PREDICTING IMPACTS OF FUTURE HUMAN POPULATION GROWTH AND DEVELOPMENT ON OCCUPANCY RATES AND LANDSCAPE CARRYING CAPACITY 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 forest loss and fragmentation in the next century. First, 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. Second, we used maximum clique analysis to calculate the landscape carrying capacity, $N_k$, for the forest-dependent Ovenbird. We sampled four developed land cover classes: urban, suburban, exurban, and rural, and estimated Ovenbird $N_k$ from occupancy probability maps for the years 2000 and 2050. Over half a million new housing units were predicted to be added to the landscape. The maximum human housing density grew from 517 housing units per hectare in the year 2000 to 530 housing units per hectare in the year 2050. However, 30% of the towns in the study area were projected to add less than 1 housing unit per ha. In the face of this predicted human growth, the overall occupancy of each species decreased by as much as 38% in certain places in the study area in the year 2050. These declines were greater outside of protected areas than within protected lands. $N_k$ was predicted to decrease 44% in the landscape classified as exurban development, 25% in urban and suburban development, and 14% in rural development. These decreases far exceeded the decreases in occupancy probabilities that ranged between 3% and 5% across the same sampled sites. This spatial approach to wildlife planning provides data to evaluate trade-offs between development scenarios and the viability of forest-dependent wildlife species. Specifically, maximum clique analysis is a tool that can be used to estimate a species population metric, $N_k$, and provide decision-makers with straightforward data to inform decisions and communicate with stakeholders.
Citations

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Chapter 1 - Literature Review

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). Human impacts on land have global, regional, and local consequences including changes in land cover, climate, atmospheric composition, biodiversity, soil condition, and water and sediment flows (Turner et al. 1994, Lambin et al. 2001). The rate that natural habitats are being lost and environmental processes are being altered is greater now than in the last 50 million years (Fastovsky and Weishampel 1996). Given the scale and pace of human-induced land transformation, more information is needed to understand how the landscape is changing, what these changes will mean for species and ecosystems distribution and persistence (Gutzwiller 2002), what natural resource managers and policy makers can do, and ultimately what impacts land use change will have on the future functioning of the globe.

Landscape Change

Land Use and Land Cover

Land use refers to the human perspective of how land is utilized (i.e., protected areas, forestry for timber products, agriculture, and human development). Land cover is the ecological state and physical appearance of the land surface (i.e. closed forests, open woodlands, or grasslands) (Turner and Meyer 1994). The commonly used National Land Cover Database divides the landscape into 29 classes of land cover ranging from deciduous forest and woody wetlands to open water and perennial ice/snow. Four
developed classes: open space, low intensity, medium intensity, and high intensity are differentiated by the percent of total cover within a pixel (Homer et al. 2004). Land cover change converts land of one type of cover to another, regardless of land use; whereas change in land use may or may not significantly change land cover. For example, a change in forest management practices from selective harvest to no harvest will cause minimal discernible land cover change. Alternatively, a change from managed forestland to cultivated land will cause a formidable change in land cover (Dale et al. 2000).

The cause of land cover change can be natural (i.e. hurricanes) or anthropogenic (i.e. agriculture) (Forman 1995, Dale et al. 2000). Natural processes such as fire, wind throw, and ice storms can cause small canopy openings or transform entire systems. In the northeast, a major natural source of land transformation is beaver. Once present in nearly all river, streams, and lakes of north temperate and boreal regions, beavers have been extirpated in some regions by humans (Forman 1995). Where they remain, however, beavers have major effects on hydrology, sedimentation, mineral nutrients, and wetland formation (Naiman et al. 1994, Jenkins and Keal 2004).

While natural processes can cause land transformation, anthropogenic modifications are the most significant modern factors resulting in these changes (Lindenmayer and Franklin 2002). One of the fundamental forces behind landscape conversion is human population growth. As population numbers increase so do competing needs for land, such as food, energy extraction, and infrastructure (Gutzwiller 2002). For example, between the years 1850 – 1900 the human population in the United States tripled. During the same period, the number of acres of cropland increased four-
fold (MacCleery 1992). Where population growth occurs is a function of multiple factors including physical constraints like terrain and climate (Gutzwiller 2002), and ease of access (Forman et al. 2003). Both natural and engineered transportation networks have made even remote areas accessible to humans. Intense and rapid landscape conversation often follows the development of reliable road and rail systems (Bockstael 1996).

Human decisions and social drivers are other fundamental forces behind land cover change (Turner et al. 1994). Accordingly, social drivers like local and global economies must be considered when discussing land use and land cover change (Bockstael 1996). “The Forest Transitions” was coined as a concept suggesting amounts of forest change in predictable ways as societies experience economic development, industrialization, and urbanization (Rudel et al. 2005). For example, tropical deforestation resulting from changing national and global-scale economic opportunities is a major contributor to global land use change. A literature review of the drivers behind tropical deforestation concluded that individual and public decisions largely result in agriculture expansion, wood extraction, and infrastructure extension, causing regional and local deforestation (Geist 2002).

**Historical Land Use and Land Cover Patterns**

Over the centuries two important trends are evident: 1) the total land area dedicated to human uses has grown significantly, and 2) increasing production of goods and services (mostly food and fiber) has intensified both use and control of the land (Richards 1990). In the recent past, the rate of change of land transformation worldwide has accelerated. More acres of grasslands and forests have been converted to other land cover types in the last from 1950 – 1980 than in the 150 years between 1700 – 1850.
(Turner et al. 2001). On a regional-level, the land use trends slightly differ. After settlement in central New England more than 80% of the land was cleared of forest by the mid-1800’s, however, at that time reforestation began and continued through the twentieth century (Foster 1992).

In Vermont, initial forest loss peaked during the early ninetieth century for agriculture and pasture; much of state reforested from this agrarian state in the 1900’s. Importantly, recent trends demonstrate that development in forestland is on the rise relative to population increases, with land currently developing at 260 times the rate of population increases (Vermont Forum on Sprawl 1999). Based on these trends, Gutzwiller (2002) has suggested a general principle relative to human disturbances of natural habitats: barring profound changes to the soil and hydrological properties of a landscape, terrestrial habitats are resilient and can revert back to a natural condition if left undisturbed. While historically in Vermont, agricultural land use has enabled reversion back to natural cover, the current trend of development could contribute to more permanent changes on the landscape.

Common, but poorly defined terms, have emerged in recent years to describe different types of human development and land use: suburban, exurban, rural sprawl, and rural. Suburban areas are typically considered to be areas of lower density residential use outside of urban centers, often thought of in concert with sprawl. Rural areas are conceptualized as simply “not urban” (Theobald 2004); while rural sprawl is thought of as low-density residential development scattered outside of suburbs and cities (Daniels 1999a). Exurban is defined as the semi-rural region outside the suburbs of a city, characterized by low density (~5 acres per unit or more), large-lot development (Daniels
Because of the overlapping nature of these terms, quantifiably defining the land use types can be helpful. The U.S. Census Bureau collects housing density that serves a basis for quantitative explanations (U.S. Census Bureau 2011). Theobald (2005) developed the following definitions: “urban” housing densities are less than 0.1 ha per unit; “suburban” housing densities are between 0.1-0.68 ha per unit, “exurban” housing densities are 0.68-16.18 ha per unit, and “rural” housing densities are greater than 16.18 ha per unit and the majority of houses support agricultural production.

Most quantitative assessments of land use change have focused on changes in metropolitan areas. However, exurban developments patterns have changed radically in the United States in the last 50 years. The first major shift occurred between 1950 and 1970 and was driven by urban growth. The majority of non-urban counties lost population to urban centers, while a significant number of people moved from urban cores to new suburbs. This pattern changed abruptly in the 1970’s, when for the first time in 150 years, rural population gains exceeded metropolitan gains. The 1980’s saw demographic trends return back to urban growth. Since the 1990’s there has been a reversal back to rural migration (Brown et al. 2005). These trends of the past five decades are a major departure from the prior century and a half.

Exurban development is extensive and widespread in nature, and often occurs adjacent to protected lands (Theobald 2005, Bierwagen et al. 2010). The geographic extent of exurban land development in the U.S. is over seven times larger than that of urban and suburban development. While each individual lot is not necessarily ecologically detrimental, the cumulative effects can be problematic. The rate of land use...
change can also be of ecological concern. In total, the rate of developing land was 25% faster that the rate of population growth from 1980 – 2000 (Theobald 2005).

**Ecological Impacts of Land Use**

The spatial extent of historic land use changes appears to coincide with the spatial distribution of species richness. Across North America, humans have settled areas that are also the most species-rich (Ricketts and Imhoff 2003). Similar patterns have been observed in other biodiversity hotspots worldwide. Roughly 20% of the world’s population is living in a biodiversity hotspot, which represents an area about 12% of Earth’s terrestrial surface (Cincotta et al. 2000).

Ecological impacts of land use are wide-ranging and varied. Nearly all human issues surrounding land (settlement, forestry, conservation, sociology) involve its transformation and fragmentation. Forman (1995) describes five main spatial processes resulting from land use change that have distinct ecological impacts. These spatial processes can be thought of as phases of land transformation and while they can overlap temporally, they are also ordered.

