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Predicting impacts of future human population growth and development on occupancy rates of forest-dependent birds

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ABSTRACT

Forest loss and fragmentation are among the largest threats to forest-dwelling wildlife species today, and projected increases in human population growth are expected to increase these threats in the next century. We combined spatially-explicit growth models with wildlife distribution models to predict the effects of human development on 5 forest-dependent bird species in Vermont, New Hampshire, and Massachusetts, USA. We used single-species occupancy models to derive the probability of occupancy for each species across the study area in the years 2000 and 2050. Over half a million new housing units were predicted to be added to the landscape. The maximum change in housing density was nearly 30 houses per hectare; however, 30% of the towns in the study area were projected to add less than 1 housing unit per hectare. In the face of predicted human growth, the overall occupancy of each species decreased by as much as 38% (ranging from 19% to 38% declines in the worst-case scenario) in the year 2050. These declines were greater outside of protected areas than within protected lands. Ninety-seven percent of towns experienced some decline in species occupancy within their borders, highlighting the value of spatially-explicit models. The mean decrease in occupancy probability within towns ranged from 3% for hairy woodpecker to 8% for ovenbird and hermit thrush. Reductions in occupancy probability occurred on the perimeters of cities and towns where exurban development is predicted to increase in the study area. This spatial approach to wildlife planning provides data to evaluate trade-offs between development scenarios and forest-dependent wildlife species.

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1. Introduction

Human modifications of natural landscapes have reached most corners of the globe. Activities such as agriculture, development, and resource extraction historically and presently continue to transform land (Dale et al., 2000; Turner et al., 2001). Of particular concern are the many adverse effects land transformation can have on wildlife (Vitousek et al., 1997; Gutzwiller, 2002; Foley et al., 2005; Brown and Laband, 2006) through changes in land use (how land is utilized) and land cover (the physical appearance of the land surface) (Turner et al., 1994). Land use changes can be caused by natural processes, but human-induced modifications are by far the most significant modern forces behind land transformation (Forman, 1995; Lindenmayer and Franklin, 2002). This presents challenges for how wildlife conservation will remain compatible with increased human development as the global population is projected to grow to over 9 billion people within the next four decades (United Nations, 2011).

In the northeastern USA, the populations of Vermont, New Hampshire, and Massachusetts are predicted to grow 16.9%, 33.2%, and 10.4%, respectively, between the years 2000 and 2030 (U.S. Census Bureau, 2011), collectively adding 1.2 million people. Importantly, the relationship between population growth and land use conversion differs across regions worldwide. For example, in Vermont the rate of land conversion is happening 260 times faster than population growth (Vermont Forum on Sprawl, 1999), and in Massachusetts residential housing accounts for 87% of land use change even in areas where population growth is roughly flat (DeNormandie et al., 2009).

Wildlife biologists and other conservation professionals are pressed to estimate the risk fauna populations will face in response to this projected human growth and increase in development. Wildlife abundance, distribution, and viability can be intricately

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tied to the condition of the landscape mosaic (Forman, 1995; Lindenmayer and Franklin, 2002). For example, landscapes with low amounts of forest cover have significantly more nest predation and lower bird densities as compared with unfragmented landscapes (Robinson et al., 1995, Donovan et al., 1997, Rosenberg et al., 1999). Bird species occurrence can also decrease in proximity to roads (Brotons and Herrando, 2001).

Because many wildlife species are responsive to both forest loss and fragmentation, there is a great need to predict where human growth and development is likely to occur, and the resulting consequences to wildlife. Some progress has been made with respect to land use change modeling (e.g., overview by Voigt and Troy, 2008), however, developing quantitative metrics that allow decision makers to link predicted land use changes with changes in forest-dependent wildlife species remains a pressing need.

Our goal in this paper is to predict changes in forest bird distribution patterns to the year 2050 as a result of increased development, and determine how the current network of reserves contributes to species' distribution patterns overall. The objectives of our study were to: (1) spatially quantify projected increases in human housing units in the study area to the year 2050, (2) based on projected human housing growth, forecast changes in four landscape variables: percent development, road density, percent forest cover, and distance to developed edge, (3) quantify the changes in probability of occupancy in each 30 m pixel for 5 forest interior bird species across the study area and in individual towns, and (4) evaluate the probability of occupancy within and outside of protected lands for the 5 bird species to the year 2050.

2. Methods

2.1. Study area and target species

The study area was the three-state region of Vermont (VT), New Hampshire (NH), and mainland Massachusetts (MA), USA (26,800 square miles). It was approximately 68% forested, 9% agriculture, and 11% developed, according to the 2001 National Land Cover Dataset (NLCD) (Multi-Resolution Land Characteristics Consortium, 2001), which was produced in a similar timeframe as the bird observations (Schwenk and Donovan, 2011). The majority of the study area occurred within the same ecoregion (Adirondack-New England highlands, province M212) (Bailey, 1995). The mean percent forest cover was 0.72 (VT), 0.78 (NH), and 0.52 (MA); the mean percent evergreen forest cover was 0.14 (VT), 0.22 (NH), and 0.12 (MA).

We selected 5 forest interior bird species for analysis based on habitat preferences and sensitivities to forest loss and fragmentation. The species were (1) black-throated blue warbler (*Setophaga caerulescens*), (2) black-throated green warbler (*Setophaga virens*), (3) ovenbird (*Seiurus aurocapillus*), (4) hermit thrush (*Catharus guttatus*), and (5) hairy woodpecker (*Picoides villosus*). In Vermont, the probability of a forest interior bird species occupying a site is dependent largely on the percent forested landscape around a site, as well as road density, distance to an edge, and percent development in the landscape (Schwenk and Donovan, 2011).

2.2. Housing density projections (Objective 1)

Projections of housing density in the study area were derived from the Spatially Explicit Regional Growth Model (SERGoM) (Theobald, 2005; Bierwagen et al., 2010). SERGoM inputs include data on housing units within each census block, county-level historic population, land cover types, and transportation infrastructure; the primary output is a 1 ha raster depicting housing density for the years 2000 and 2050.

