



The loss of forest birds habitats under different land use policies as projected by a coupled ecological-econometric model



Frederic Beaudry^{a,*}, Volker C. Radeloff^b, Anna M. Pidgeon^b, Andrew J. Plantinga^c, David J. Lewis^d, David Helmers^b, Van Butsic^b

^a Environmental Studies Division, Alfred University, 1 Saxon Drive, Alfred, NY 14802, USA

^b Department of Forest & Wildlife Ecology, University of Wisconsin – Madison, Madison, WI 53706, USA

^c Department of Agricultural and Resource Economics, Oregon State University, Corvallis, OR 97331, USA

^d Department of Economics, University of Puget Sound, 1500 N. Warner St., Tacoma, WA 98416, USA

ARTICLE INFO

Article history:

Received 14 January 2013

Received in revised form 17 May 2013

Accepted 20 May 2013

Available online 20 June 2013

Keywords:

Coupled models

Econometrics

Habitat loss

Land use

Wisconsin

ABSTRACT

Land use is driven by socio-economic factors that must be understood in order to mitigate habitat loss. Econometric land-use models describe how land use is affected by socio-economic factors, such as financial returns to different uses of land, and they can be linked to biological models to provide new insight for conservation. Our goal was to evaluate the effects of future land use change on the habitat of forest breeding bird species in northern Wisconsin. Specifically, we estimated the effects of land use change on the amount of habitat available and compared the effects of economic policy scenarios on bird habitat. To do this, we coupled a spatially-explicit econometric model of land use change on private lands with models of northern Wisconsin forest bird potential habitat, comparing a 50-yr baseline projection with a scenario providing incentives for forest growth and a high urban growth scenario. The baseline scenario suggests an average of 438,705 ha of forest lost (10%), with 1.9% of that saved under the Forest Incentive scenario, and a 1.6% greater loss for the Urban Growth scenario. Under baseline projections boreal birds experienced the least amount of habitat loss (2–3%), and deciduous forest birds the most (6–8%). For some species, the projected loss of habitat exacerbates ongoing long-term declining population trend. Coupled economic-ecological models can be used to evaluate alternative incentive programs and to explore the complex interactions between policy, land use change, and broad spatial scale ecological processes that are highly relevant to conservation.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Habitat loss due to land use is the single most important cause of terrestrial biodiversity loss (Wilcove et al., 1998). Globally, 34% of the land area is devoted to cropland and pastures (Ramankutty et al., 2008), and human dominated land use has converted over 60% of temperate forests (Millennium Ecosystem Assessment, 2005). Land use change is forecasted to remain the largest driver of biodiversity loss for at least the next 100 years (Sala et al., 2000). This underscores the urgency of successful conservation of terrestrial biodiversity, which requires a thorough understanding of habitat loss and the agents of land use change (Balmford et al., 2003).

Determinants of land use include natural factors such as soil quality and climate, along with a host of socioeconomic factors operating at a range of spatial scales. At the broadest scales, global macroeconomic conditions determine commodity prices which, in turn, influence land prices and use decisions, and national policies govern land ownership rights and provide subsidies for production (agriculture and forestry) and conservation. At finer scales regional and local regulatory frameworks (e.g., zoning) and local land markets further drive land use. Those human factors are part of socio-economic systems that are highly dynamic: for example, the price paid to farmers for corn in the United States more than tripled between 2000 and 2011, from 1.85 to 6.22USD per bushel (US Department of Agriculture, 2013). If ecological models ignore the underlying economic drivers of land use change, they will have limited practical policy use (Wätzold et al., 2006). Most conservation approaches treat a particular habitat's underlying land tenure as stable and uniform, limiting their usefulness in real-world applications as land use economics are rarely integrated (Margules and Pressey, 2000). In reality, ecologically-defined conservation targets aimed at reducing habitat loss face trade-offs with socio-economic

* Corresponding author. Tel.: +1 607 871 2604.

E-mail addresses: beaudry@alfred.edu (F. Beaudry), radeloff@wisc.edu (V.C. Radeloff), apidgeon@wisc.edu (A.M. Pidgeon), plantinga@oregonstate.edu (A.J. Plantinga), djlewis@pugetsound.edu (D.J. Lewis), helmers@wisc.edu (D. Helmers), vanbutsic@gmail.com (V. Butsic).

outputs that depend on varying land prices (Ando et al., 1998; Polasky et al., 2001).

Ecological models based on land cover quantify the connection between wildlife presence (or abundance) and the land, and can predict habitat for conservation planning at broad spatial scales (Noss, 1983; Mladenoff et al., 1995; Sanderson et al., 2002; Hansen and DeFries, 2007; Otte et al., 2007). For example, landscape-scale habitat suitability index models can be useful when the functions relating environmental variables with habitat quality are well known (Rittenhouse et al., 2010b), whereas maximum entropy modeling is powerful for situations where only presence data are available (Phillips et al., 2006). Potential habitat distribution models are another approach for broad spatial scale wildlife habitat models, especially when available data are limited (Beaudry et al., 2010). Pairing habitat models with time-series of satellite images allows evaluating how past land use may have led to habitat loss, and making projections of future land use change and its effects (e.g., Lütolf et al., 2009). However, the use of land use trajectories that are based simply on observed trends in land use can be limiting, as in reality land use is largely determined by the prices of the commodities (tangible or not) that can be obtained from that land (Radeloff et al., 2012).

Econometric models, as quantitative analyses of economic relationships, describe how land use is affected by prices. Recent advances in spatially-explicit econometrics make land use projections at both grains and extents that are relevant to many ecological processes and pertinent for conservation (Lewis, 2010). Economic theory that describes individual land use decisions is the basis for modeling land use change using econometrics (Bockstael, 1996). Empirically observed individual land use decisions, such as the US Department of Agriculture's Natural Resource Inventory (NRI; Lubowski et al., 2006) or time series of plat maps showing the land use history of individual land parcels (Lewis et al., 2009a; Butsic et al., 2010), form the input for econometric models. The output of econometric models are point estimates which describe the effects of physical, spatial, and economic covariates on the likelihood a parcel will transition to an alternative land use. Once these transition probabilities are estimated, econometric land use models can describe future land use changes through the use of landscape simulations (Lewis and Alig, 2009), either

deterministically (Chomitz and Gray, 1996), or stochastically (Lewis and Plantinga, 2007).

Econometric models provide new opportunities to link economics and ecology, and to integrate economic drivers and biological models to provide reliable and realistic projections of land use, land cover, and their effects on wildlife. The landscape simulations obtained from econometric models can be assessed for ecologically important patterns such as forest patch size (Lewis and Plantinga, 2007; Lewis et al., 2009a), watershed health indices (Langpap et al., 2008), or lakefront development density (Lewis et al., 2009b). Recent studies have explored ecological responses to simulated landscape patterns, linking econometric models with biodiversity indices (Nelson et al., 2008), anadromous fish spawning habitat quality (Lohse et al., 2008), green frog (*Rana clamitans*) habitat quality (Lewis, 2010), and fish growth rates (Butsic et al., 2010, 2012). Landscape simulations derived from spatially-explicit econometric models thus provide an opportunity to explore how land use change interacts with the main threat to biodiversity, habitat loss.