Land cover change often begins with perforation - the creation of a gap in the existing cover. This can occur through natural processes like blow down or anthropogenic means like logging or scattered housing developments (Brown et al. 2005). Alternatively, land can begin its conversion through fragmentation - the breaking up of a large habitat into smaller pieces (Forman 1995). The third spatial land transformation process that affects ecology is dissection – subdivision by equal-sized modifications. The most common examples of dissection are roads, which divide landscapes across the globe (Forman et al. 2003). Dissection may be considered a
specific example of fragmentation, however, the processes driving the land cover change are different (i.e., roads and power lines versus clearcutting and housing developments). While forest fragmentation refers to the spatial configuration of remaining habitat, forest loss refers to the outright amount of forest left, (Lindenmayer and Franklin 2002). Forest loss defines Forman’s fourth land transformation process – shrinkage. Shrinkage is simply the size reduction of a given land-cover element (i.e. a forest patch or woodlot) (Forman 1995). Finally, as a landscape continues to change and shrink, attrition becomes inevitable. Attrition is the complete loss of a land element (i.e. patch) and is commonly observed through the loss of small forest patches and corridors (Forman 1995, Trani and Giles 1999).

The modification of the relative abundances and spatial distribution of natural habitats and land cover types can affect biodiversity in distinct ways. First, species distributions can change. The scale of species distribution changes can be local (i.e., within a forest patch), or regional. The second effect of land cover change on biodiversity is change in population dynamics. There are four general principles that determine whether a population will grow or decline over time. These factors are often referred to as the BIDE factors – birth, immigration, death, and emigration (Donovan and Welden 2002). Third, habitat amount and distribution can affect population structure. Metapopulations, populations that consist of multiple subpopulations that occupy many different habitat patches, can change over time based on colonization, extinction, and dispersal events (Donovan and Welden 2002). Each of these effects on biodiversity will be discussed with respect to forest dissection, forest fragmentation, and forest loss (shrinkage).
Forest Dissection

Roads have stretched across nearly all of North America. Roughly five million miles of road networks provide corridors for a quarter billion vehicles. There are very few places roads do not go, including mountains, valleys, and rivers (Forman et al. 2003). In addition to facilitating human modification of the landscape, roads have specific impacts to wildlife. First, roads may impact the distribution of species. Many species exhibit road avoidance behavior and prefer not to cross particular roads, thus exacerbating the impacts of dissection in the landscape. For example, in northern Montana black bears seem to avoid habitat within 274 m of open roads (Kasworm and Manley 1990), while cougars in California seem averse to paved roads, but tolerate dirt roads (Dickson et al. 2005). Road density, the average total road length per unit area of landscape, is a commonly used metric to measure ecological impacts to species and ecosystem (Forman et al. 2003), and is correlated with lower moose population density (Beazley et al. 2005). In addition, existing evidence suggests that large carnivores may only persist in landscapes with low road densities (1 mi/ mi²) (Forman and Alexander 1998). Often the traffic volume determines whether or not roads are a barrier to wildlife. Among roads that black bears navigate, low-volume roads are crossed more frequently than high volume roads (Forman et al. 2003).

A second impact of dissection is direct species mortality. In some cases, the rate of mortality caused by roads exceeds the rate of natural mortality in a population. For example, mass kill events have been recorded during salamander and toad migrations across the globe. These are often the results of roads being constructed between wetland and upland habitat, thus in the migration path of species that need both habitats to
complete their lifecycle (Johnson et al. 2002, Fahrig and Rytwinski 2009). While it is difficult to assess the impact of these mortalities to entire populations of amphibians and reptiles, studies have demonstrated population level consequences (Forman 1995). The population structure of other taxa groups, like wide-ranging carnivores, may be impacted greater by each individual road kill incident. The effect of dissection on population structure is evident in the case of the Florida panther, where 35% of the mortality was caused by vehicle collision (Taylor et al. 2002). Shifting the age structure of populations to younger age classes is also a typical affect of mortality and may be a consequence of dissection to fauna populations (Forman 1995).

**Forest Fragmentation**

Forest dissection is a specific example of forest fragmentation. Therefore, forest fragmentation also affects species distribution, BIDE, and population structure. The focus here is on additional impacts of fragmentation to forest-dwelling species.

Forest fragmentation has been widely described as a cause of species decline and reduced viability. The interpretation of fragmentation effect, however, can be complicated especially when considering landscape condition and individual species response (Lindenmayer and Franklin 2002). In other words, the effect on wildlife of fragmenting a million acre forest patch will likely be different than the effect of fragmenting a small forest patch within a matrix of agriculture. Despite these variables, there is ample evidence that forest fragmentation can have a negative effect on forest-dwelling wildlife.

Forest fragmentation impacts the viability of species populations. Decreased birth rates and increased mortality rates in birds are well-documented effects of fragmentation.
For example, the fecundity of ten forest-nesting passerines was reviewed across a gradient of fragmentation in a variety of geographies and shown to be negatively impacted by fragmentation (Donovan and Flather 2002). Similarly, it has been demonstrated that highly fragmented landscapes have significantly more nest predation than unfragmented landscapes (Robinson et al. 1995, Donovan et al. 1997).

The distribution and population structure of birds can also be impacted by fragmentation. Occurrences of scarlet tanagers, a forest interior species, is correlated with overall amounts of fragmentation and the probability of finding breeding pairs is < 0.5 in highly fragmented landscapes (Rosenberg et al. 1999a).

**Forest Loss (Shrinkage and Attrition)**

It has been suggested that habitat loss has the greatest consequence to species viability (Lindenmayer and Franklin 2002). When comparing total amount of habitat lost to the spatial arrangement of habitat, habitat lost is a better predictor of species loss (Fahrig 1998). Outright species extinctions are the ultimate negative consequences of land transformation processes on fauna. For example, over 80% of the world’s endangered birds are threatened by habitat loss (Temple 1986). Similarly, the chief factor contributing to invertebrate extinctions is thought to be a reduction in habitat (Thomas and Morris 1995).

In addition to outright species loss, the distribution of many forest-dwelling species is dependent on amount of forestland. For example, western martens were found to be virtually absent from landscapes with >25% non-forest cover even where forest connectivity was present (Hargis et al. 1999). In another study martens were found more
frequently in larger forest patches (median 27 ha) than smaller patches (median 1.5 ha) (Chapin et al. 1998).

The impacts of forest loss to species populations and the BIDE principles are readily documented as well. The amount of forested habitat within a 5 km distance was strongly and negatively related to the per capita birth rates, nesting success, and abundance of nesting success of Black-throated Blue Warblers, forest-nesting birds (Cornell and Donovan 2010). As habitat patch size decreases, not only is the total amount of available habitat smaller, but the functional area of available habitat may also be smaller. In other words, edge effects associated with the fragmentation of a landscape have been documented negatively impacting the birth rates for certain species (Turner et al. 2001).

Finally, population structure and the ability of species to disperse to other viable habitat patches and maintain healthy subpopulation are also affected by habitat loss. For example, martens are found more often in forest patches close to other forest patches (Chapin et al. 1998). Mobile amphibian species have been shown to be more impacted by habitat loss than less mobile species, suggesting challenges with successful dispersal (Forman 1995).

**Predicting Future Land Use Change**

Empirically evaluating human land-use has often been approached by using land-cover data as a proxy for human activities (Brown et al. 2005). For example, the commonly used National Land Cover Database (2001) divides the landscape into 29 classes of land cover ranging from deciduous forest and woody wetlands to open water and perennial ice/snow. There are four developed classes: open space, low intensity,
medium intensity, and high intensity, which are differentiated by the percent of total cover within a pixel (Homer et al. 2004). Therefore, an assumption is made at the pixel scale relative to human-use severity and the development land cover class, ignoring any subtleties in development patterns on the fringes of those land cover class categories (i.e. exurban development) (Theobald 2005). Another standardized dataset commonly used to monitor land cover change with respect to natural and anthropogenic factors is produced by NOAA (National Oceanic and Atmospheric Administration) through the Coastal Change Analysis Program (C-CAP). Similar to the NLCD dataset, C-CAP data are derived from remotely sensed imagery focused on coastal regions of the U.S. The data have improved wetland and intertidal inventories, and are re-processed every five years to provide land cover rasters and an assessment of change for that period of time.

A second method used to analyze human land-use is to map distributions of human populations. Human populations can be used as an indicator of human demand for various goods and services provided by ecological systems. The U.S. Census Bureau collects population data in ten-year intervals that allows for assessments to consider population changes and their associated demographic components (Brown et al. 2005). Changes in human population densities are often used as a proxy for urbanization (Vesterby and Heimlich 1991), though this is not necessarily geographically precise enough decipher between different types of land-use change (i.e. exurban or rural). Additionally, U.S. Census population data is based on primary place of residence, which can underestimate landscape change in resort and second home communities (Theobald 2005).
In order to more accurately account for development on the urban-rural fringe, methods to quantify land-use change using housing density as the metric have emerged (Bierwagen et al. 2010). Along with population, the U.S. Census also provides data on housing units, which represent a physical manifestation of development. These data can help differentiate between land-use change and population change, various degrees of intensity of development types, and capture vacation and second homes (Brown et al. 2005).