We allocated the historic (defined as year 1990) and current (defined as year 2000 throughout the manuscript) housing density on the landscape (defined as the number of housing units per hectare) in three steps within SERGoM (Fig. 1). First, we obtained the number of housing units per census block in the year 2000 from the U.S. Census Bureau (Fig. 1a). Census blocks vary in size from roughly 1–2 ha in urban areas to 100–1000 ha in rural areas (Theobald, 2005). Second, we allocated housing units within each census block using a GIS raster that reflected patterns of growth from 1990 to 2000 upon which the new housing units were allocated (Fig. 1j). This required the identification of land potentially available for development (Fig. 1e). We removed water features such as lakes, reservoirs, and wide rivers to ensure no housing units were placed on those features (Fig. 1c). Like the water features, housing units were not placed on lands that prohibit development like parks and other public lands (Fig. 1b). Third, we considered the influence of roads on the spatial distribution of housing units within a census block. Existing major roads (Esri, 2009) were converted to road density (Fig. 1d), defined as the density of roads within 800 meters of each pixel (Fig. 1f) because undeveloped lands with a high road density tend to be more readily developed (and have effects on wildlife habitat) (Forman et al., 2003). Thus, the final allocation of housing units per hectare (Fig. 1g) resulted from available developable lands and road density (Bierwagen et al., 2010), and the total number of housing units within a block were not assigned homogeneously throughout a block.

We estimated future housing density on the landscape for each hectare in the next decadal time step (Fig. 1l). We used county-level population forecasts (Fig. 1k; Bierwagen et al., 2010) to estimate the increased population size for each county, which are based on a gravity-based model that relate amenity variables such as public land as well as recent county-to-county migration patterns. This was a non-spatial rate of growth that needed to be applied spatially to housing units. We allocated new housing units to each 1 ha pixel in several steps. Location-specific growth rates were computed for 16 development classes (from Theobald, 2005) which were combinations of housing density classes (urban: <0.1 ha/housing unit, suburban: 0.1 to 0.68 ha/housing unit, exurban: 0.68–16.18 ha/housing unit, and rural: >16.18 ha/housing unit) and accessibility classes (measured as travel time from the nearest urban core: 0–10, 10–30, 30–60, and >60 min) (Fig. 1h). The allocation of housing units were adjusted based on proximity to urban areas (Fig. 1i), expressed in the amount of travel time from an urban center along major roads. Finally, we added the newly allocated housing units to a map of current housing units to forecast the future housing unit density. In other words, the calculated housing units for time $t+1$ were added to the housing units at time t.

The number of houses per ha in the study area was derived decadally between the years 2000 and 2050, but we report only on 2000 and 2050. We then applied a moving window analysis to sum the number of houses within a 1 km radius circle for each 1 ha pixel; thus, each pixel indicated the total number of houses within a 1 km radius circle. This radius was selected because it is strongly associated with avian occurrence (Bakermans and Rodewald, 2006) and was used to develop the bird occupancy models in this analysis (Schwenk and Donovan, 2011). Finally, we produced current (year 2000) and future (year 2050) housing unit maps from the outputs of SERGoM (number of housing units summed to 1 km radius circles) for Objective 2.

2.3. Landscape change scenarios (Objective 2)

Increases in housing density will affect landscape features such as land cover. We developed a landscape change model to predict changes in road density (km of roads within a 1 km radius circle),

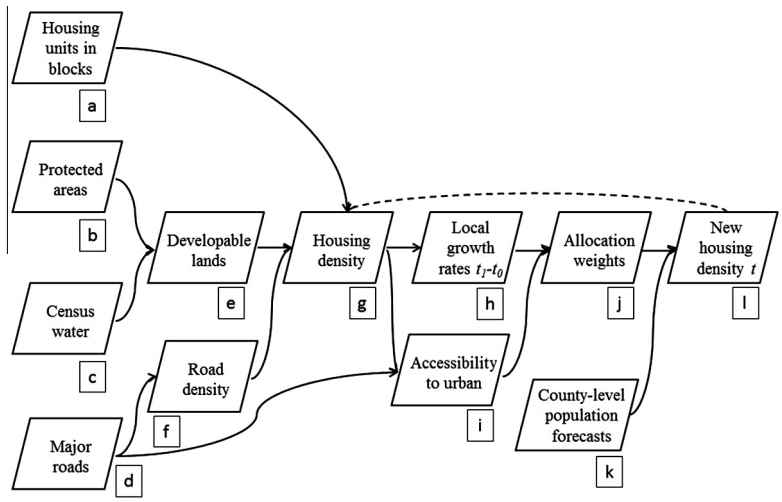

Fig. 1. An illustration of SERGoM depicting the method to spatially allocate future human housing density across a landscape (U.S. Environmental Protection Agency, 2009). Two main phases of SERGoM derive housing projection outputs: (1) calculating current housing density values, and (2) calculating future housing density values. The first phase, Fig. 1a – 1f uses U.S. Census data and available developable lands to create current spatially-explicit housing density values. The second phase of SERGoM, Fig. 1h–l, uses future population growth rates and proximity to urban centers to project spatially-explicit future housing density values.

percent development within a 1 km radius circle, percent forest cover within a 1 km radius circle, and distance to the edge of the nearest different land cover class. These four variables are known to influence bird distributions (Schwenk and Donovan, 2011). We created spatially-explicit GIS rasters for each variable in two years: 2000 and 2050.

We used a 1 km moving window analysis in ArcGIS to calculate road density for each pixel (i.e., km of roads within a 1 km radius circle) on all roads in the U.S. Census Bureau TIGER roads dataset (U.S. Census Bureau, 2011). This resulted in a baseline road density map for the year 2000. To establish the baseline percent forest and development maps, we recoded cells in the 2001 NLCD raster as developed if they coincided with TIGER roads, and categorized the NLCD into six categories that were expected to be perceived by birds as distinct: developed (including roads and bare land); non-forested wetland; open water; agriculture and grassland; forest; and scrub or shrub (Schwenk and Donovan, 2011). Then, we used a 1 km moving window on the reclassified land cover categories to estimate percent development and percent forest cover for each pixel. To establish a baseline minimum distance-to-edge map, we calculated the Euclidean distance for each of the 6 land cover types from the center of each pixel to the nearest pixel of a different land cover class (see Schwenk and Donovan, 2011). Thus, each pixel had 5 distances to alternative land cover types (e.g., if the pixel itself was forested, we computed a distance-to-developed grid, a distance-to-agriculture grid, a distance-to-non-forested-wetland grid, a distance to scrub-shrub grid, and a distance-to-open-water grid). We used the minimum of these 5 grids to compute a minimum distance-to-edge grid, which was the minimum distance in meters to the nearest *different* land cover class for the year 2000.