Temperate forests may receive less conservation attention than other threatened ecosystem types such as grasslands or wetlands, partly because temperate forests are not as rare, but nevertheless habitat degradation and fragmentation continue to threaten temperate forests (Millennium Ecosystem Assessment, 2005). The threats in northern Wisconsin are representative of those elsewhere in northern temperate forests: a lack of large patches and old forests, invasive plant species, overabundant large herbivores populations (e.g., white-tailed deer), loss of specialized ground flora, invasive earthworms, and motorized recreation (Wisconsin Department of Natural Resources, 2005). Migratory birds of temperate forests in the United States have experienced recent significant declines in diversity and abundance (Rittenhouse et al., 2010a). Our goal was to evaluate the effects of future land use change on the habitat of temperate forest breeding bird species of conservation concern in northern Wisconsin. We linked an econometric model of land use with an ecological model of potential habitat, to (1) estimate the effects of land use change on the amount of habitat available, (2) compare the relative effects of land use change on species relying on different forest types, and (3) compare the effects of economic policy scenarios on bird habitat.

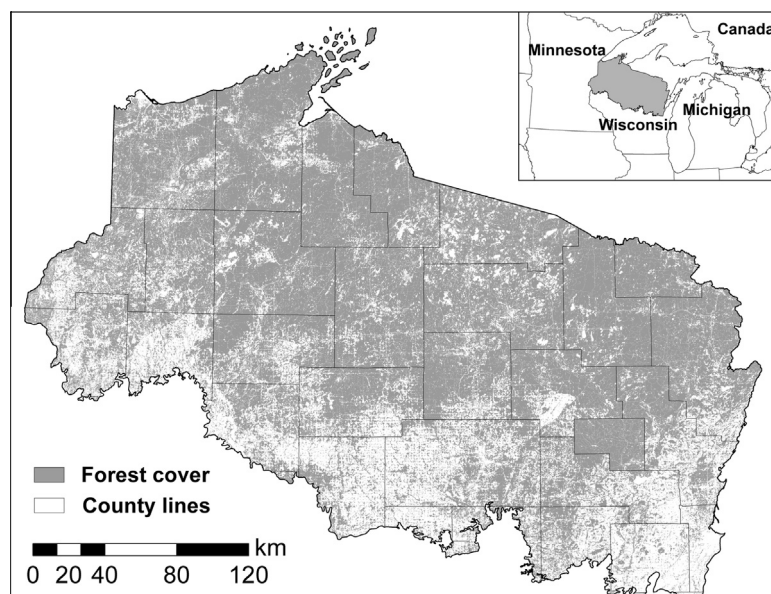


Fig. 1. Study area: northern Wisconsin Laurentian Mixed Forest Ecoregion.

To do this, we evaluated the potential habitat of forest breeding birds on simulated landscapes built with a spatially-explicit economic model of land use change.

2. Methods

2.1. Study area

Our study area included most of northern Wisconsin, USA, and is part of the Laurentian Mixed Forest Ecoregion (Bailey, 1995; Fig. 1). This area encompasses 7 million ha, 4.6 million of which were classified as forest in the 2001 National Land Cover Database (NLCD; Multi-Resolution Land Characteristics Consortium, <http://www.epa.gov/mrlc/nlcd-2001.html>). Extensively logged in the first half of the 20th century, the study area has since largely reverted to forests that have re-grown on former clear-cuts and abandoned fields (Radeloff et al., 2005). Common land uses included forestry, recreation, small private woodlots, and agriculture on the best soils. A substantial portion of the study area's forested land was publicly owned (35%), 5% was owned by American Indian tribes, and 60% was in non-tribal, private properties. On these private lands, second-home building has flourished since the 1950s, with development concentrated along lakeshores and resulting in substantial forest fragmentation (Radeloff et al., 2005).

2.2. Study species

As a strategic approach to encourage regional conservation planning, the U.S. Congress mandated in 2001 that in order to receive federal funding for wildlife conservation, each state must develop a Wildlife Action Plan. In Wisconsin, the State Wildlife Action Plan identified 152 vertebrate species of greatest conservation need, 84 of which were birds, and the goal is to conserve these species and their habitat before they become rare and require more costly protection (Wisconsin Department of Natural Resources, 2005). Of the 84 avian species of greatest conservation need in Wisconsin, 20 regularly breed in northern forests (Table 1), and

of those, 15 are migratory, and five are year-long residents. We used distribution models that had recently been developed for these 20 species (Beaudry et al., 2010). These models map potential habitat using data on landscape features, landscape patterns, and land cover. We first obtained general habitat requirements from published studies, breeding bird atlases, and species accounts, and organized that information into three nested habitat components that reflect levels of specificity, category resolution and data availability:

- (1) *Habitat groups* are broad vegetation cover types (e.g. deciduous, mixed or coniferous forest) that capture the general habitat requirements for a given species. A species may rely on more than one habitat group. Habitat groups' distributions are well mapped at the regional scale.
- (2) *Constraints* are species-specific modifiers to the habitat groups, and refine habitat requirements by taking into account the more specific conditions needed by birds (e.g. edge-sensitivity, exclusion of some stand types, proximity to water). Constraints refine habitat models using parameters that are mapped at broad spatial scales.
- (3) *Intrinsic elements* are fine scale habitat selection requirements. These elements are not usually mapped at the regional scale, but most can be maintained within habitat groups under appropriate management (e.g. snags, understory vegetation).

We combined habitat groups and habitat constraints into habitat distribution models that identified potential habitat at a 30-m resolution. Each species was associated with one or more habitat groups corresponding to the 2001 NLCD land cover classes (Multi-Resolution Land Characteristics Consortium, <http://www.epa.gov/mrlc/nlcd-2001.html>). We then extracted areas by applying the identified habitat constraints. For some species constraints included area sensitivity and edge effects, modeled using morphological image processing applied to the 2001 NLCD image classification (Vogt et al., 2007). For other species we used tree species composition from the Wisconsin Initiative for Statewide

Table 1

Northern Wisconsin forest breeding study species, with amount of modeled potential habitat and dominant habitat association.