A nationwide, fine-grained database of housing density based on census data is available and provides quantifiable historic, current, and forecasted housing density projections (Theobald 2005). Unlike other nationwide land use/land cover datasets like NRI (National Resources Conservation Service 2001) and NLCD (Homer et al. 2004), the housing density database was developed from census data. Forecasted projections for housing units are generated by the Spatially Explicit Regional Growth Model (SERGoM), which seeks to project future housing densities across the full rural-to-urban spectrum (i.e. exurban) at broad regional and national extents. The rate of density increase is based on the past decades growth pattern in a particular geographic area.

Five main inputs are utilized in SERGoM to estimate housing density (Bierwagen et al. 2010). The first model input is U.S. Census data. The number of housing units and population for each census block were compiled. Water features such as lakes, reservoirs, and wide rivers were removed to ensure no housing units were placed on those features. The second model input is undevelopable lands. This is a modified dataset that contains nation-wide data on land ownership. As with water features, housing units are not placed on lands that prohibit development, such as parks and other public lands. The
third model input is road and groundwater density. The spatial distribution of housing units within a census block will be influenced by the existing location of roads and groundwater wells. In other words, the amount of housing units per census block will be determined by census data and county projections, but the spatial allocation of those housing units per census block will be driven by the location of roads and groundwater wells. The fourth types of information utilized by SERGoM are county population projections. The growth forecasts are derived from county population projections (U.S. Census data) and the number of new housing units are added based on the needs of the projected new population. The final model input is commercial and industrial land use. These are land use types that would typically not be available for new housing units. These industrial areas were identified and eliminated using NLCD urban categories that had >25% built up area per hectare (Bierwagen et al. 2010).

The strength of SERGoM lies in its comprehensive coverage of housing unit density across the U.S. The outputs are spatially-explicit and are derived from the finest-scale data available. The methods are consistent and not sample-based. Finally SERGoM has achieved high accuracy rates and has performed well in comparison to other data (i.e. aerial photography and parcel-scale data) (Theobald 2005).

Predicting Effects of Land Use Change on Biodiversity

Recent studies have demonstrated the impacts of exurban growth on biodiversity. Many native species have reduced survival and reproduction near homes; native species richness often drops with increased exurban densities. Exotic species, some human-adapted native species, and species from early successional stages often increase with exurban development (Hansen et al. 2005). Negative consequences for wildlife include
ecosystem fragmentation, edge effects and nest predation, creation of source-sink dynamics, disruption of wildlife dispersal and movement patterns, and changes in community composition and structure, among others (Glennon and Kretser 2005). In Vermont, for example, black bears demonstrated significant avoidance of houses of all types (Hammond 2002). There may be a lag time in these effects for several decades following exurban development, so that biodiversity is likely still responding to the wave of exurban expansion that has occurred since 1950 (Hansen et al. 2005).

**Predicting Species Occurrences**

Species-environment models are designed to assess the relationship between environmental variables and the distribution of a given species or assemblage of species. It is these relationships that enable the prediction of where species may occur given known locations (Scott et al. 2002). Three fundamental principles underlie species-environment models. First, space and time will influence observable patterns. Although species-environment studies tend to focus on habitat use, many additional variables determine whether a species occurs in a particular place. For example, temporal patterns associated with preferred habitat and social interactions are often drivers of where species will occur, but these are also difficult to incorporate into models (Greco et al. 2002).

Second, relationships between species and their habitats are essentially nonlinear and depend on the scale of investigations. Habitat selection occurs at multiple scales, most simply an evolutionary scale (i.e. fitness rates) and a local scale (i.e. physiology and behavior) (Tobalske 2002). Species-environment models are necessarily based on the scale of habitat data available, not necessarily the scale at which the species responds, third, the dynamic nature of species distributions will influence models over space and
time. The variables that influence distribution can change hourly, daily, annually, or over centuries. Similarly, environmental variables are dynamic and population responses to change may occur in the short or long term (Johnson and Krohn 2002).

**Occupancy Modeling**

While it is important to consider the three principles that underlie species-environment studies, available data will often guide the modeling effort. Landscapes of interest are often too large to survey completely and data can be limited. Available data are often restricted to presence or absence survey data. A key issue with these data is differentiating between species that are absent from a landscape unit and species that are not being detected. Presence-absence refers to whether a species is biologically located at a site, whereas detection-nondetection refers to the observed outcome of the sampling process (MacKenzie 2005). In other words, a species can be present at a site and simply not detected. Many factors may contribute to the successful detection of a species in the field, including: sampling effort, landscape characteristics (i.e., habitat), survey conditions (i.e. weather conditions), and surveyor expertise. An occupancy modeling framework explicitly accounts for the variability in detection success and incorporates whether a site is occupied and the probability that the species of interest was detected.

Occupancy modeling utilizes a likelihood framework. This means that models assess the likelihood that a given species may occur based on estimates of occupancy ($\psi$), the probability of detection ($p$), and covariates that describe something about occupancy or detection. There are many benefits of utilizing a likelihood framework. First, it allows for assessment of the weight of evidence in data across multiple hypotheses. Second, it allows for the use of multiple kinds of observations. Third, because multiple hypotheses
can be assessed, likelihood frameworks allow for combining results through model averaging, which often yields a better result than accepting or rejecting a single hypothesis (Hobbs and Hilborn 2006).

**Focal Species**

Five forest-dependent birds were selected for study based on their affinities for forest and sensitivities to forest loss and fragmentation: Black-throated Blue Warbler, Black-throated Green Warbler, Hairy Woodpecker, Hermit Thrush, and Ovenbird. This guild of birds is often referred to as forest-interior because they prefer to breed in larger tracts of forests away from forest edges. The size and shape of forest patches are critical to the breeding success of this suite of species (Rosenberg et al. 1999b). In Vermont, the forest-interior guild increased in occupancy probability as percent forest cover and distance to edges increased (Schwenk and Donovan 2011).

**Black-throated Green Warbler** (*Setophaga virens*)

Black-throated Green Warblers are common breeding birds in northeastern coniferous forests. They are also found in mixed forests, but usually near conifer stands (McGowan and Corwin 2008). Black-throated Green Warblers prefer large forest patches and are more common in the interior than near road edges. They are sensitive to forest loss and fragmentation. Black-throated Blue Warblers have disappeared from areas where fragmentation decreased the size and increased the isolation of forest patches (Morse and Poole 2005). In areas where hemlock wooly adelgid persists, significant declines in Black-throated Green Warbler populations have been observed following hemlock death (Tingley et al. 2002).

**Black-throated Blue Warbler** (*Setophaga caerulescens*)
Black-throated Blue Warblers are migratory songbirds that breed in the northeastern U.S. and southern Canada, and along the high elevations of the Appalachian Mountains. They prefer large continuous areas of relatively undisturbed hardwood and mixed deciduous-coniferous forests (McGowan and Corwin 2008). Black-throated Blue Warblers are sensitive to extensive deforestation and probably declined during European settlement. Populations seem to be on the rise in recent years, however, likely due to reforestation in breeding grounds (Holmes et al. 2005). A key habitat feature seems to be closed canopy cover, as Black-throated Blue Warblers can be common in both managed and unmanaged forests (Buford and Capan 1999).

**Hairy Woodpecker (Picoides villosus)**

Hairy Woodpeckers are the most widespread woodpecker in North America. They are primarily birds of mature forests, but will breed in a variety of habitats including forests, woodlots, residential areas with large trees, and small woodlots, although at lower densities (McGowan and Corwin 2008). Considered a forest-interior species, Hairy Woodpeckers have declined throughout its range due to forest fragmentation and they are becoming less common in less forested landscapes like farms and suburbs (Jackson et al. 2002). It has been suggested that the maturation of forests in the northeast U.S. could support increased habitat for Hairy Woodpeckers in the future (McGowan and Corwin 2008).

**Hermit Thrush (Catharus guttatus)**

The Hermit Thrush is a widely-distributed migratory bird in North America, nesting and foraging in lower branches or forest floor in coniferous and mixed forest types (McGowan and Corwin 2008). The Hermit Thrush appears to be the only thrush
whose population has increased or remained stable in the last 20 years (Sauer et al. 2005, Dellinger et al. 2012). Sensitive to forest loss and fragmentation, Hermit Thrush occurrences are more strongly affected by landscape scale changes versus local scale changes. Nests tend to be found in undisturbed forests away from edges and in closed canopies (Dellinger et al. 2012).

**Ovenbird (Seiurus aurocapilla)**

Ovenbirds are common throughout eastern North American forests. They nest in mature deciduous and mixed forests and are known to prefer large blocks of continuous forests with structural diversity and high canopy closure (60 – 90%) (McGowan and Corwin 2008). Ovenbirds are negatively impacted by fragmentation, and sensitive to habitat edges and forestry. The effect of forest roads, powerlines, and chronic noise have been found to be damaging to Ovenbird populations (Porneluzi et al. 2011). While fragmentation has a demonstrated negative impact on Ovenbird fecundity, other variables like behavior, also contribute to nesting success. In the face of heavy nest predation in the interior forest by chipmunks, Ovenbirds have been shown to nest in forest edges with greater nest productivity (Morton 2005).