Given the baseline land cover and road density maps, we then developed a four-step framework to create the future landscape variables for the year 2050 that resulted from increased human housing density. First, we increased road density based on its relationship with housing density. To estimate the relationship between these two variables, we obtained a random sample of 300 pixels (spatially separated by over 10 km) from the study area baseline rasters, and regressed mean road density per 1 km radius circle on the summed number of housing units within the same area for the year 2000. Then, we used the resulting equation to forecast road density for each pixel in the next time step.

Second, we increased the number of developed pixels based on the relationship between development and road density. From our random sample of baseline map locations, we used logistic regression to estimate the association between road density within a 1 km radius circle surrounding a pixel and the percent development within this same area. Then, we used this statistical relationship to predict the increases in percent development in each pixel in each time step. To calculate the total amount of increases in developed land between time steps, we subtracted the percent development in time step t from time step $t + 1$.

Third, for those pixels where the proportion of developed land was expected to increase from one time step to the next, we applied two development scenarios to decrease a corresponding proportion of a non-developed land class. In the first scenario, we assumed that development would occur entirely on forested lands. In the second scenario, we assumed that development occurred half in forest and half in another land cover class.

Finally, as development increased in the landscape, we updated the distance-to-developed-edge grid for all non-developed pixels. First, we regressed the baseline distance-to-developed-edge per 1 ha against housing density and applied this formula to create a 2050 distance-to-developed-edge grid. We compared the 2000 and 2050 grids and in pixels where housing density increased, we retained the new distance-to-developed-edge values for 2050. The final step was to recalculate the minimum distance-to-edge layer for year 2050 by incorporating the new distance-to-developed-edge grid values. The only places where the minimum distance-to-edge decreased in the year 2050 were locations on the landscape where distance-to-developed-edge decreased.

2.4. Species occupancy models (Objective 3)

To examine how the forecasted changes in road density, distance-to-edge, and percent forest cover affect different birds, we used single-species occupancy models for 5 target species, described fully in Schwenk and Donovan (2011). Occupancy models predict the probability that a species will occur (ψ) based on empirical presence-absence data and species' sensitivities to variables like forest amount, forest arrangement, development, and roads (MacKenzie et al., 2006). These models were used to calculate the probability of occupancy (ψ) within each 30 m^2 pixel in the study area based on bird surveys at 693 sites across the state of Vermont in 2003 and 2004. Schwenk and Donovan (2011) selected 6 covariates to predict occupancy: (1) binary forest value within 25 m of bird count point locations (forest), (2) topographic

wetness index (TWI), (3) distance-to-edge of nearest different land cover type (edge), (4) percent evergreen forest within 300 m of point (evergreen), (5) percent forest within 1 km of point (percent_forest), and (6) road density within 1 km of point (roads). The logit equation for the model containing all the occupancy covariates was:

$$\begin{aligned}\text{logit}(\psi) = {} & \beta_0 + \beta_1(\text{forest}) + \beta_2(\text{TWI}) + \beta_3(\text{TWI})^2 + \beta_4(\text{edge}) \\ & + \beta_5(\text{edge} \times \text{forest}) + \beta_6(\text{evergreen}) + \beta_7(\text{evergreen})^2 \\ & + \beta_8(\text{percent_forest}) + \beta_9(\text{percent_forest})^2 + \beta_{10}(\text{roads}) \\ & + \beta_{11}(\text{roads})^2\end{aligned}$$

Quadratic terms were included because many bird species are known to have nonlinear relationships between probability of occurrence and landscape variables. Schwenk and Donovan (2011) evaluated 32 alternative models to determine which variables were the most important predictors of occupancy for each of the 5 target species. Here, we used the model averaged coefficient estimates, which are the weighted averages of the parameter coefficients (betas) where the weights are the AIC weights of each model (Table 1) (Burnham and Anderson, 2002). For our dataset, using the model averaged coefficients to estimate occupancy patterns produced nearly identical results as predicting occupancy patterns for each model weighted by the AIC weight, and then summing the results. Model performance was assessed by running bootstrap goodness-of-fit tests for each species (Schwenk and Donovan, 2011), and all models used in our analysis performed adequately. Across these species, the variable with the strongest effect on occupancy probability was percent forest cover within a 1 km window.

To examine the change in species occupancy based on projected increases in development and roads as a result of increased human housing density, we applied the occupancy models to two years: 2000 and 2050. We used the occupancy logit equation and baseline rasters to establish occupancy patterns in year 2000. We then estimated occupancy in 2050 for both landscape change scenarios by applying the occupancy models to the 2050 covariate rasters for road density, distance-to-edge, and percent forest cover while retaining the 2000 covariate values for TWI, evergreen, and forest. The new equation for species occupancy in 2050 was:

$$\begin{aligned}\text{logit}(\psi) = {} & \beta_0 + \beta_1(\text{forest}) + \beta_2(\text{TWI}) + \beta_3(\text{TWI})^2 + \beta_4(\text{edge_2050}) \\ & + \beta_5(\text{edge_2050} \times \text{forest}) + \beta_6(\text{evergreen}) \\ & + \beta_7(\text{evergreen})^2 + \beta_8(\text{percent_forest_2050}) \\ & + \beta_9(\text{percent_forest_2050})^2 + \beta_{10}(\text{roads_2050}) \\ & + \beta_{11}(\text{roads_2050})^2\end{aligned}$$

Note that even if the development within 1 km of a pixel increased greatly, we assumed that the development did not occur on the pixel itself if it was forested (forest), and the new development did not change TWI or the percentage of evergreen forest within 300 m of the pixel (evergreen). Our analysis, therefore, presents a cautious estimate of land use change in response to future human population growth. We examined changes in occupancy patterns throughout the study area and summarized results by town, which allowed us to comprehensively partition the landscape into comparable units.