Species	Code	Scientific name	Potential habitat (ha) ^a	Dominant habitat association ^a
Black-backed Woodpecker	BBWO	<i>Picoides arcticus</i>	198,097	Boreal forest ^b
Black-billed Cuckoo	BBUC	<i>Coccyzus erythrophthalmus</i>	1,721,958	Edge habitat
Black-throated Blue Warbler	BTBW	<i>Dendroica caerulescens</i>	446,221	Interior deciduous
Blue-winged Warbler	BWWA	<i>Vermivora pinus</i>	2,879,657	Early successional ^c
Boreal Chickadee	BOCH	<i>Poecile hudsonica</i>	130,474	Boreal forest
Brown Thrasher	BRTH	<i>Toxostoma rufum</i>	344,630	Edge habitat
Canada Warbler	CAWA	<i>Wilsonia canadensis</i>	570,187	Mixed coniferous-deciduous forest
Cerulean Warbler	CEWA	<i>Dendroica cerulea</i>	511,537	Deciduous forest ^d
Connecticut Warbler	CONW	<i>Oporornis agilis</i>	326,752	Boreal forest
Golden-winged Warbler	GWWA	<i>Vermivora chrysoptera</i>	2,413,886	Early successional
Least Flycatcher	LEFL	<i>Empidonax minimus</i>	2,425,749	Deciduous forest
Northern Goshawk	NOGO	<i>Accipiter gentilis</i>	1,881,216	Large forest blocks
Olive-sided Flycatcher	OSFL	<i>Contopus cooperi</i>	261,734	Coniferous forest ^e
Red Crossbill	RECR	<i>Loxia curvirostra</i>	388,902	Coniferous forest
Red-shouldered Hawk	RSHA	<i>Buteo lineatus</i>	850,095	Deciduous forest
Spruce Grouse	SPGR	<i>Falcapennis canadensis</i>	155,527	Boreal forest
Veery	VEER	<i>Catharus fuscescens</i>	1,739,160	Deciduous forest
Whip-poor-will	WHIP	<i>Caprimulgus vociferus</i>	2,394,748	Various forest habitat
Wood Thrush	WOTH	<i>Hylocichla mustelina</i>	2,638,032	Deciduous forest
Yellow-billed Cuckoo	YBCU	<i>Coccyzus americanus</i>	1,721,958	Edge habitat

^a See methods in Beaudry et al. (2010).

^b Forest with boreal-forest associated trees such as white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*).

^c Young forest often dominated by trembling aspen (*Populus tremuloides*), cherry (*Prunus* sp.), and white birch.

^d Forest dominated by broad-leaf deciduous trees, commonly sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and red oak (*Quercus rubra*).

^e Forest dominated by red pine (*Pinus resinosa*) and eastern hemlock (*Tsuga canadensis*).

Cooperation on Landscape Analysis and Data (WISCLAND, <http://www.sco.wisc.edu/wiscland>) and the U.S. Forest Service Forest Inventory Analysis data (Miles et al., 2001).

Full occupancy of the resulting mapped potential habitat should not be expected. Our model structure was centered on potential habitat, and was not influenced by variations in bird occupancy associated with weather, metapopulation dynamics, or other factors affecting models relying on correlations between habitat variables and animal occupancy or abundance (Early et al., 2008). However, independently acquired empirical data were used in model training and evaluation. Out of the 20 models, eight showed a significant correlation between the model and independently obtained point-count locations, and seven had too few empirical data to permit a meaningful evaluation. Models for species associated with mature or interior forest performed best, while models for edge-associated and early successional species performed unevenly. See Beaudry et al. (2010) for details on model development and evaluation and Appendix A in Supplementary Content for maps of the potential habitat models.

2.3. Econometric model and landscape simulations

In prior work, we build an econometric model to estimate the effects of net returns from five land uses (cropland, pasture, forest, urban, or rangeland) on decisions by private landowners to allocate their land to a different use (Lubowski, 2002; Lubowski et al., 2008; Radeloff et al., 2012). The model was parameterized with data from the U.S. Department of Agriculture's Natural Resources Inventory (NRI), a nation-wide survey of the status, conditions, and trends of land, soil and water on private land repeated at 5-year intervals during 1977–1997 on 844,000 plots (Nusser and Goebel, 1997). For each county in the conterminous U.S., estimates of real per-acre net revenues between 1992 and 1997 for each of the five land uses were assembled (Lubowski, 2002). This information was used to estimate land-use change probabilities for each county and land capability class, which is a measure of soil quality and agriculture potential (U.S. Department of Agriculture, 1973). The land capability class allowed for plot-level deviations from the county-averaged discounted net returns per land use type. These net returns are the average annual profit (revenue less costs) observed in each county for each land use, including federal agricultural subsidies for crops. The econometric model was specified as a series of multinomial logit models, one for each land use, to express a choice of keeping a cell to the same land use or to transition to a different one. Finally, a random variable was included to account for unobservable factors, for example private non-market benefits from the land such as recreation and aesthetics (Lubowski et al., 2006; Radeloff et al., 2012). We assumed static land use on federal and tribal lands because the NRI does not monitor land use there.

We used the econometric model to create land-use transition probability matrices for each county and each land capability class. Through matrix multiplication we projected these matrices over a 50-year period. Each element of the matrix provided the probability that a parcel starting in one land use will end up in a different land use, accounting for all possible outcomes (except for transitions from urban to any other land use, as it was not observed in the NRI data).

In addition to a baseline scenario (i.e., where the net revenue values for land were held constant at the 1992–1997 levels used to estimate the econometric model), we identified two economic scenarios to explore the effects of policies on bird habitat. First, the Forest Incentive scenario imposed on the baseline scenario a \$247.11/ha (\$100/acre) subsidy for afforestation and a \$247.11/ha tax on deforestation. This type of subsidy/tax combination simulated efforts to boost carbon sequestration. To explore the effects of various incentive levels, the Forest Incentive scenario was

repeated for incentive values of \$0 to \$400/ha in \$25/ha increments. Second, the Urban Growth scenario is based on a 25% increase in net returns for urban uses, which could occur with increases in population or income growth.

We used landscape simulations based on the matrices of estimated transition probabilities to depict future land use change (Fig. 2). The 2001 NLCD, a satellite derived land cover classification grid, provided a land use starting point for the landscape projections. We resampled the 30-m grid to 100-m cells (1 ha), to resemble the average patch size of land use changes (Radeloff et al., 2012). We used the Soil Data Mart (National Resources Conservation Service) as our soil quality data source. Using the econometric model we generated a set of transition probabilities for each 100-m grid cell, based on land use in 2001, soil quality rating, and county. We then simulated land use change stochastically, based on the fitted transition probabilities, for 50 years. For example, suppose a cell is matched with an estimated probability of developing equal to 0.1. The simulations repeat the land-use decision many times such that the parcel will be in a developed use during 10% of the simulations. When applied to the entire landscape, the output was a number of landscape projections (one for each simulation), all consistent with the stochastic decision rules generated by the underlying econometric land use model (Lewis and Plantinga, 2007). We conducted 20 landscape projections for each scenario, because initial results showed that sample size sufficient for the metrics' standard deviations to level off (Radeloff et al., 2012). In summary, each landscape projection had a spatial resolution of 1 ha, consistent with the county-level transition probabilities but modified by the finer-grained soil data.

2.4. Analysis

For each landscape simulation from all three scenarios, we quantified forest loss, and applied that loss to each forest breeding bird potential habitat model. We calculated potential habitat loss mean and standard deviation for the 20 projections of each scenario \times species combination. We correlated, for each species, proportional potential habitat loss with total amount of potential habitat using a Pearson Product Moment correlation. We used a one-way ANOVA with a Holm–Sidak multiple comparisons test to compare the mean potential habitat change resulting from the Urban Growth and Forest Incentive scenarios to the loss resulting from the baseline scenario. We completed all spatial analyses using GDAL (Open Source Geospatial Foundation), Numerical Python (NumPy.org), and ArcGIS (ESRI Inc.), and conducted statistical analyses using SYSTAT 12 (Systat Software Inc.).