**Implications for Conservation**

Recent studies suggest that urban land in the United States is projected to increase from 3.1% in 2000 to 8.1% in 2050, and projected amount of forest land estimated to be subsumed by urbanization between 2000 and 2050 is about 118,300 km$^2$, an area approximately the size of Pennsylvania (Nowak and Walton 2005). These development and forest loss trends threaten the viability of certain native fauna. The location of development, specifically exurban development, is often nonrandom relative to
biodiversity because both exurban development and biodiversity are influenced by biophysical factors. Consequently, the effects on biodiversity may be disproportionately large relative to the area of the development (Hansen et al. 2005). Wildlife management decisions are often based on current and future species population estimates. Therefore, decision makers need tools that can provide spatially explicit predictions of development and its impact on the population and distribution of wildlife.

Ecological effects of resource management are sensitive to temporal and spatial scales (i.e., of land development). Factors that deserve consideration include the configuration of the landscape mosaic and its change over time, the distribution regime and likely consequences for pattern and process, the responses of species that operate at various scales, and the effects of change on ecosystem function (Turner et al. 2001). Understanding these dynamics can help ecologists better contribute to policy and land management and planning debates.
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Chapter 2 - 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 forest loss and fragmentation 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 human housing density grew from 517 housing units per hectare in year 2000 to 530 housing units per hectare in year 2050. However, 30% of the towns in the study area were projected to add less than 1 housing unit per ha. In the face of predicted human growth, the overall occupancy of each species decreased by as much as 38% in certain places in the study area 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 Woodpeckers 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 the viability of forest-dependent wildlife species.
Keywords: Occupancy modeling, human population growth, landuse change modeling, Ovenbird, Black-throated Blue Warbler, Black-throated Green Warbler, Hermit Thrush, Hairy Woodpecker, forest ecosystem, protected lands.
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). Land cover change refers to the conversion of the ecological state and physical appearance of the land surface (Turner et al. 1994), such as converting a forested parcel of land to a developed parcel. Land use changes can be caused by natural processes, but human-induced modifications are by far the most significant modern forces behind land transformation (Lindenmayer and Franklin 2002).

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 and resulting in additional land cover change. Importantly, the growth rate of human populations is not the only crucial factor; the growth rate of developed land cover classes must also be considered. 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 are pressed to estimate the risk fauna populations will face in response to this projected human growth and increase in developed land cover classes. Wildlife abundance, distribution, and viability can be intricately 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. Much progress has been made with respect to land use change modeling. For instance, several new land use change models exist for the Northeast U.S., ranging in complexity from regression analysis to integrated system models (Voigt and Troy 2008). However, developing quantitative metrics that allow decision makers to link predicted 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 overall distribution patterns. 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 landscape variables such as, 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.

Methods

Study Area and Target Species
The study area was the three-state region of Vermont, New Hampshire, and mainland Massachusetts, 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).

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).

**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 historic population and growth patterns as well transportation infrastructure; the primary output is a 1 ha raster depicting housing density for the years 2000 and 2050.

We estimated historic 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 one city block to many square miles. Second, we allocated housing units within each census block using a GIS raster that reflected historic patterns of growth 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). Finally, in step 3 we considered the influence of roads on the spatial distribution of housing units within a census block. Existing major roads (Fig. 1d) were converted to road density, defined as the density of roads within 800 meters of any pixel (Fig. 1f) because open lands with a high road density tend to be more readily developed. Thus, the final allocation of housing units per hectare for year 2000 (Fig. 1g) resulted from available developable lands and road density.

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) to estimate the increased population size for each county. 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 three steps. First, location-specific growth rates were computed for 16 development classes, 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 minutes) (Fig. 1h). Second, the allocations 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. Third, a GIS surface was created that reflected location-specific growth rates and proximity to urban areas called allocation weights (Fig. 1j). New housing units were distributed based on this new raster. The final step in forecasting future housing unit density was to add the newly allocated housing units to a map of current housing units. 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 for the years 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 consistent with the scale of bird occupancy models (see below). This final map output was the base map for Objective 2.

**Landscape Change Scenarios (Objective 2)**

Given the number of housing units within a 1 km radius circle, we developed a landscape change model to predict changes in road density (km of roads within a 1 km radius circle), 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. To establish the baseline road density map (year 2000), we used a 1 km moving window analysis in ArcGIS on U.S. Census Bureau TIGER roads to create an estimate for each pixel (U.S.Census Bureau 2011). To establish the baseline percent
forest and development maps, we burned TIGER roads into the 2001 NLCD raster and reclassified 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. (The distance-to-developed grid was updated for the 2050 landscape scenario; see below).

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 build-out 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 smaller of the two values. This resulted in a new distance-to-developed layer in 2050 based on where housing density increased. The final step was to recalculate the minimum distance-to-edge layer
for year 2050 using all of the land cover classes. In other words, the only places where the total minimum distance-to-edge decreased in the year 2050 were locations on the landscape where distance-to-developed-edge decreased.

**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 ($\psi$) 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 ($\psi$) 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) forest with 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:

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

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 (Burnham and Anderson 2002). Parameter coefficients for each species are provided in Table 1. Across these species, the variable that was the most significant predictor of occupancy was percent forest 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:

$$\text{logit}(\psi) = \beta_0 + \beta_1(\text{forest}) + \beta_2(\text{TWI}) + \beta_3(\text{TWI})^2 + \beta_4(\text{edge}_2050) + \beta_5(\text{edge}_2050 \times \text{forest}) + \beta_6(\text{evergreen}) + \beta_7(\text{evergreen})^2 + \beta_8(\text{percent}_\text{forest}_2050) + \beta_9(\text{percent}_\text{forest}_2050)^2 + \beta_{10}(\text{roads}_2050) + \beta_{11}(\text{roads}_2050)^2$$

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 this new development did not change TWI or the percentage of evergreen forest within 300 m of the pixel (evergreen). Our analysis, therefore, presents a very conservative estimate of
the response of forest birds to future human population growth. We examined changes in
occupancy patterns throughout the study area and by town.

**Conserved Lands and Species Habitat (Objective 4)**

The probability of occupancy maps represented 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 $\psi$ values across each raster cell
in the year 2000. Then, we summed the total $\psi$ 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.

**Results**

**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 were expected to gain the 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 human housing density grew from 517 housing units per hectare in year 2000 to 530 housing units per hectare in year 2050. The maximum change in housing density was nearly 30 houses per ha (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).

**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). This model explained approximately 84% of the variation ($R^2 = 0.8391, P < 0.0001$). The maximum road density in 2000 was 35.3 km/km² and the maximum road density in 2050 was 36.9 km/km², given housing densities in 2050. The mean road density across the
study area rose from 2.37 to 2.83 km/km² and the highest road density increase in any one pixel throughout the study area was 20.6 km/km² (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

\[
\ln(\text{odds})_{\text{percent development}_{1\text{km}}} = -3.20 + 2.83 \times \log(\text{road density}_{1\text{km}}) + 0.60 \times (\log \text{road density} - 0.15)^2.
\]

This model explained approximately 86% of the variation in the data \(R^2 = 0.8645, P < 0.0001\). 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 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 ex-urbia 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

\[
\log(\text{distance to develop edge within 1 hectare}) = 2.73 - 0.34 \times \log(\text{housing density within 1 ha}_{2000}) (P < 0.0001, R^2 = 0.15).
\]
Overall, the mean change in minimum edge distance across the landscape was 15.85 meters; whereas in places distance-to-edge decreased by almost 1000 meters (Fig. 3d). The spatial pattern of minimum distance-to-edge was different than the other forecasted variables in the year 2050 (Fig. 3). Existing roads were more prominent in shaping the future minimum distance to edge than was apparent with percent forest cover and developed land cover. The overall spatial pattern of change was more irregular across much of the landscape rather than the overt exurban development patterns of the other variables.

**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 Warblers 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 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 Woodpeckers to 8% for Ovenbird and Hermit Thrush (Fig. 5). For instance, 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.

**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% - 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% - 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.

**Discussion**

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 – 0.68 ha per unit; (3) “exurban” densities are between 0.68 – 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 (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 $\psi$ is contained within USFS boundaries. For instance, 10% of the total $\psi$ 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 $\psi$ 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. These estimates are conservative because 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. Therefore,
any reduction in future total $\psi$ values across the landscape could 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 $\psi$ 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. In other parts of the study area where protected parcels were small, this phenomenon was further exacerbated. 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.

Several challenges and considerations remain. First, our study assumed that development would occur on certain land cover classes based on scenarios we designed. 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 was not spatially explicit in that we did not predict the exact location of land cover change on a pixel by pixel basis. More sophisticated land use change modeling could produce more accurate land cover forecasts (Voigt and Troy 2008). For instance, forest succession on abandoned farm land is an important offset to increases in development in Vermont, and our model does not account for that.

Second, we assumed a linear relationship between road density and the number of housing units. There is likely a temporal aspect of housing development that this does not account for. Over time the marginal amount of road constructed per marginal amount of new housing unit could be nonlinear and instead decrease. Similarly, second home and vacation home development is driven more by the distribution of amenities than the density of roads. This is partially accounted for because we map housing rather than population density.