2.5. Conserved lands and species habitat (Objective 4)

The probability of occupancy maps represented potential species distributions across the landscape. For each species, we calculated the proportion of the total occupancy probability that occurred within boundaries of protected lands. We considered this proportion a quantitative metric of species conservation (e.g., if 30% of the total occupancy probabilities in year *t* occurred within protected areas, 0.30 represents the degree to which protected lands in year *t* support a species distribution).

We used a conservation lands database developed by The Nature Conservancy to examine the distribution and amount of protected lands across the study area. We considered a parcel to be protected if it had a Gap Status of 1, 2, or 3; meaning it was permanently protected for biodiversity, in a natural state, or secured for multiple uses (The Nature Conservancy, 2010). To estimate the proportion of total occupancy that occurred on protected lands for each species, we summed ψ values across each raster cell in the year 2000. Then, we summed the total ψ values that occurred on protected lands in the year 2000 and divided the summed amount of occupancy probability protected by the total amount of occupancy probability in the study area. We conducted this analysis for each of the 5 study species in two years, 2000 and 2050. If species occupancy patterns declined overall in the year 2050, we expected that the protected areas would house a greater proportion of species' total occupancy due to the protected status of conserved lands.

3. Results

3.1. Human housing density projections (Objective 1)

Objective 1 was to develop human housing density projections between the years 2000 and 2050. Over half a million new housing units were predicted to be added to the landscape in VT, NH, and MA. The forecasted pattern of development followed similar development patterns as in other parts of the United States (Theobald, 2005; Bierwagen et al., 2010); lands outside of urban areas, but within close proximity to urban areas, were expected to gain the

Table 1
Betas obtained through single-species occupancy model analysis for 5 forest interior bird species: hairy woodpecker (HAWO), black-throated green warbler (BTNW), hermit thrush (HETH), ovenbird (OVEN), and black-throated blue warbler (BTBW) (Schwenk and Donovan, 2011).

Coefficient values	HAWO	BTNW	HETH	OVEN	BTBW
Psi intercept	−2.06	−4.76	−3.97	−3.05	−4.74
TWI (topographic wetness index)	−0.0001	0.051	−0.18	0.024	0.016
TWI^2 (topographic wetness index)^2	0.000082	−0.0043	0.011	−0.0039	−0.0016
Edge (minimum distance to edge of nearest different land cover class)	−0.0070	−0.00073	−0.011	−0.0096	−0.012
Forest (binary forest or non-forest value within 25 m of bird count location)	0.064	0.79	1.13	1.06	0.28
Forest * Edge (interaction term for forest and edge)	0.0075	0.0014	0.012	0.011	0.011
Percent forest (percent forest within 1 km radius of pixel)	2.12	6.48	5.90	5.77	7.79
Percent forest^2 (percent forest within 1 km radius of pixel)^2	−0.89	−1.91	−2.46	−2.96	−2.29
Road (road density within 1 km radius of pixel)	0.15	0.058	0.00052	−0.071	−0.043
Road^2 (road density within 1 km radius of pixel)	−0.019	−0.0075	−0.0015	−0.0079	0.0052
Evergreen (percent evergreen forest within 300 m of pixel)	−0.56	2.46	0.39	2.80	−5.64
Evergreen^2 (percent evergreen forest within 300 m of pixel)	0.93	−1.35	−0.38	−4.20	5.78

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most housing units and many rural places were not predicted to grow at all. Towns around metropolises like Boston, MA, Manchester, NH, and Burlington, VT were expected to grow the most. The maximum change in housing density was nearly 30 houses per hectare between the years 2000 and 2050 (Fig. 2). Alternatively, rural areas were expected to grow very little. Thirty percent of the towns in the study area were projected to add less than 1 housing unit per ha between the years 2000 and 2050 (Fig. 2).

3.2. Landscape change scenarios (Objective 2)

Objective 2 was to forecast landscape variables based on projected human housing growth. We predicted future changes to four landscape variables including road density (increase), percent developed land cover (increase), percent forested land cover (decrease), and minimum distance-to-edge (decrease).

First, the model that best predicted the relationship between mean road density in a 1 km radius circle and summed housing density within the same area for the baseline year 2000 was road_1k_2000 = 0.065 + 0.0075 ∗ sqrt(housing density_2000) ($P < 0.0001$, $R^2 = 0.8391$). The maximum road density in 2000 was 35.3 km/km^2 and the maximum road density in 2050 was 36.9 km/km^2, given housing densities in 2050. The mean road density across the study area rose from 2.37 to 2.83 km/km^2 (Fig. 3a).

Second, the model that best predicted the relationship between mean road density and the mean percent developed land class in a 1 km radius window for the year 2000 was ln(odds)_percent development_1 km = −3.20 + 2.83 ∗ log(road density_1km) + 0.60 ∗ (log road density − 0.15)^2 ($P < 0.0001$, $R^2 = 0.8645$). Across the study area, the mean proportion of developed land cover within 1 km increased 3% between the years 2000 and 2050 (Fig. 3b). We used this model to examine two future land scenarios that resulted from predicted housing unit development. The first land scenario assumed that all of the increased development would occur on forested lands. In this scenario, despite the overall mean increase in development being small, some areas experienced up to 32% forest loss within 1 km of a pixel (Fig. 3c). The second land scenario assumed that half of the increased development would occur on