3. Results

Our 50-yr projections suggested that on average 438,705 ha (SD: 577) of forest will be lost under the baseline scenario, which represents almost 9.5% of the forest cover in the study area. We observed a predicted forest loss of 430,263 ha (SD: 538) for the Forest Incentive scenario, and 445,751 ha (SD: 520) under the Urban Growth scenario. This represents 1.9% less loss for the Forest Incentive scenario compared to baseline, and 1.6% more loss to urban use for the Urban Growth scenario.

The amount of potential habitat in the study area varied widely by species, with species dependent on boreal forest elements having the smallest amount of potential habitat (e.g., Spruce Grouse, Black-backed Woodpecker, Boreal Chickadee all with <200,000 ha; Table 1). In contrast, species relying on deciduous forests and edge habitat had comparatively large amounts of potential habitat (e.g., Least Flycatcher, Blue-winged Warbler, Wood Thrush all with >2 million ha; Table 1).

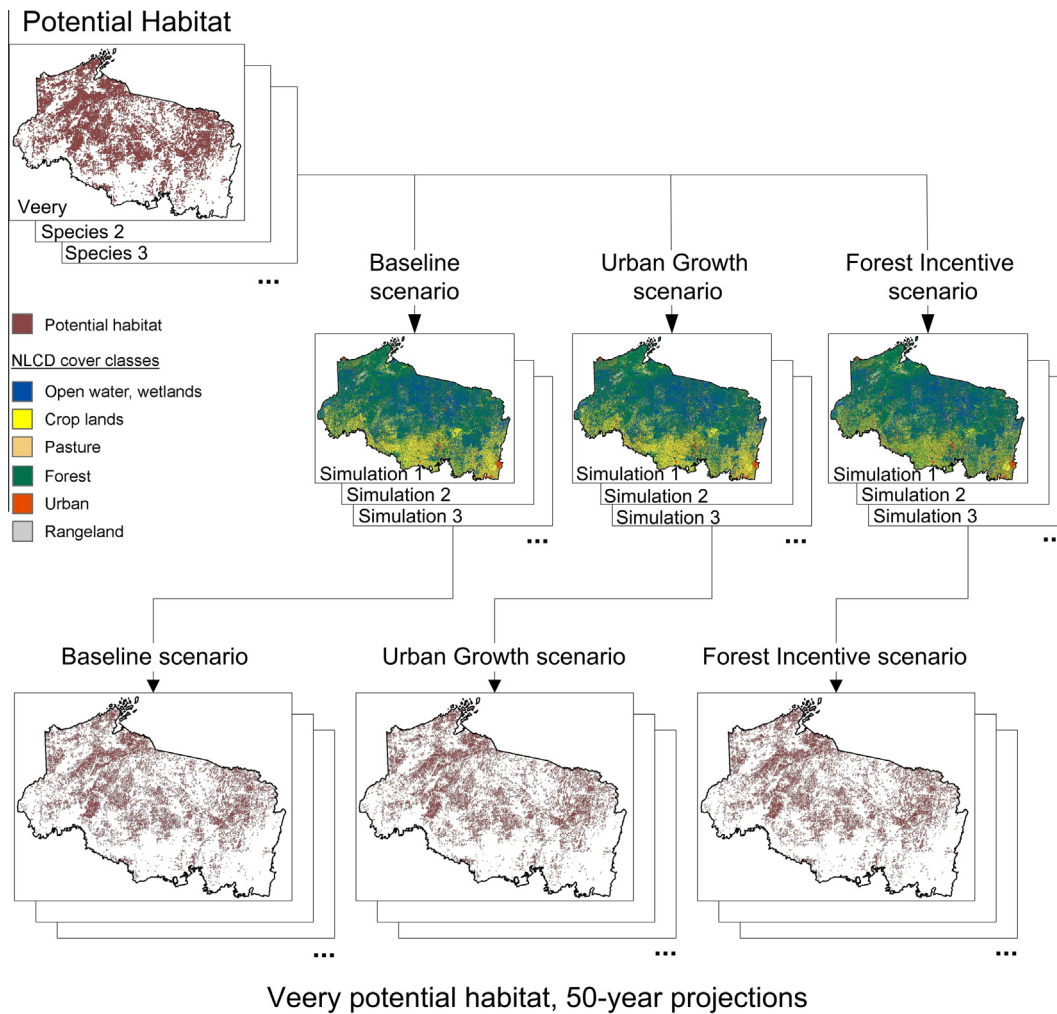


Fig. 2. Analysis flowchart, with species-specific potential habitat models as starting point. An econometric model was used to estimate land use transition probabilities for three scenarios, and from these transitions 20 projections were simulated for a period of 50 years. Forest loss incurred in each simulation was then applied to each species potential habitat map.

The amount of potential habitat was significantly correlated with the amount of habitat loss, with species with more potential habitat experiencing proportionally more habitat loss (for baseline scenario, Pearson correlation $r = -0.646$, $p = 0.002$). Notable exceptions to that relationship were Brown Thrasher, which showed both a low amount of potential habitat, and a large amount of habitat loss, and both species of Cuckoo, which are projected to experience less habitat loss than expected based on the amount of potential habitat (Fig. 3).

In general, species relying on boreal forests were projected to experience 3% or less habitat loss based on baseline projections (Fig. 3). Species associated with the study area's more common deciduous forests, such as Veery, Least Flycatcher, Wood Thrush, and Blue-winged Warbler, were forecasted to suffer proportionally greater habitat loss, around 6–8% of their potential habitat.

For 16 species out of the 20, the Urban Growth scenario led to a greater habitat loss, while the Forest Incentive scenario resulted in a reduced loss of habitat (Fig. 3). For Connecticut Warbler, Black-backed Woodpecker, and Red Crossbill, only the Urban Growth Scenario had a significant (negative) effect compared to the baseline scenario. For Boreal Chickadee, it was the Forest Incentive scenario that had a significant (positive) effect. For all species the reported effects were statistically significant but small, with a maximum difference in habitat loss of 2.2% for Blue-winged

Warbler (Forest Incentive scenario vs. Baseline), summing up to a difference of approximately 6400 ha.

When increasing the incentive value in the Forest Incentive scenario, two patterns were apparent. Deciduous or mixed-forest dependent species all showed an almost linear relationship where less habitat loss was observed at higher incentive value (Fig. 4). The difference between the extremes values (\$0 and \$400/ha) was highest for Black-throated Blue Warbler with a difference of 0.85% in habitat loss between the high and low Forest Incentive scenarios. The habitat of coniferous forest dependent species showed no response when the monetary incentives were below approximately \$200/ha (Fig. 4). Above that value, most showed a small decrease in habitat loss with increasing incentive value. Connecticut Warbler habitat did not show any clear relationship with changes in forest incentive values.