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. In spatially allocating each housing unit, SERGoM does not explicitly account for the varying sizes of census blocks,
which potentially alters the levels of precision in predicting the number of housing units per unit area.

Fourth, we used species occupancy probabilities as proxies for habitat suitability. It is important to recognize that we used the occupancy coefficient point estimates in our analyses. However, all coefficients are imprecise (as measured by the standard error), and 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. In a companion paper, we 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 (Brown et al. In review). The key result from this analysis was that relatively small decreases in occupancy can result in large decreases in landscape carrying capacity.

Finally, we assumed that species models developed in VT could be extended to the study region including NH and MA. The species models utilized in this study were for forest-interior species. Other non-forest core species may increase in occupancy as forests decrease, roads increase, and distance-to-developed edge decreases.

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). The question of how wildlife will respond to eminent land use change is widespread, and 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. A benefit of our approach is that town planners can take advantage of spatial mapping and use the maps proactively for future conservation efforts. The results provide replicable, spatially-explicit information about the risks of development that largely, to date, have been unavailable.

Acknowledgements

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Literature Cited


Tables

Table 2.1. Model averaged parameter coefficients 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).

<table>
<thead>
<tr>
<th>Coefficient values</th>
<th>HAWO</th>
<th>BTNW</th>
<th>HETH</th>
<th>OVEN</th>
<th>BTBW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psi intercept</td>
<td>-2.06</td>
<td>-4.76</td>
<td>-3.97</td>
<td>-3.05</td>
<td>-4.74</td>
</tr>
<tr>
<td>TWI (topographic wetness index)</td>
<td>-0.0001</td>
<td>0.051</td>
<td>-0.18</td>
<td>0.024</td>
<td>0.016</td>
</tr>
<tr>
<td>TWI² (topographic wetness index)²</td>
<td>0.000082</td>
<td>-0.0043</td>
<td>0.011</td>
<td>-0.0039</td>
<td>-0.0016</td>
</tr>
<tr>
<td>Edge (minimum distance to edge of nearest different land cover class)</td>
<td>-0.0070</td>
<td>-0.00073</td>
<td>-0.011</td>
<td>-0.0096</td>
<td>-0.012</td>
</tr>
<tr>
<td>Forest (binary forest or non-forest value within 25 m of bird count location)</td>
<td>0.064</td>
<td>0.79</td>
<td>1.13</td>
<td>1.06</td>
<td>0.28</td>
</tr>
<tr>
<td>Forest*Edge (interaction term for Forest and Edge)</td>
<td>0.0075</td>
<td>0.0014</td>
<td>0.012</td>
<td>0.011</td>
<td>0.011</td>
</tr>
<tr>
<td>Percent forest (percent forest within 1 km radius of pixel)</td>
<td>2.12</td>
<td>6.48</td>
<td>5.90</td>
<td>5.77</td>
<td>7.79</td>
</tr>
<tr>
<td>Percent forest² (percent forest within 1 km radius of pixel)²</td>
<td>-0.89</td>
<td>-1.91</td>
<td>-2.46</td>
<td>-2.96</td>
<td>-2.29</td>
</tr>
<tr>
<td>Road (road density within 1 km radius of pixel)</td>
<td>0.15</td>
<td>0.058</td>
<td>0.00052</td>
<td>-0.071</td>
<td>-0.043</td>
</tr>
<tr>
<td>Road² (road density within 1 km radius of pixel)²</td>
<td>-0.019</td>
<td>-0.0075</td>
<td>-0.0015</td>
<td>-0.0079</td>
<td>0.0052</td>
</tr>
<tr>
<td>Evergreen (percent evergreen forest within 300 m of pixel)</td>
<td>-0.56</td>
<td>2.46</td>
<td>0.39</td>
<td>2.80</td>
<td>-5.64</td>
</tr>
<tr>
<td>Evergreen² (percent evergreen forest within 300 m of pixel)²</td>
<td>0.93</td>
<td>-1.35</td>
<td>-0.38</td>
<td>-4.20</td>
<td>5.78</td>
</tr>
</tbody>
</table>
Table 2.2. 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).

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

**Figure 2.1.** 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 – 1l, uses future population growth rates and proximity to urban centers to project spatially-explicit future housing density values.

**Figure 2.2.** 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.

**Figure 2.3.** 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, b) percent development within a 1 km radius circle, c) percent forest cover within a 1 km radius circle, and d) minimum distance to the nearest edge of a different land cover class within a 1 ha radius circle. Dark areas indicate large differences in the landscape metric values between 2000 and 2050 and white areas indicate little or no difference.
**Figure 2.4.** 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.

**Figure 2.5.** Differences in mean town 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.
Figures

Fig. 2.1.
Fig. 2.2.
Fig. 2.5.
Chapter 3 - Predicting Effects of Future Human Population Growth and Development on a Territorial Forest Songbird: Small Declines in Occupancy Equates to Large Declines in Landscape Carrying Capacity

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Abstract

Projected increases in human population growth are expected to increase forest loss and fragmentation in the next century at the expense of forest-dwelling wildlife species. In the face of increased development, managers need a spatial quantitative metric to inform decisions that benefit wildlife. We used maximum clique analysis to calculate the landscape carrying capacity, $N_k$, across the northeastern states of Vermont, New Hampshire, and Massachusetts, USA for the forest-dependent Ovenbird. We classified the year 2000 landscape into four land cover classes based on human housing density: urban, suburban, exurban, and rural development. We sampled each land cover class and estimated Ovenbird $N_k$ from occupancy probability maps for the years 2000 and 2050. The forecasted occupancy maps represented landscape conditions in the year 2050 derived from spatially-explicit growth models. In response to human population growth and development, $N_k$ was predicted to decrease 44% in the landscape classified as exurban development, 25% in urban and suburban development, and 14% in rural development. These decreases far exceeded the decreases in occupancy probabilities that ranged between 3% and 5% across the same sampled sites. Maximum clique analysis is a tool that can be used to estimate a species population metric, $N_k$, and provide decision-makers with straightforward information to inform decisions and communicate with stakeholders.

Keywords: Occupancy modeling, human population growth, $N_k$, landscape carrying capacity, Ovenbird, forest ecosystem
Introduction

Projected increases in human population growth are expected to increase forest loss and fragmentation in the next century. The populations of Vermont, New Hampshire, and Massachusetts, USA, are predicted to grow 16.9%, 33.2%, and 10.4%, respectively, between the years 2000 and 2030, collectively adding 1.2 million people (U.S.Census Bureau 2011). In addition to adding more people to the landscape, each person is taking up more space. Currently, residential housing accounts for 87% of land use change in Massachusetts even in areas where population growth is roughly flat (DeNormandie et al. 2009).

In addition to the amount of human population growth, the distribution of people and houses on a landscape can affect forest loss and fragmentation. Theobald (2005) defines four categories of developed land use relative to human housing density: urban, suburban, exurban, and rural development. Exurban development is low-density residential development that occurs outside of cities and suburbs (Daniels 1999). Land classified as exurban often contains viable forest habitat for species (Brown et al. in review), but is under the gravest threat of conversion due to disproportionate rapid development pressures (Theobald 2005).

In the face of future human population growth, wildlife biologists are pressed to estimate the risk of increased development to wildlife populations – how will species respond? Their abundance, distribution, and viability can be intricately tied to the condition of the landscape mosaic (Forman 1995, Turner et al. 2001); however, wildlife managers often cannot manipulate the landscape mosaic on behalf of wildlife. Given these challenges, spatially-explicit tools are needed to quantify how individual species are
expected to change in response to increased development. Additionally, metrics are needed that can be easily communicated to wildlife practitioners and decision-makers alike (Burdett et al. 2010, Brown et al. In review).

One common method used to estimate the distribution of animal patterns is to calculate the probability that a species will occur in the landscape based on spatial covariates. Occupancy models calculate the probability that a species will occur ($\psi$) based on empirical presence-absence data and species’ sensitivities to variables such as forest amount, forest arrangement, development, and roads (MacKenzie et al. 2006). In a recent paper, Schwenk and Donovan (2011) modeled $\psi$ for over 60 bird species using a single-species occupancy modeling framework and several landscape covariates including forest cover, road density, and distance to edge. These models were used to calculate and map the probability of occupancy within each 30 m$^2$ pixel in the study area for each species in the year 2000.

This methodology was expanded to predict $\psi$ in future decades (to the year 2050) for 5 forest-dependent birds species in the northeastern USA based on projected changes in human housing density, developed lands, forest cover, and distance to the nearest edge (Brown et al. In review). The probability of occupancy for each species decreased by as much as 38% in some places in the study area and 97% of towns experienced species occupancy decline between the years 2000 and 2050. However, average declines in occupancy across the study area were fairly minimal, ranging from 0% (Hairy Woodpecker) to 2% (Black-throated Green Warbler, Ovenbird, and Hermit Thrush). These results suggested that distribution patterns of these species may not change dramatically in response to future land use change.
Although calculating changes in occupancy probability is a rigorous quantitative metric, research suggests that probability can be a difficult concept for people to understand (Rottenstreich and Hsee 2001). People tend to overestimate the odds of things that are obscure, underestimate the odds of common things, and ignore everything in between (Welch 2001, Rosenthal 2006). Additionally, cognitive bias results in people disregarding probability when making a decision (Baron 2000). Thus, expecting land and wildlife managers to use probabilities to make critical decisions on behalf of wildlife populations may be unrealistic.