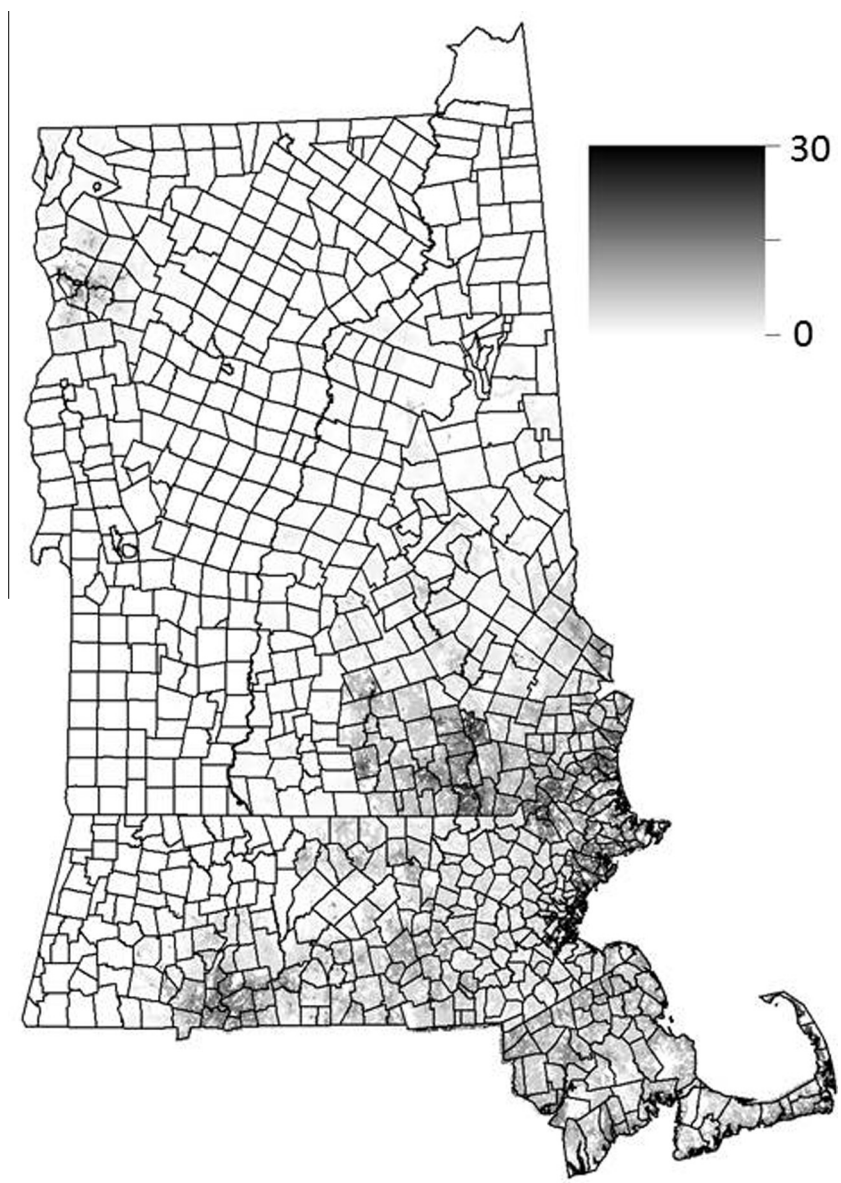

Fig. 2. The amount of projected housing density increase in Vermont, New Hampshire, and Massachusetts, USA, from 2000 to 2050. Housing density values were derived using SERGoM for the years 2000 and 2050. Dark areas illustrate large increases in the number of projected housing units, whereas white areas indicate little or no increase in the number of predicted housing units. Town boundaries are illustrated for geographic reference.

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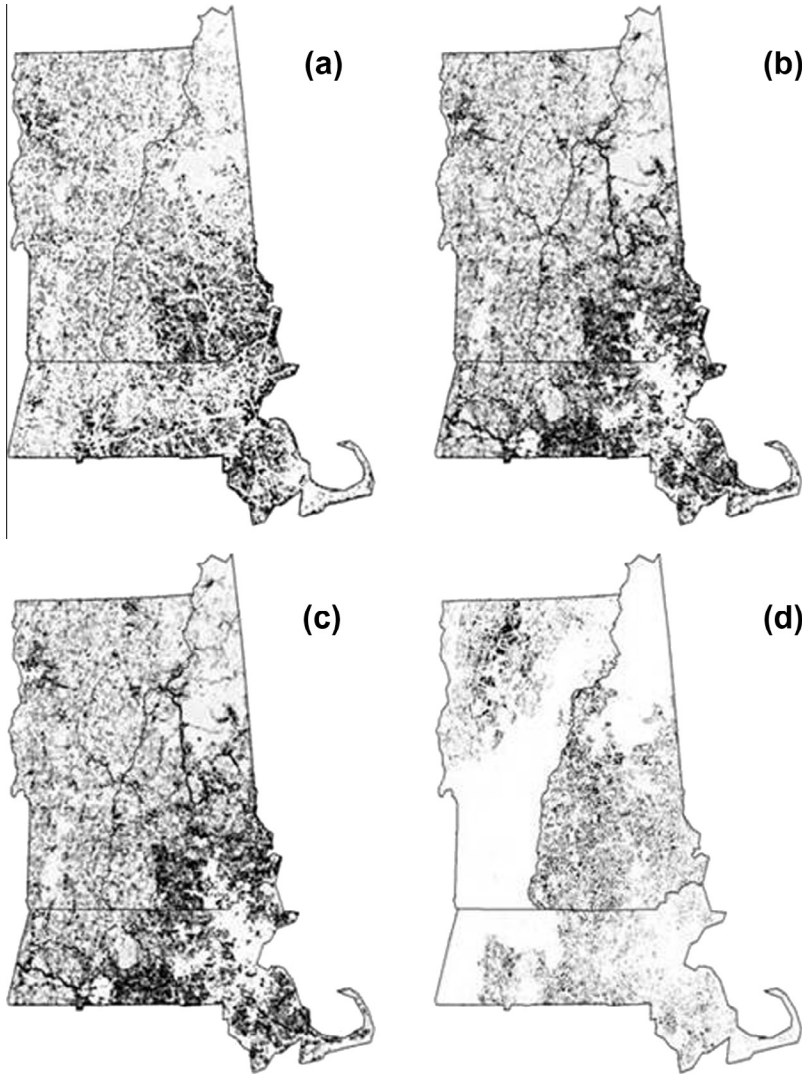

Fig. 3. Changes in four landscape metrics from 2000 to 2050 in Vermont, New Hampshire, and Massachusetts, USA: (a) road density within a 1 km radius circle (values range between 0–20.62 km/km^2), (b) percent development within a 1 km radius circle (values range between 0–0.51), (c) percent forest cover within a 1 km radius circle (values range between 0–0.32), and (d) minimum distance to the nearest edge of a different land cover class within a 1 ha radius circle (values range between 0–973 m). Dark areas indicate large differences in the landscape metric values between 2000 and 2050 and white areas indicate little or no difference.

forested lands. In this scenario, there was up to 16% forest loss within 1 km of a pixel. Although the magnitude of forest loss was smaller in the second scenario, the spatial effects of fragmentation were similar. The urban centers showed very little change in developed land cover given they were already saturated with development. Most of the forest loss was in exurbia outside and between cities. For example, large, forested habitats were degraded between Concord, NH and Brattleboro, VT, along existing infrastructure.