4. Discussion

Based on a record of landowner decisions, current land use and land conditions, and prices obtained from alternative uses, our 50-yr landscape projections suggest a loss of potential habitat for all the northern Wisconsin forest breeding birds examined. For some of the study species, the projected loss of potential habitat is of particular concern. The Golden-winged Warbler under the baseline

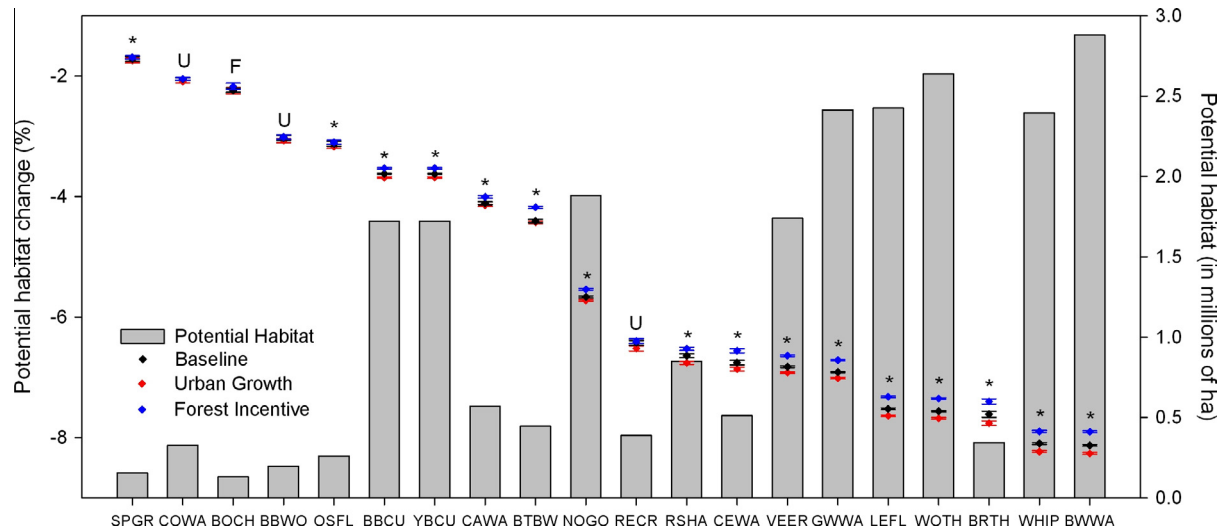


Fig. 3. For 20 northern Wisconsin species of forest breeding birds, mean habitat change expected between 2001 and 2052 from an econometric model of land use transitions (three scenarios are shown; left axis), and amount of potential habitat estimated for 2001 (right axis). Error bars are standard deviations based on 20 simulations per species \times scenario combination. The letters U (Urban Growth) and F (Forest Incentive) identify the mean habitat change for that scenario as significantly different from Baseline. An asterisk indicates that both the Urban Growth and Forest Incentive scenarios were significantly different from the Baseline scenario.

scenario is projected to lose 6.9% of its potential habitat over a 50-yr period, which is substantial given a annual population decline of -2.9% yearly since 1966 (Sauer et al., 2008). Wisconsin's conservation responsibility towards Golden-winged Warblers is high, as the state holds approximately 20% of the global population (Panjabi et al., 2005). Another neotropical migrant projected to suffer large potential habitat losses (6.8% under the baseline scenario), the Cerulean Warbler, has already declined by 4.1% annually between 1966 and 2007 (Sauer et al., 2008). The loss of potential habitat is possibly most consequential for the Northern Goshawk, a species for which all the current potential habitat must remain in suitable condition and occupied in order to meet Partners in Flight conservation objectives (Panjabi et al., 2005; Beaudry et al., 2010).

A surprising result was that the species with the least amount of potential habitat in northern Wisconsin were projected to have the smallest amount of habitat loss, proportionally. The observed pattern of large amount of habitat/high habitat loss may be due to the latitudinal distribution of forest types. Boreal forest occupied a small area in the northern part of the study region ($\sim 100,000$ ha) in counties far away from urban centers and major agricultural areas, which are thus less likely to experience land use change from forest to either urban or to agricultural use. Species such as Boreal Chickadee, Black-backed Woodpecker and Spruce Grouse rely on these rarer habitats and were projected to experience less habitat loss. Additionally, boreal forest bird species rely on, among other types of forests, lowland spruce forests which have soil types that prevent transition to urban or agriculture uses (for example, poorly-drained mucks and peats [Web Soil Survey, 2013]). Mixed coniferous–deciduous forests are also in the northern portion of the study area, occupying approximately 400,000 ha. Canada Warblers are associated with these mixed forests, and they showed an intermediate amount of habitat loss. The most common forest type was deciduous forest, with almost 3 million ha, home to a number of bird species that were predicted to proportionally lose the most habitat in the next 50 years under all three scenarios. This stronger effect of land use change is likely due to deciduous forests being more prevalent in the central and southern portions of the study area in counties where net revenues from urban and agricultural land uses were higher. Land in those counties is closer, in general, to urban centers, transportation networks, and existing agriculture, and has better soil quality making the transition from forest to agriculture more likely. Overall, this pattern of large amounts of

habitat combined with high habitat loss may be specific to our study area's geographic idiosyncrasies.

The land use policies that we examined could reduce (i.e., the Forest Incentive scenario) or worsen (i.e., the Urban Growth scenario) habitat loss had generally significant but surprisingly small effects on the projected potential habitat. We believe this may be because the differences in net returns between land uses were large enough in the baseline scenario that the modeled incentives (or disincentives) did not often meet the revenue threshold needed to trigger a change to a different use. The lesson from this is that if policies to decrease forest loss are to be implemented, the amount of the incentive (or disincentive in the case of a tax) has to be a high enough fraction of the baseline revenue in order to effectively force a substantial number of parcels to transition to a desired land use. Higher monetary incentives to maintain forests (the Forest Incentive scenarios) did indeed lead to lower habitat loss projected, most clearly for deciduous or mixed forest dependent species in an incremental manner with no apparent threshold. Species dependent on more northern habitats, whether boreal forests or coniferous stands, showed a weaker response to increased incentives, probably due to the much lower probabilities that these regions would experience transition to urban or agricultural use.

An alternative policy approach to influence land use could include local land use controls, such as zoning. A large number of local governments in the U.S. already use zoning ordinances. Zoning can produce significant ecological effects by regulating land use: for example, a minimum lakeshore frontage zoning rule in northern Wisconsin was estimated to result in lower residential density, higher coarse woody debris along the shoreline, and increased bluegill (*Lepomis macrochirus*) growth rate (Butsic et al., 2010). Zoning, however, is not uniformly effective over the entire landscape (Lewis et al., 2009b; Butsic et al., 2010), and must be targeted to areas where ecologically sensitive habitats exist and where there is an actual threat of land conversion. Additionally, zoning is usually governed at the county level, so regional conservation would require cooperation between multiple counties. Given that most states lack the institutional framework necessary to enable regional planning, this may be a difficult task.