There is a great need, therefore, to create metrics that can be used by land managers and policy makers alike to critically evaluate changes in wildlife distribution patterns that may result from future human population growth. One measure that is readily understood by decision makers in assessing responses to future land use change is wildlife population size (Rosenberg & Blanche 2005). Maximum clique analysis, a branch of mathematical graph theory, provides a novel way to estimate the maximum potential population size a given landscape is capable of supporting, $N_k$ (Donovan et al. 2012). In other words, $N_k$ is the maximum number of species territories that a landscape can support. Although the actual population size may be less than $N_k$, unlike probabilities, $N_k$ is a metric that most decision makers can understand relative to assessing species responses to future land use change.

To estimate $N_k$ using maximum clique analysis, it is helpful to understand some basic graph theory. A graph consists of a set of objects called points (also called vertices) along with a set of edges that link the points. Each edge indicates a relationship between its associated pair of points. Two points so linked are said to be adjacent. A clique in a
graph is a subset of the points in which every pair of points is adjacent. For example, in a social network where points indicate people and edges indicate friendships, a clique would correspond to a group of mutual friends. A clique is said to be maximum if a clique with more points does not exist (e.g. the largest group of friends). The drawings in Figure 1a and 1b represent the same graph. We have drawn this graph in two different ways to emphasize that the positions of the points are immaterial; what matters is the same pairs of points are adjacent in each drawing. Cliques of size two and three are highlighted in Figure 1a. A maximum clique of size four is highlighted in Figure 1b.

In this paper, we use occupancy models as inputs for maximum clique analysis to predict changes in the landscape carrying capacity ($N_k$) as a result of predicted future development. Figure 2 illustrates how to transform an occupancy map into an estimate of $N_k$ with maximum clique analysis under the assumption that probability of occupancy is directly related to habitat suitability (Martin et al. 2010). First, an occupancy map has pixel values that range between 0 and 1 (Fig. 2a). In this example, a focal pixel in row 3, column 3 has an occupancy probability of 0.6 (Fig. 2a). The circle represents a buffered polygon that simulates a territory. Second, the occupancy probabilities in each pixel are recalculated to represent the average $\psi$ of the pixels within the territory boundary, essentially scoring each pixel as if it were the center of a hypothetical breeding territory. A numeric threshold is set based on what is considered a suitable territory score for the target species. In Figure 2b, all pixels that are $\geq$ to a hypothetical threshold of 0.8 are shaded, indicating that they have sufficient resources in the surrounding cells to support a territorial bird. The two locations that meet the habitat threshold are retained, numbered 1 and 2, and buffered to simulate the placement of pseudo territories on the landscape.
(Fig. 2c). The pseudo territory locations are converted from spatial locations to points in a graph, and edges are drawn between points that can co-exist without overlapping territorial boundaries (Fig. 2d). In this example, a maximum clique analysis of this graph yields $N_k = 2$. By converting occupancy maps (or other habitat suitability maps) to estimates of $N_k$, decisions can be informed by an understandable metric that is often used in setting conservation objectives (Rosenberg and Blancher 2005).

For this study we selected a forest-dependent songbird that is sensitive to development and forest fragmentation, the Ovenbird (*Seiurus aurocapillus*). The goal of this study was to compare occupancy probability and $N_k$ as quantitative metrics and examine their use in informing conservation and management. The objectives of our study were to: 1) Estimate landscape carrying capacity ($N_k$) for the Ovenbird in four development classes: urban, suburban, exurban, and rural, for the years 2000 and 2050 and 2) Compare changes in occupancy probability with changes in $N_k$.

**Methods**

**Study Area and Target Species**

The study area was the three-state region of Vermont, New Hampshire, and mainland Massachusetts, USA (26,800 square miles; Fig. 3). 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). We defined the development categories based on housing unit density thresholds from Theobald (2005): (1) “urban” housing densities are < 0.1 ha per unit; (2) “suburban” housing densities are between 0.1 – 0.68 ha per unit; (3) “exurban” densities are between 0.68 – 16.18 ha per unit; and (4) “rural” housing densities are > 16.18 ha per unit (Fig. 3).
Approximately 50% of the landscape was categorized as exurban, 36% as rural, and 12% suburban and 3% urban development categories in the year 2000. Between the years 2000 and 2050, Brown et al. (in review) predicted that roughly half a million new housing units will be added to the landscape in VT, NH, and MA. The pattern of development was forecasted to follow similar development patterns as in other parts of the United States (Theobald 2005); the areas outside of urban areas were expected to gain the most housing units, but many rural places were not predicted to grow.

The Ovenbird was selected for analysis based on its habitat preferences and sensitivities to forest loss and fragmentation. This neotropical migrant songbird breeds throughout eastern North American forests. Ovenbirds nest in mature deciduous and mixed forests and are known to prefer large blocks of continuous forests with structural diversity and high canopy closure (60 – 90%) (McGowan and Corwin 2008). Ovenbirds are negatively impacted by fragmentation; nesting success declines as the percentage of forest in the landscape decreases (Robinson et al. 1995) and as the distance to edge decreases (Ortega and Capen 1999). Ovenbirds respond negatively to forest roads, power lines, and chronic noise (Porneluzi et al. 2011). As territorial breeders, Ovenbirds are a good target species for calculating $N_k$ through time.

**Ovenbird Occupancy Mapping: 2000 and 2050**

Brown et al. (in review) developed raw occupancy probability maps for singing male Ovenbirds across the study area for the years 2000 and 2050. These maps were derived from single-season occupancy models (MacKenzie et al. 2006), described fully in Schwenk and Donovan (2011). Briefly, birds were surveyed at 693 points across the state of Vermont in either 2003 or 2004. Six environmental characteristics (covariates)
were quantified for each point: (1) forest or not forest; (2) topographic wetness index; (3) distance to the edge of a different land cover type; (4) percent evergreen forest within 300 m; (5) percent forest within 1 km; and (6) road density within 1 km. Thirty-two models, consisting of various combinations of the 6 covariates, were analyzed in a single-season occupancy framework (MacKenzie et al. 2002). Models were compared and evaluated in an AIC framework (Burnham and Anderson 2002), which estimated the weight of support for each model. Model averaged coefficient estimates for each of the 6 covariates were estimated (Table 1), and indicated that the probability a 30 m² pixel would be occupied by an Ovenbird increased as distance to a non-forest edge increased and percentage of forest cover within 1 km increased (Fig. 4). Brown et al. (in review) used the model averaged coefficient estimates to predict occupancy for each pixel in the study area for the year 2000 (Table 1; Fig. 5a). To predict occupancy probabilities of Ovenbird to the year 2050, Brown et al. (in review) applied the model-averaged occupancy parameter estimates (Table 1) to a landscape that represented conditions in the year 2050 (Fig. 5b).

**Objective 1: Estimate landscape carrying capacity \( N_k \) for the Ovenbird in four development classes for the years 2000 and 2050**

The Ovenbird occupancy maps for the years 2000 and 2050 were the main inputs for maximum clique analysis (Donovan et al. 2012). Because the computational time to run maximum clique analysis on the entire landscape was prohibitive, we estimated \( N_k \) for sample sites that were roughly 100 ha in size within each of the four development categories (urban, suburban, exurban, and rural).
To select random study sites, we assigned each pixel in the study area to one of four development categories (urban, suburban, exurban, or rural) based on housing density in the year 2000. Next, we used a moving window analysis to reclassify each pixel into one of the four development categories based on the category that most frequently occurred within a 576 m radius circle (area ~ 100 ha). We randomly placed points on the resultant raster grid for the year 2000, and selected eligible points in each development category that were at least 2000 m away from each other. Points were considered to be eligible if at least one pseudo territory could occur within the sample site boundaries. Forty points were selected for the rural and exurban development categories, while only 5 and 10 points were selected for the urban and suburban development categories, respectively (Fig. 3). Fewer sample sites were selected for the urban and suburban development categories because the number of eligible pseudo territories was much lower than in rural and exurban development (see below). Each selected point was buffered by a circle with a radius of 576 m (area ~ 100 ha; N = 95 sample sites in total).

We clipped the occupancy maps for the years 2000 and 2050 (Fig. 5) to each sample site, and estimated \( N_k \) for each site and time period with maximum clique analysis.

**Maximum Clique Analysis**

To convert the Ovenbird occupancy probabilities within each sample site to estimates of \( N_k \), several steps were necessary and are described fully in Donovan et al. (2012). Briefly, given the pixel size of the occupancy map was smaller than the territory size of an Ovenbird, the first step was to convert the occupancy map so that pixel scores depicted the territory capacity (sensu Compton et al. 2006). This was achieved by assuming each pixel was the center of a pseudo territory, and computing a score so that
the pixel value reflected the suitability of the pixel itself plus the surrounding area. We created pseudo territories by simulating circular territories with a radius of 77.6 m, which is equivalent to a territory size of 1.89 ha (Porneluzi et al. 2011). Second, locations not meeting a 0.77 occupancy threshold were eliminated. We assumed those locations did not contain sufficient resources to constitute an Ovenbird pseudo territory. This occupancy probability threshold was determined by calculating probabilities in locations where Ovenbirds were known to occur with certainty in Vermont based on singing male surveys (Schwenk and Donovan 2011). Third, each cell that met the threshold criteria for a pseudo territory was assigned a unique number within each sample site. These represented points in a mathematical graph.