The distance-to-developed edges decreased as housing density increased. The model that best predicted this relationship was log(distance to develop edge within 1 ha) = 2.73–0.34 $*$ log(housing density within 1 ha_2000) ($P < 0.0001$, $R^2 = 0.15$). Overall, the mean change in minimum edge distance across the landscape was 15.85 m; distance-to-edge decreased by almost 1000 m in some places (Fig. 3d). The spatial pattern of minimum distance-to-edge was different than the other forecasted variables in the year 2050 (Fig. 3). In addition to development, existing roads were more prominent in shaping the future minimum distance to edge than was apparent with percent forest cover and developed land cover.

3.3. Species occupancy models (Objective 3)

Objective 3 was to predict the change in species occupancy models for 5 forest-interior bird species. In both development scenarios, all 5 species occupancy probabilities decreased between the years 2000 and 2050. In the scenario where all development occurred on forested lands, occupancy probabilities decreased by as much 38% for ovenbird and as little as 19% for hairy woodpecker (Fig. 4). Slight increases in occupancy were observed in some places across the landscape for some species. For example, although black-throated blue warbler were expected to decrease in occupancy patterns overall, in some places they exhibited as much as a 20% increase in occupancy probability, especially in places across the landscape where distance-to-edge decreased but overall forest cover remained high.

The trends of decreased occupancy were the same for the second landscape change scenario where only half of development occurred on forestland, although the magnitude of changes decreased. For example, the maximum decrease in occupancy was less for every species except hairy woodpecker. As with the first scenario, the most drastic changes in occupancy occurred

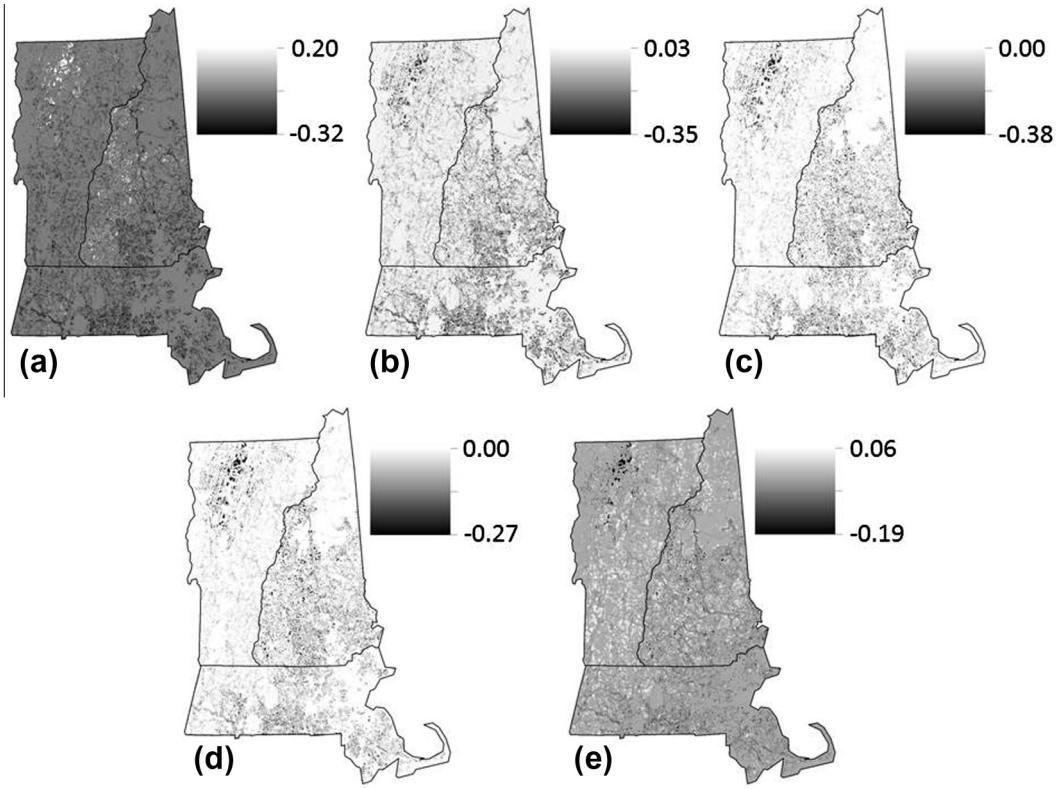

Fig. 4. Differences in occupancy probabilities for 5 forest interior bird species from 2000 to 2050 in Vermont, New Hampshire, and Massachusetts, USA: (a) black-throated blue warbler, (b) black-throated green warbler, (c) ovenbird, (d) hermit thrush, and (e) hairy woodpecker. The range of the change in occupancy probabilities for each species is shown.

outside of city centers where the highest amount of increased housing density was forecasted.

Occupancy change was variable across towns. Ninety-seven percent of towns saw at least some decrease in occupancy for one or more forest interior bird species. The mean decrease in occupancy probability within towns ranged from 3% for hairy woodpecker to 8% for ovenbird and hermit thrush (Fig. 5). At least 78% of all towns decreased in mean occupancy for black-throated blue warbler, black-throated green warbler, hermit thrush, and ovenbird. Hairy woodpecker occupancy, on the other hand, decreased in 24% of towns but remained stable in 76% of towns. Within towns, decreasing patterns of occupancy occurred in areas predicted to increase in human population as expected.

3.4. Conserved lands and species habitat (Objective 4)

Objective 4 was to evaluate the probability of occupancy within and outside of protected lands for bird species in the year 2050. In the year 2000, the total summed occupancy across the study area ranged from 19,017,878 (hairy woodpecker) to 39,191,372 (ovenbird; Table 2). In the baseline year, between 27.8% and 30.2% of the total occupancy score for any given species occurred within protected lands. For the year 2050, the total occupancy across the study area ranged from 18,938,758 (hairy woodpecker) to 37,757,788 (ovenbird), representing a 0.4% to 4.7% decline overall (Table 2). In the year 2050, between 28.1% and 30.9% of the total occupancy score for any given species occurred within protected lands, indicating a slight increase in the relative value of protected lands. These declines were greater outside of protected areas than inside (Table 2). For example, ovenbird overall occupancy declined by 1.5% within protected lands, and 4.5% outside protected lands.