We also caution that the modeled habitat loss is a conservative estimate of the likely effect on wildlife populations. The two most common types of land use transitions away from forest, towards urban and agriculture, both have strong negative effects on forest

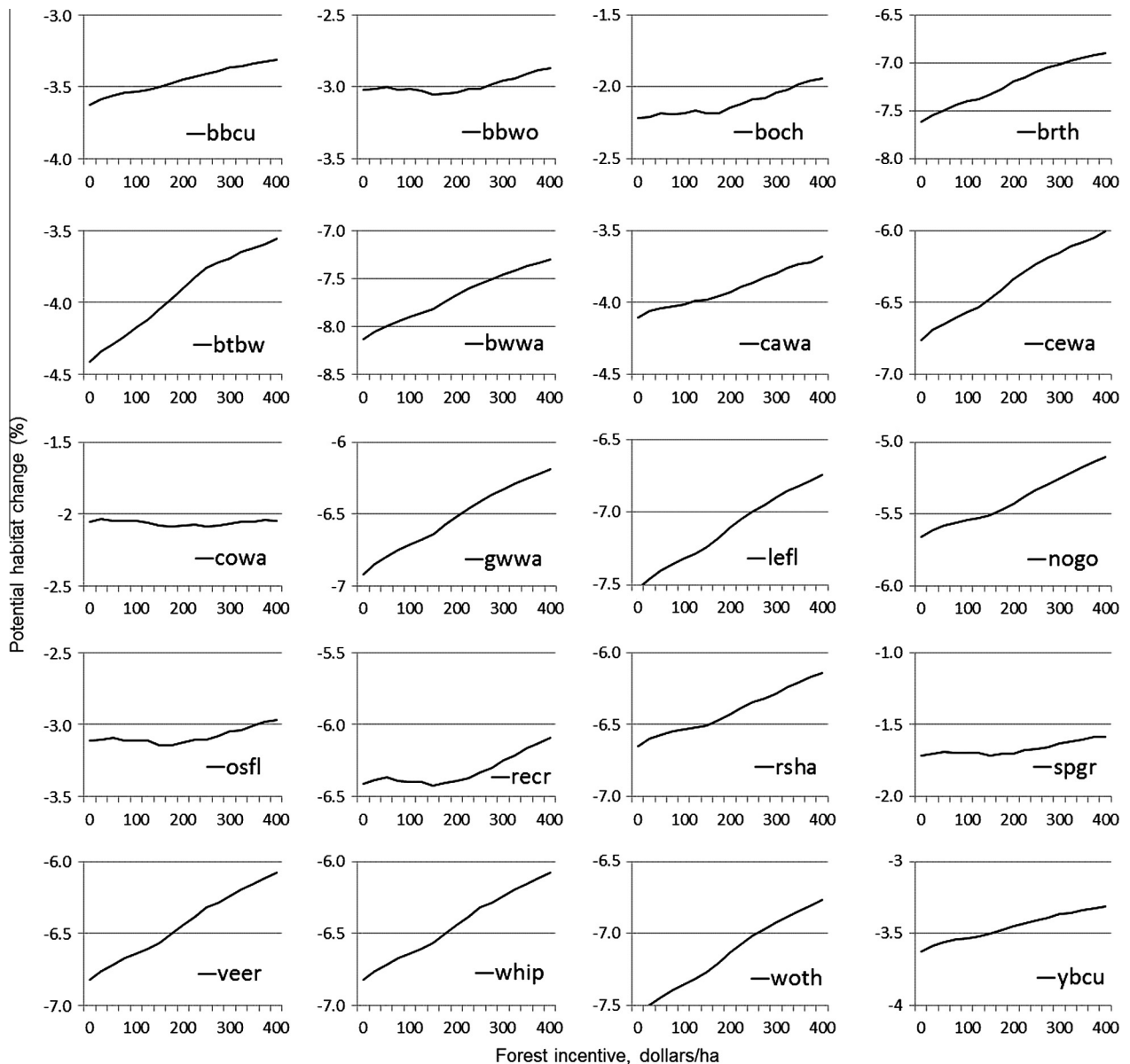


Fig. 4. For 20 northern Wisconsin species of forest breeding bird, mean habitat change expected between 2001 and 2052 from an econometric model of land use transitions under Forest Incentive scenarios with incentive values ranging from \$0 to \$400/ha, with \$25 increments.

bird habitat that go beyond the direct loss over the area affected. Rural housing development results in negative effects on many species of wildlife beyond the developed lot boundary (Theobald et al., 1997; Odell and Knight, 2001), including birds (Pidgeon et al., 2007) and anadromous fish (Lohse et al., 2008). Specific negative disturbances outside the housing lot include increasing wildlife predation from pets (Lepczyk et al., 2004), the introduction of invasive plant species that alter the surrounding forest composition (Hansen et al., 2005; Gavier-Pizarro et al., 2010), an increase in edge habitat and forest fragmentation due to the roads and driveways serving new development (Theobald, 2000; Hawbaker et al., 2006), as well as an increase in vehicle traffic (Foreman and Alexander, 1998). The transition to agriculture can change the conditions within adjacent forest, for example by altering temperature, moisture and light regimes a significant distance inside the forest from the edge (Matlack, 1993), subsidizing nest predators (Chalfoun et al., 2002), and creating pesticide drift harmful to understory plants (Grove et al., 2007).

In our analysis, grid cell characteristics, such as current land use and soil type, influenced the transition to an alternative land use, but the spatial arrangement of these characteristics relative to other nearby cells was not simulated. In reality, spatial autocorrelation in land use is common (Overmars et al., 2003; Müller et al., 2009), with a given land use type more likely found next to an area with the same land use. Similarly, the patterns of habitat loss affect the value of the remaining habitat. For example, the conversion of an interior forest pixel has more deleterious effects on an edge-sensitive species than the conversion of a similar-sized parcel at the edge of that species' habitat. This absence of spatial autocorrelation in the analysis, both in the land use transition simulations and the estimated change in potential habitat loss, might lead to underestimated habitat losses. However, this bias is at least partially offset by the patterns of those areas that revert back to forest cover. These new forest cells issued from the conversion of agricultural areas back to forest represented a comparatively rarer transition during the simulations (approximately 4% of the transitions).

We did not integrate the effects this reforestation might have on bird potential habitat, as we could not forecast the time and successional path these transitioning lands will take to become forest bird habitat. The condition of abandoned agricultural land can be affected by the tree species involved, the presence of invasive shrub species, available seed banks in the soil, or by management intervention. Nevertheless, we suggest that the strength of our analysis is in the marked patterns of forest loss and their general effects on potential habitat, consistent with the broad spatial scale of the study area (i.e., the mapped results should not be used to interpret change over small, specific areas). In general, habitat loss has stronger negative effects than changes in spatial arrangement of habitat, including fragmentation (Fahrig, 1997; St-Laurent et al., 2009).