Points were linked by an edge (i.e., made adjacent) if the corresponding locations could support both pseudo territories without overlapping or violating territory boundaries. We used maximum clique analysis to calculate the maximum number of non-overlapping pseudo territories within each sample in the study area in both 2000 and 2050. We then used the public domain C software Cliquer to find the maximum clique size for each Ovenbird sample site in each year (Niskanen and Ostergard 2003). Finally, we conducted paired two-sample t-tests for each development category (urban, suburban, exurban, and rural development) to test for differences in $N_k$ among time periods.

Estimates of $N_k$ are known to be sensitive to both habitat threshold and territory size (Donovan et al. 2012). Therefore, we evaluated the sensitivity of $N_k$ to changes in territory size and habitat quality (i.e., habitat thresholds). We varied the territory sizes from 0.5 to 1.89 to 4.0 ha, which represented the range of published estimates of Ovenbird territory size (Porneluzi et al. 2011). We also varied the habitat threshold (i.e.,
ψ) from 0.72 to 0.77 to 0.82, which represented a range of average ψ values within a 1.89
ha area where Ovenbirds were known to occur (Schwenk and Donovan 2011).

**Objective 2: Compare changes in occupancy probability with changes in N_k**

We calculated the average occupancy probability for each sample site for the
years 2000 and 2050, and then calculated the average differences in occupancy
probabilities for each development category. We also calculated differences in N_k for
each sample for the years 2000 and 2050, and compared changes in occupancy
probabilities with changes in N_k.

**Results**

In the year 2000, average N_k estimates for Ovenbirds ranged between 28.8 birds
per 100 ha for urban (range 11 - 44; SD = 13.6) and 33.8 for rural development categories
(range 8 - 45; SD = 9.4; Fig. 6a). The high standard deviations of N_k within each
development category suggests that the 2000 landscape was heterogeneous in terms of
landcover (percent forest cover within 1km, distance to edge, roads, etc) within a given
development category. The high estimates of N_k for the urban and suburban development
categories are due to the fact that we considered only those samples that contained at
least one pseudo territory. These estimates would be much lower if we had included in
our random sample those areas that had 0 pseudo territories.

Objective 1 was to estimate the difference in N_k for Ovenbirds between the years
2000 and 2050. Landscape carrying capacity decreased in all development categories
(rural, exurban, suburban, and urban) between the years 2000 and 2050 (Fig. 6a). The
most dramatic decreases in Ovenbird N_k were observed in the exurban development
category, where N_k declined from 33 to 23 territories (-44%; Fig. 6a). The least amount
of change was observed in rural development where a 14% reduction in $N_k$ was observed; 25% reductions were estimated in each of the urban and suburban development categories (Fig. 6a). The reductions in percent $N_k$ were significant in suburban, exurban, and rural development categories, but not significant for urban development (Fig. 6a; paired two-sample t-tests within each development category). The test for the urban development, however, had low statistical power because the sample size was restricted to 5.

Finally, we evaluated the sensitivity of $N_k$ to changes in pseudo territory threshold and Ovenbird territory size (Fig. 6b-6e). In each case evaluated, generally speaking, $N_k$ increased as territory size decreased and as threshold decreased. $N_k$ was most sensitive to changes in the threshold level used to define pseudo home ranges; territory size affected $N_k$ to a much lesser degree. For example, in rural categories in the year 2000, the baseline $N_k$ estimate was 33.8 (threshold = 0.77, territory size = 1.89 ha; Figure 6a). The change in $N_k$ when the threshold was reduced to 0.72, $N_k$ estimates were 41.2 for territory size of 0.5 ha and 39.3 when territory size was 4 ha. In contrast, when the threshold was 0.82, $N_k$ dropped to ~22 regardless of the territory size evaluated (Fig 6b-6e). This pattern was generally consistent across analyses.

Objective 2 was to compare changes in occupancy probability from 2000 to 2050 for the study area with changes in $N_k$. Pixel values in the raw (original) probability of occupancy map for Ovenbird ranged from 0 to 0.94 in both 2000 and 2050 across the study area (Fig. 5). The mean probability of occupancy was 0.50 in 2000 and 0.48 in 2050. In our sample sites, the mean decrease in occupancy probability between the years 2000 and 2050 ranged from 3% in urban, suburban, and rural development to 5% in
exurban development (Fig. 7). In contrast, $N_k$ decreased between 14% (rural) and 44% (exurban; Fig. 7). Thus, a relatively small decrease in occupancy probability (e.g. exurban = -5%; Fig. 7) resulted in a large decrease in $N_k$ (exurban = -44%; Fig. 7).

**Discussion**

Making decisions based on quantitative metrics is challenging, but essential, for managers, town planners, and politicians. Metrics need to be biologically meaningful, easy to understand, and straightforward to communicate. For example, the future change in occupancy probability is hardly discernible at a landscape scale in VT, NH, and MA (Fig. 5) and it is challenging to communicate to stakeholders exactly what the probabilities mean and how to implement solutions to change them (Rottenstreich and Hsee 2001). However, we demonstrated that significant changes will happen in the landscape at the expense of populations of forest-dwelling birds using the metric $N_k$.

Species population numbers are more intuitive to understand than probabilities, are commonly used as conservation objectives, and lend themselves to policy and management solutions (Rosenberg and Blancher 2005). Maximum clique analysis is a methodology that can translate occupancy probabilities and other habitat suitability maps to yield more intuitive results in terms of species population parameters.

Why is there such a divergence in occupancy probability and $N_k$? For Ovenbirds, small changes in forest cover can reduce occupancy probability (Fig. 4). Between the years 2000 and 2050, some places in the landscape lost as much as 32% forest cover within a 1 km window (Brown et al. In review). Overall, the decline in occupancy probability was only 2% for the entire study area; these varied spatially, with highest declines occurring in exurban areas. In maximum clique analysis, however, when pseudo
territories are placed in the landscape, the average occupancy within the pseudo territory is computed. Only those pseudo territories that meet the habitat threshold are retained as points for the clique analysis. In our sensitivity analysis, the clique estimate was much more sensitive to changes in habitat threshold than to changes in territory size (Fig. 6). That is, a small change in habitat threshold affected the $N_k$ result. Decreasing occupancy within pseudo territories, even by a small amount, reduced the average occupancy score such that the pseudo territories no longer met the habitat threshold. This reduced the number of points in the clique analysis, and $N_k$ was reduced because there were fewer non-overlapping pseudo territories in the landscape for year 2050. Upon visual inspection of the pseudo territory maps, it was clear that the pseudo territories were being lost at the edges of habitat patches.

Human population growth and development will significantly decrease $N_k$ for Ovenbirds in the future. The spatial pattern of where $N_k$ will decrease in the landscape has consequences for managers and decision-makers as well as wildlife. The predicted percent reduction of Ovenbird $N_k$ was high in every development category (urban, suburban, exurban, and rural), ranging from a 14% decrease in rural development to a 44% decrease in exurban development. In the USA, exurban areas have been growing disproportionately in comparison to the other three development classes in recent years both in terms of absolute amount of hectares and rates of development (Vermont Forum on Sprawl 1999, Theobald 2001). In our study area, land classified as exurban development contained a large amount of viable habitat for the forest-dwelling Ovenbird, in part because exurban development occupied a large portion of the landscape (50% in the year 2000) and in part because sizable forest patches can exist within exurban
development. The changes in each development category between the years 2000 and 2050 was minimal: 0% change in urban, 1% growth in suburban, 1% growth in exurban, and 2% decline in rural. Even though these changes are small, a 1% increase in exurban development equates to roughly 268 square miles, and because the development categories contain a range of housing unit values, houses can still be added to the landscape without changing development categories. The land use change model used in this analysis focused on increasing number of housing units, causing the further fragmentation of wildlife habitat despite relative low change in development category; wildlife are responding to the increased number of housing units in the landscape and not the broad development categories.

Even in rural areas, where human population growth is limited, \( N_k \) is expected to decrease by 14%. This decline is due to the fact that even small increases in housing density can fragment the forested landscape and cause reductions in estimated occupancy probability and \( N_k \). This is a result of the strength of the forest cover and road density covariates in the Ovenbird occupancy model.

Ovenbirds were also predicted to decline in urban and suburban land classes. We were limited to a small number of samples in both of these development categories (\( N = 5, N = 10 \), respectively). We pre-selected sample sites where there was habitat for at least 1 viable pseudo territory. This significantly limited the amount of land in urban and suburban development categories. As a result of requiring at least 1 viable pseudo territory per sample site, we self-selected areas in urban and suburban development classes that contained high quality habitat. This created large numbers of pseudo territories per sample site in urban and suburban development categories that are not
representative of those development categories as a whole. If we had included 0’s in our sampling scheme, these areas would likely show no difference in $N_k$ between 2000 and 2050 because most randomly selected sample sites would have had 0 pseudo territories and thus not changed between time periods. By restricting our analysis to locations where pseudo territories existed in the landscape in the year 2000, our sampling design did not permit us to estimate $N_k$ across the study area, but this is a natural next step.