4. Discussion

The effects of land use change on wildlife populations is a topic of importance not only across the Northeast, but in many places across the world (Millenium Ecosystem Assessment, 2005; Brown and Laband, 2006; Glennon and Porter, 2007; Pidgeon et al., 2007). Recent studies suggest that in the next 50 years urban land in the United States is projected to increase by 5% and forestland is projected to decrease by about the size of Pennsylvania (Nowak and Walton, 2005). These development growth and forest loss trends threaten the viability of certain native fauna. We demonstrated that projected development in VT, NH, and MA, decreased the probability of occupancy for a suite of forest-dwelling bird species.

In addition to *how much* land will be developed, the pattern of *where* this development will happen is a critical factor to understand how wildlife will respond to increased human population growth. The location of development, specifically exurban development, is often nonrandom relative to biodiversity because both are influenced by biophysical factors (Theobald, 2005). Theobald (2005) defines four categories of developed land use: (1) "urban" housing densities are <0.1 ha per unit; (2) "suburban" housing densities are between 0.1 and 0.68 ha per unit; (3) "exurban" densities are between 0.68 and 16.18 ha per unit; and (4) "rural" housing densities are >16.18 ha per unit. In our study area, the greatest declines in species occupancy occurred in exurban areas beyond the urban fringe. There was very little change in occupancy in urban centers given they were built-out and amongst the places with the lowest occupancy probabilities in time step 2000. Consequently, the effects on biodiversity in future time steps can be disproportionately large relative to the area of the development

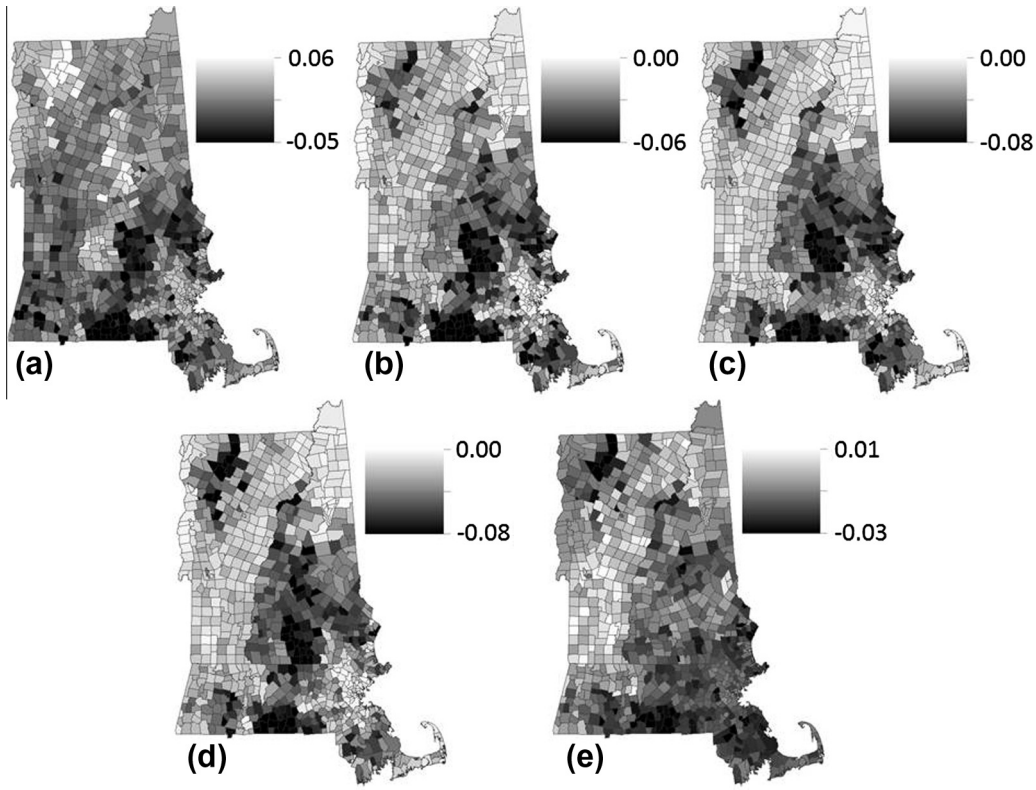

Fig. 5. Differences in mean occupancy probabilities for 5 forest interior bird species from 2000 to 2050 for towns in Vermont, New Hampshire, and Massachusetts, USA: (a) black-throated blue warbler, (b) black-throated green warbler, (c) ovenbird, (d) hermit thrush, and (e) hairy woodpecker. The range of the change in mean occupancy probabilities for each species is shown.

Table 2
Total occupancy probabilities (ψ) across the study area and within protected lands for 5 forest-dwelling birds: hairy woodpecker (HAWO), black-throated green warbler (BTNW), hermit thrush (HETH), ovenbird (OVEN), and black-throated blue warbler (BTBW).

Species	Total ψ 2000	Total ψ 2050	Total percent decline in ψ	Percent decline in ψ within protected areas	Percent decline in ψ outside protected areas
HAWO	19,017,878	18,938,758	0.42	−0.62	0.81
BTNW	35,107,452	33,763,196	3.83	1.70	4.72
HETH	28,212,578	26,940,834	4.51	1.89	5.63
OVEN	39,191,372	37,757,788	3.66	1.51	4.50
BTBW	21,285,360	20,288,046	4.69	3.11	5.37

(Hansen et al., 2005). Our results suggest that even in rural areas where projected increases in human housing density was less than one percent, species occupancy was still declining for forest-interior bird species.

Our study developed a framework for quantifying the contribution of protected lands to species distribution patterns. This has many benefits for both public and private land protection and management including the ability to quantify wildlife and habitat goals, measure conservation success, and monitor environmental changes over time. For example, from the ovenbird habitat perspective, 10% of the total summed ovenbird probabilities occurred on U.S. Forest Service (USFS) lands. This does not imply anything about habitat quality or population numbers; this number simply reveals what proportion of the total ψ is contained within USFS boundaries. For instance, 10% of the total ψ for ovenbirds could be achieved with low occupancy probabilities across large areas, or high occupancy probabilities across small areas. This approach can also be used to examine the contribution of different land management agencies to ovenbird distributions within protected lands. For example, considering the entire suite of protected ovenbird habitat (in terms if summed ψ values) in the study area, USFS lands accounted for 36% of protected habitat, conservation easements accounted for 11%, and state lands accounted for 31% of protected occupancy values.