Ideally, existing spatial patterns of land use should be taken into account to make conservation incentives most effective (Lewis et al., 2009a). In our study's Forest Incentive scenario, any afforestation effort will be rewarded, regardless of where it is on the land. Concentrating conservation efforts spatially can lead to greater ecological benefits (Wu and Boggess, 1999). For example, the location of forested parcels could be arranged to provide more interior forest, less edge, and greater connectivity with other existing forest. Rewarding landowners with an agglomeration bonus for conserving adjacent parcels is an incentive mechanism that can lead to an effective spatial arrangement of the conserved land (Parkhurst and Shogren, 2007), and benefits for the landowner (Grout, 2009). Novel conservation incentive systems could also be evaluated and compared using the coupled economic-ecological linkage presented here but would require more complex simulation algorithms to account for neighborhood relationships. This approach could be used to investigate the effects of land use policies on other important ecological processes. In particular, coupled models could be further refined to evaluate the complex interactions between policy, land use change, and broad spatial scale ecological processes highly relevant to conservation, such as dispersal, gene flow, metapopulation dynamics, and metapopulation viability. Furthermore, we see great value in coupled models in helping to foresee the intricate relationships expected between global climate change, economics-driven land uses, land cover, and biodiversity.

To plan for effective land stewardship requires a long-term vision and sound ecologically-defined conservation targets, but also an understanding of land use's dynamic nature. Socio-economic factors can help us understand land use change, and we can use policies as economic levers to steer such change. We need to simultaneously address ecological and economic sustainability, without either of which the conservation of terrestrial biodiversity will fail.

Acknowledgements

We gratefully acknowledge support for this research by the NSF Couple Natural-Human Systems program, and by the Wisconsin Department of Natural Resources. We thank Steve Polasky for his help in initiating this project, and three anonymous reviewers for valuable comments.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.05.016>.

References

Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. *Science* 279, 2126–2128.

- Bailey, R.G., 1995. Description of the Ecoregions of the United States, second ed. Miscellaneous Publications No. 1391 (rev), U.S. Department of Agriculture, Forest Service, Washington, DC, USA.
- Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. *Trends Ecol. Evol.* 18, 327.
- Beaudry, F., Pidgeon, A.M., Radeloff, V.C., Howe, R.W., Mladenoff, D.J., Bartelt, G.A., 2010. Modeling regional-scale habitat of forest birds when land management guidelines are needed but information is limited. *Biol. Conserv.* 143, 1759–1769.
- Bockstael, N.E., 1996. Modeling economics and ecology: the importance of a spatial perspective. *Am. J. Agric. Econ.* 78, 1168–1180.
- Butsic, V., Lewis, D.J., Radeloff, V.C., 2010. Lakeshore zoning has heterogeneous ecological effects: an application of a coupled economic-ecological model. *Ecol. Appl.* 20, 867–879.
- Butsic, V., Gaeta, J.W., Radeloff, V.C., 2012. The ability of zoning and land acquisition to increase property values and maintain largemouth bass growth in an amenity rich region. *Landscape Urban Plan.* 107, 69–78.
- Chalfoun, A.D., Thompson III, F.R., Ratnaswamy, M.J., 2002. Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.* 16, 306–318.
- Chomitz, K.M., Gray, D.A., 1996. Roads, land use, and deforestation: a spatial model applied to Belize. *World Bank Econ. Rev.* 10, 487–512.
- Early, R., Anderson, B., Thomas, C.D., 2008. Using habitat distribution models to evaluate large-scale landscape priorities for spatially dynamic species. *J. Appl. Ecol.* 45, 228–238.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildlife Manage.* 61, 603–610.
- Foreman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* 29, 207–231.
- Gavier-Pizarro, G.I., Stewart, S.I., Huebner, C., Keuler, N.S., Radeloff, V.C., 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecol. Appl.* 20, 1913–1925.
- Grout, C.A., 2009. Incentives for spatially coordinated land conservation: a conditional agglomeration bonus. *West. Econ. Forum* 8 (fall), 29–36.
- Grove, B., Power, S.A., Buckley, G.P., Ghazoul, J., 2007. Effects of herbicide spray drift and fertilizer overspread on selected species of woodland ground flora: comparison between short-term and long-term impact assessments and field surveys. *J. Appl. Ecol.* 44, 374–384.
- Hansen, A.J., DeFries, R., 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecol. Appl.* 17, 974–988.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecol. Appl.* 15, 1893–1905.
- Hawbaker, T.J., Radeloff, V.C., Clayton, M.K., Hammer, R.B., Gonzalez-Abraham, C.E., 2006. Road development, housing growth, and landscape fragmentation in northern Wisconsin: 1937–1999. *Ecol. Appl.* 16, 1222–1237.
- Langpap, C., Hascic, I., Wu, J., 2008. Protecting watershed ecosystems through targeted local land use policies. *Am. J. Agric. Econ.* 90, 684–700.
- Lepczyk, C.A., Mertig, A.G., Liu, J., 2004. Landowners and cat predation across rural-to-urban landscapes. *Biol. Conserv.* 115, 191–201.
- Lewis, D.J., 2010. An economic framework for forecasting land use and ecosystem change. *Resour. Energy Econ.* 32, 98–116.
- Lewis, D.J., Alig, R.J., 2009. Empirical methods for modeling landscape change, ecosystem services, and biodiversity. *West. Econ. Forum* 8 (spring), 29–36.
- Lewis, D.J., Plantinga, A.J., 2007. Policies for habitat fragmentation: combining econometrics with GIS-based landscape simulations. *Land Econ.* 83, 109–127.
- Lewis, D.J., Plantinga, A.J., Wu, J., 2009a. Targeting incentives to reduce habitat fragmentation. *Am. J. Agric. Econ.* 91, 1080–1096.
- Lewis, D.J., Plantinga, A.J., Butsic, V., 2009b. The dynamic effects of open-space conservation policies on residential development density. *J. Environ. Econ. Manage.* 57, 239–252.
- Lohse, K.A., Newburn, D.A., Opperman, J.J., Merenlender, A.M., 2008. Forecasting relative impacts of land use on anadromous fish habitat to guide conservation planning. *Ecol. Appl.* 18, 467–482.
- Lubowski, R.N., 2002. Determinants of Land-use Transitions in the United States: Econometric Analysis of Changes among Major Land-use Categories. Ph.D. Dissertation, Harvard University, Cambridge, MA.
- Lubowski, R.N., Plantinga, A.J., Stavins, R.N., 2006. Land-use change and carbon sinks: econometric estimation of the carbon sequestration supply function. *J. Environ. Econ. Manage.* 51, 440–457.
- Lubowski, R.N., Plantinga, A.J., Stavins, R.N., 2008. What drives land-use change in the United States? A national analysis of landowner decisions. *Land Econ.* 84, 529–550.
- Lütolf, M., Nolliger, J., Kienast, F., Guisan, A., 2009. Scenario-based assessment of future land use change on butterfly species distributions. *Biodivers. Conserv.* 18, 1329–1347.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Matlack, G.R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66, 185–194.
- Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.F., Woudenberg, S.W., Glover, J.F., Ezell, E.N., 2001. The Forest Inventory and Analysis Database Description and Users Manual. General Technical Report NC-218. U.S. Department of Agriculture, Forest Service, St. Paul, MN.
- Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis, World Resource Institute, Washington, DC, USA. <<http://>