It is often difficult to demonstrate the negative effect of incremental land use change even though cumulative impacts can be detrimental to natural resources and wildlife (Theobald et al. 1997, Conway and Lathrop 2005, Johnson et al. 2005). Therefore, our results suggest three important considerations for decision makers. First, occupancy probability modeling and other habitat suitability approaches are becoming more widespread. While these are rigorous assessments of the likelihood of species occurrences, our results suggest that small incremental changes in these metrics cumulatively result in big changes in $N_k$. Second, since probabilities are not fully understood by most people (Rottenstreich and Hsee 2001), $N_k$ provides a bridge between commonly used occupancy or habitat suitability maps with population parameters that are often defined in management objectives. Third, $N_k$ estimates can be applied at multiple scales. At a landscape scale, $N_k$ can potentially strengthen our understanding of metapopulation or source-sink dynamics that are hypothesized to characterize songbird populations (Tittler et al. 2006, With et al. 2006). Local land use decisions, however, often drive landscape changes on-the-ground. At a local scale, the $N_k$ metric can be used to assess alternative land use change scenarios that might affect species population size. In turn, these local scale decisions affect broader regional population dynamics.
An important source of uncertainty in estimating $N_k$ is due to territory size and habitat threshold. We examined a range of habitat thresholds and territory sizes above and below the mean values of these metrics which resulted from Vermont field data (Schwenk and Donovan 2011) and literature for singing males (Porneluzi et al. 2011). Territory sizes are difficult to measure and vary with space, time, habitat quality, and population parameters (Andren 1990, McLoughlin 2000). However, in our analysis, habitat threshold was much more sensitive than territory size resulting in varying numbers of pseudo territories considered viable for an Ovenbird (Fig. 6). When changing the habitat threshold, the amount of change in $N_k$ will vary over time although the relative trend will be the same.

Despite of these considerations, we have demonstrated an approach for understanding the potential consequences of land use change on territorial species. These approaches can be adapted for other species (e.g.,(Donovan et al. 2012)), and can be used to provide a more holistic ecosystem approach. Common understanding of the trade-offs between human development and species viability is needed to make informed decisions about the future of wildlife populations.

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Tables

Table 3.1. Model averaged parameter coefficients obtained through single-species occupancy model analysis for Ovenbirds (OVEN) (Schwenk and Donovan 2011).

<table>
<thead>
<tr>
<th>Coefficient values</th>
<th>OVEN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Psi intercept</td>
<td>-3.05</td>
</tr>
<tr>
<td>TWI (topographic wetness index)</td>
<td>0.024</td>
</tr>
<tr>
<td>TWI² (topographic wetness index)²</td>
<td>-0.0039</td>
</tr>
<tr>
<td>Edge (minimum distance to edge of nearest different land cover class)</td>
<td>-0.0096</td>
</tr>
<tr>
<td>Forest (binary forest or non-forest value within 25 m of bird count location)</td>
<td>1.06</td>
</tr>
<tr>
<td>Forest*Edge (interaction term for Forest and Edge)</td>
<td>0.011</td>
</tr>
<tr>
<td>Percent forest (percent forest within 1 km radius of pixel)</td>
<td>5.77</td>
</tr>
<tr>
<td>Percent forest² (percent forest within 1 km radius of pixel)²</td>
<td>-2.96</td>
</tr>
<tr>
<td>Road (road density within 1 km radius of pixel)</td>
<td>-0.071</td>
</tr>
<tr>
<td>Road² (road density within 1 km radius of pixel)</td>
<td>-0.0079</td>
</tr>
<tr>
<td>Evergreen (percent evergreen forest within 300 m of pixel)</td>
<td>2.80</td>
</tr>
<tr>
<td>Evergreen² (percent evergreen forest within 300 m of pixel)</td>
<td>-4.20</td>
</tr>
</tbody>
</table>
Figure Legends

Figure 3.1. Two drawings of a single graph with seven points (vertices). Points are joined by an edge if they have a specified relationship; edges are displayed here with lines (either thin red or thick black lines). In this study, each point represents the center of a pseudo territory on the landscape; an edge is drawn between two points if the two points can co-exist on the landscape, i.e., their pseudo territory polygons do not overlap. Point “a” can co-exist with points f, d, and c. Its pseudo territory boundaries overlap with points b, e, and g; therefore “a” is not joined with these points. Point “b” can co-exist with points e and d only; its pseudo territory boundaries overlap with points a, c, f, and g. Left Graph: A clique of size two (points b and e) is highlighted with thick lines, indicating that points b and e can co-exist on the landscape. A clique of size three is also highlighted (points a, c and d), indicating that all three points can co-exist on the landscape. Right Graph: The same graph (just re-oriented) highlighting the maximum clique for this seven point graph (points a, c, d and f).

Figure 3.2. (a) Hypothetical occupancy map showing pixel values that range between 0 and 1. A focal pixel in row 3, column 3 has an occupancy score of 0.6. The circle represents a buffered polygon that simulates a territory; (b) Hypothetical territory capacity map based on Figure 1a, in which the pixel score is the average of the focal pixel plus the 8 surrounding cells. All pixels that are ≥ to a hypothetical pseudo territory threshold of 0.8 are shaded; (c) The two locations that meet the threshold are retained, numbered 1 and 2, and buffered to simulate the placement of pseudo territories on the
landscape. In this example, we used circular buffers to simulate pseudo territories of the same size, resulting in a maximum of 2 territories that can co-exist on the landscape without overlap, and $N_k = 2$; (d) The pseudo territory locations are de-spaced and converted to points on a graph, and edges are drawn between points that can co-exist without overlapping boundaries. A maximum clique analysis of this graph yields $N_k = 2$; (e) The same occupancy map as (a) is duplicated for a new analysis; (f) A new hypothetical territory capacity map is created with a hypothetical pseudo territory threshold of 0.7; (g) The six locations that meet the 0.7 threshold are numbered retained and numbered 1-6; (h) The pseudo territory locations are de-spaced and converted to points on a graph as in (d). The maximum clique of this graph ($N_k$) is 3. The maximum clique ($N_k$) can be achieved in 6 ways: Examples include points 1, 2, and 4 and points 1, 3, and 5 (Donovan et al. 2012).

**Figure 3.3.** Study area of Vermont, New Hampshire, and Massachusetts, USA, illustrating four developed land classes in 2000: urban (red), suburban (orange), exurban (yellow), and rural (green). White areas represent undevelopable lands such as conserved lands, public lands, or water. Developed land classes are defined based on the number of housing units per hectare; where urban housing densities are $< 0.1$ ha per unit; suburban housing densities are between $0.1$–$0.68$ ha per unit; exurban densities are between $0.68$–$16.18$ ha per unit; and rural housing densities are $> 16.18$ ha per unit. Ninety-five sample sites (576 m radius circles; ~100 ha) are shown as points.
Figure 3.4. The effect of two covariates (1) percent forest cover and (2) distance to a non-forest edge on the probability of occupancy for Ovenbird in Vermont, New Hampshire, and Massachusetts, USA. As the distance to a non-forest edge increases, the probability of occupancy increases; as percent forest cover increases, the probability of occupancy increases.

Figure 3.5. Probability of occupancy maps for the Ovenbird in year 2000 (a) and 2050 (b) in Vermont, New Hampshire, and Massachusetts, USA. Probabilities range from 0 (black) to 0.94 (white) and have a mean of 0.50 (a) and 0.48 (b) (Brown et al. In review).

Figure 3.6. Changes in mean $N_k$ between the years 2000 (white) and 2050 (gray) in four developed land classes: urban, suburban, exurban, and rural. Standard deviations are illustrated by bars around each mean. Threshold for habitat quality (occupancy probability) and territory size vary by illustration: (a) habitat threshold = 0.77, territory size = 1.89 ha; (b) habitat threshold = 0.82, territory size = 0.5 ha; (c) habitat threshold = 0.72, territory size = 0.5 ha; (d) habitat threshold = 0.82, territory size = 4.0 ha; (e) habitat threshold = 0.72, territory size = 4.0 ha.

Figure 3.7. Percent declines in occupancy probabilities and $N_k$ between the years 2000 and 2050 in four developed land classes: urban, suburban, exurban, and rural, in Vermont, New Hampshire, and Massachusetts, USA.
Figures

![Diagram a](image1.png)
![Diagram b](image2.png)

Fig. 3.1.
Fig. 3.2.
Fig. 3.3.
Fig. 3.5.
Fig. 3.6.

Habitat Threshold = 0.77
Territory Size = 1.89 ha

Habitat Threshold = 0.82
Territory Size = 0.5 ha

Habitat Threshold = 0.72
Territory Size = 0.5 ha

Habitat Threshold = 0.82
Territory Size = 4.0 ha

Habitat Threshold = 0.72
Territory Size = 4.0 ha
Fig. 3.7.
Comprehensive Literature Cited


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