In the year 2050, we found that the values of protected lands increased for the 5 study bird species. In other words, the area around protected lands degraded as development increased causing the habitat within protected lands to become relatively more important for the conservation of species habitat. We assumed the amount of protected habitat in the 2000 landscape would remain constant in the future; i.e., we could not account for future protected lands. Any reduction in future total ψ values across the landscape (e.g., through increased housing density) will lead to an increase in the importance of the proportion of habitat conserved.

Protected lands also deteriorated in quality, even though over time protected habitat increased in relative importance for the conservation of species. The boundaries of protected areas were

subject to effects from both within and outside of the protected area. Encroachment on protected lands decreased the value of the habitat within protected lands because habitat quality is affected at scales considerably larger than the size of breeding territories (Whitaker and Warkentin, 2010). The occupancy models assessed variables at a 1 km window. Therefore, if the area within 1 km of a protected area is developed, the occupancy probability inside the protected area will decrease.

To illustrate, we examined one large protected area, the White Mountain National Forest in northern NH. Over 50 years, capacity of the National Forest to support forest interior birds decreased as measured by total summed occupancy values. The decreased capacity was based on predicted increased development and a corresponding decrease in occupancy for all 5 species within 1 km of the protected boundary. We considered occupancy trends within boundary areas (within 1 km of the protected boundary) and core areas (the interior portion of the National Forest). The values of ψ within boundary areas decreased for all 5 forest interior birds. Although protected, the boundary areas were subject to degradation because the pixel scores reflect landscape conditions both within and outside the protected area itself. Human-caused degradation outside of nature reserves has been shown to reduce their conservation capacity in other studies (Beaumont and Duursma, 2012) and have the potential to reduce species viability within protected areas (Hansen and Rotella, 2002). This phenomenon was further exacerbated in other parts of our study area where protected parcels were small. Small protected parcels with little interior core habitat were subject to nearly the same levels of reduced species occupancy as non-protected lands. Therefore, to maintain and increase the value of protected lands for forest species, it is best to conserve large blocks of forest that have ample interior habitat buffered from the edge effects of nearby development.

Future work could refine some components of our analysis. First, our study assumed that future development would occur on certain land cover classes based on scenarios grounded in historic development patterns (DeNormandie et al., 2009, Vermont Monitoring Cooperative, 2009). We forecasted landscape changes based on statistical relationships between development and (1) road density, (2) percent forest in the landscape, (3) percent development in the landscape, and (4) distance to edge. Thus, our model did not predict the exact location of forest conversion on a pixel by pixel basis. It is possible that alternative land use change modeling approaches could produce more accurate land cover forecasts (Verburg et al., 2004; Voigt and Troy, 2008), but these were not available for our broad study area. For instance, forest succession on abandoned farmland can be an important offset to increases in development in the study area, and our model does not account for that. However, numbers of farms, which have long been decreasing, are finally on the rise (U.S. Department of Agriculture, 2009). While recovery from historic deforestation has been prolific, regional forest cover has peaked and is declining in every New England state (Foster et al., 2010). With these changes, species affiliated with non-forest habitats may increase in occupancy patterns.

Second, vacation home and second home development is likely driven more by the distribution of amenities than the density of roads. These effects are largely accounted for in our land use model because all housing units (primary and so-called second or vacation homes) and amenities are a variable in the population growth model that drives the land use forecast model. However, because urban areas have larger absolute gains in population and often higher rates of growth than rural areas, the population model in SERGoM can under-represent growth in rural areas. Future work should compare results to demographic models created by state and/or regional governments.

Third, the spatially-explicit housing growth model (SERGoM) removed protected lands from potential housing development, but did not account for environmental development constraints like wetlands and steep slopes. SERGoM explicitly accounts for the varying sizes of census blocks because the number of housing units is measured independently for each block, but the level of uncertainty of our housing density estimates may increase in larger block sizes because of larger spatial variability.

Finally, we used species occupancy probabilities as proxies for habitat suitability and did not consider the precision of the occupancy probability estimates in our analyses; this imprecision represents a source of uncertainty. Additionally, this approach does not consider the territorial behavior and home range requirements of each species (Donovan et al., 2012). Thus, it is difficult to infer what the overall effect of human growth is on the viability of species populations based on occupancy maps alone. For example, Brown et al. (in preparation) used occupancy maps from 2000 and 2050 to estimate the landscape carrying capacity for our study area; this provided an estimate of the maximum number of territorial birds that could inhabit the study area in each time period. The key result from this analysis was that relatively small decreases in occupancy can result in large decreases in landscape carrying capacity (Brown et al., in preparation).

Ecological effects of resource management are sensitive to the temporal and spatial scales of land development. The current and projected rates of population growth, land development, and forest loss threaten the viability of native fauna (Theobald, 2005; Brown and Laband, 2006; Glennon and Porter, 2007). The question of how wildlife will respond to eminent land use change requires spatially-explicit tools and methods for understanding population responses as well as management recommendations for conservation. This study integrated wildlife habitat modeling with GIS models of human population growth and quantified how and where forest-interior birds will respond to projected increases in human population growth for the study area. Ameliorating the effects of future development on wildlife will require decision-making and policy implementation at several geographic scales. Wildlife populations require enough habitat to meet their life cycle needs and for some common wide-ranging species mean home range size can be upwards of 170 km^2 (Costello, 1992; Hammond, 2002); whereas, land use policy is often set at town scales, as in New England, USA. A benefit of our approach is that our results, which take into account regional patterns of human population growth, can be applied at local scales. Local and regional planners can take advantage of spatial habitat and human development mapping and use the information proactively for future conservation efforts or land use plans. For example, local developments can be planned to minimize habitat loss or mitigate negative affects to wildlife and our maps can be incorporated directly into town comprehensive plans. A wide range of strategies at multiple scales will be required for wildlife populations to persist in the face of human population growth. Our study and results provide replicable, spatially-explicit information about the risks of development to wildlife that could aid wildlife managers, conservation practitioners, and decision-makers in these efforts.

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