclusion of this work is that the 250-foot buffers around vernal pools may not protect sufficient matrix habitat by themselves to maintain connectivity between pools or between pools and upland forests. This suggests that additional measures may be needed to avoid a long-term decline in landscape permeability, which would thus jeopardize the long-term stability of vernal pool-breeding metapopulations. The use of multiple buffer zones with different levels of conservation measures appears to be an improvement over simple, protective buffers.

It should be noted that these results are likely very sensitive to the cost values assigned to various habitat types and to the maximum dispersal distance used in the permeability model. Future efforts should focus on improving knowledge of wood frogs' dispersal abilities in different habitats, and sensitivity analysis should be undertaken to examine the robustness of these results. Another important direction for future work is to improve the method of predicting locations of new houses. The random placement used in this paper ignores the fact that houses tend to be built next to one another and in a linear fashion along new or existing roads. It also makes no effort to incorporate new roads that inevitably must be built to accommodate residential growth and to provide access to previously undeveloped land. Roads, aside from taking up additional space, are a major source of landscape fragmentation (Gibbs 1998, Carr and Fahrig 2001, Mazerolle 2004), so this is admittedly a significant omission. Better understanding of the determinants of road and house placement is critical to the integration of economic models of land use and landscape ecology models of permeability. Nonetheless, future research should continue to use interdisciplinary methods to examine landscape permeability and search for growth management and conservation policies that more effectively preserve important corridors between vernal pools and between breeding pools and upland forest.

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APPENDIX: MELCD RECLASSIFICATION TABLE

MELCD description	Reclassified Description
High intensity developed	Developed
Medium intensity developed	
Low intensity developed	
Roads/runways	
Open space developed	Field/lawn
Cultivated crops	
Pasture/hay	
Grassland/herbaceous	
Blueberry field	
Deciduous forest	Forest
Evergreen forest	
Mixed forest	
Scrub/shrub	
Wetland forest	
Recent clearcut	
Light partial cut	
Heavy partial cut	
Regenerating forest	
Wetlands	Water
Unconsolidated shore	
Open water	
Bare land	Bare Land