- www.millenniumassessment.org/documents/document.354.aspx.pdf (accessed 09.08).
- Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. *Conserv. Biol.* 9, 279–294.
- Müller, D., Kuemmerle, T., Rusu, M., Griffiths, P., 2009. Lost in transition: determinants of post-socialist cropland abandonment in Romania. *J. Land Use Sci.* 4, 109–129.
- Nelson, E., Polasky, S., Lewis, D.J., Plantinga, A.J., Lonsdorf, E., White, D., Bael, D., Lawler, J., 2008. Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proc. Nat. Acad. Sci.* 105, 9471–9476.
- Noss, R.F., 1983. A regional landscape approach to maintain diversity. *Bioscience* 33, 700–706.
- Nusser, S.M., Goebel, J.J., 1997. The natural resources inventory: a long-term multi-resources monitoring programme. *Environ. Ecol. Stat.* 4, 181–204.
- Odell, E., Knight, R.L., 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. *Conserv. Biol.* 15, 1143–1150.
- Otte, A., Simmering, D., Wolters, V., 2007. Biodiversity at the landscape level: recent concepts and perspectives for multifunctional land use. *Landscape Ecol.* 22, 639–642.
- Overmars, K.P., de Koning, G.H.J., Veldkamp, A., 2003. Spatial autocorrelation in multi-scale land use models. *Ecol. Model.* 164, 257–270.
- Panjabi, A.O., Dunn, E.H., Blancher, P.J., Hunter, W.C., Altman, B., Bart, J., Beardmore, C.J., Berlanga, H., Butcher, G.S., Davis, S.K., Demarest, D.W., Dettmers, R., Easton, W., Gomez de Silva Garza, H., Iñigo-Elias, E.E., Pashley, D.N., Ralph, C.J., Rich, T.D., Rosenberg, K.V., Rustay, C.M., Ruth, J.M., Wendt, J.S., Will, T.C., 2005. The Partners in Flight handbook on species assessment, Partners in Flight Technical Series No. 3. <<http://www.rmbo.org/pubs/downloads/Handbook2005.pdf>>.
- Parkhurst, G.M., Shogren, J.F., 2007. Spatial incentives to coordinate contiguous habitat. *Ecol. Econ.* 64, 344–355.
- Phillips, S.J., Anderson, R.P., Shapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Pidgeon, A.M., Radeloff, V.C., Flather, C.H., Lepczyk, C.A., Clayton, M.K., Hawbaker, T.J., Hammer, R.B., 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. *Ecol. Appl.* 17, 1989–2010.
- Polasky, S., Camm, J.D., Garber-Yonts, B., 2001. Selecting biological reserves cost effectively: an application to terrestrial vertebrate conservation in Oregon. *Land Econ.* 77, 76–78.
- Radeloff, V.C., Hammer, R.B., Stewart, S.J., 2005. Sprawl and forest fragmentation in the U.S. Midwest from 1940 to 2000. *Conserv. Biol.* 19, 793–805.
- Radeloff, V.C., Nelson, E., Plantinga, A.J., Lewis, D.J., Helmers, D., Lawler, J.J., Withey, J.C., Beaudry, F., Martinuzzi, S., Butsic, V., Lonsdorf, E., White, D., Polasky, S., 2012. Economic-based projections of future land use in the conterminous US under alternative economic policy scenarios. *Ecol. Appl.* 22, 1036–1049.
- Ramankutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* 22, GB1003. <http://dx.doi.org/10.1029/2007GB002952>.
- Rittenhouse, C.D., Pidgeon, A.M., Albright, T.P., Culbert, P.D., Clayton, M.K., Flather, C.H., Huang, C., Masek, J.G., Stewart, S.J., Radeloff, V.C., 2010a. Conservation of forest birds: evidence of a shifting baseline in community structure. *PLoS ONE* 5 (8), e11938. <http://dx.doi.org/10.1371/journal.pone.0011938>.
- Rittenhouse, C.D., Thompson III, F.R., Dijak, W.D., Millsbaugh, J.J., Clawson, R.L., 2010b. Evaluation of habitat suitability models for forest passerines using demographic data. *J. Wildlife Manage.* 74, 411–422.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity – global diversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B., Ward, S.E., 2002. A conceptual model for conservation planning based on landscape species requirements. *Landscape Urban Plan.* 58, 41–56.
- Sauer, J.R., Hines, J.E., Fallon, J., 2008. The North American Breeding Bird Survey, Results and Analysis 1966–2007, Version 5.15.2008, USGS Patuxent Wildlife Research Center, Laurel, MD, USA.
- St-Laurent, M.H., Dussault, C., Ferron, J., Gagnon, R., 2009. Dissecting habitat loss and fragmentation effects following logging in boreal forest: conservation perspectives from landscape simulations. *Biol. Conserv.* 142, 2240–2249.
- Theobald, D.M., 2000. Fragmentation by inholdings and exurban development. In: Knight, R.L., Smith, F.W., Buskirk, S.W., Romme, W.H., Baker, W.L. (Eds.), *Forest Fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, Colorado, USA, pp. 157–174.
- Theobald, D.M., Miller, J.R., Hobbs, N.T., 1997. Estimating the cumulative effects of development on wildlife habitat. *Landscape Urban Plan.* 39, 25–36.
- US Department of Agriculture, 1973. Land Capability Classification. Soil Conservation Service, Agricultural Handbook No. 210, Washington, DC.
- US Department of Agriculture, 2013. Feed Grains Database. Economic Research Service <<http://www.ers.usda.gov/data-products/feed-grains-database.aspx>> (accessed 13.05).
- Vogt, P., Ritters, K.H., Estreguil, C., Kozak, J., Wade, T.G., Wickham, J.D., 2007. Mapping spatial patterns with morphological image processing. *Landscape Ecol.* 22, 171–177.
- Wätzold, F., Drechsler, M., Armstrong, C.W., Baugärtner, S., Grimm, V., Huth, A., Perrings, C., Possingham, H.P., Shogren, J.F., Skonhofs, A., Verboom-Vasiljev, J., Wissel, C., 2006. Ecological-economic modeling for biodiversity management: potential, pitfalls, and prospects. *Conserv. Biol.* 20, 1034–1041.
- Web Soil Survey, 2013. Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture. <<http://websoilsurvey.nrcs.usda.gov/>> (accessed 05.13).
- Wilcove, D., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48, 607–615.
- Wisconsin Department of Natural Resources, 2005. Wisconsin's Strategy for Wildlife Species of Greatest Conservation Need, Bureau of Endangered Resources, Pub-ER-641, Madison, Wisconsin, USA.
- Wu, J., Boggess, W.G., 1999. The optimal allocation of conservation funds. *J. Environ. Econ. Manage.* 38, 302–321.