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

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\section*{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 socioeconomic 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...
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.

![Figure 1](image_url) - 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 econometric 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 (Radloff 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 (Radloff 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>
<thead>
<tr>
<th>Species Code</th>
<th>Scientific name</th>
<th>Potential habitat (ha)</th>
<th>Dominant habitat association</th>
</tr>
</thead>
<tbody>
<tr>
<td>BBWO</td>
<td>Picoides arcticus</td>
<td>198,097</td>
<td>Boreal forest</td>
</tr>
<tr>
<td>BBCU</td>
<td>Coccothraustes virens</td>
<td>1,721,958</td>
<td>Edge habitat</td>
</tr>
<tr>
<td>BBBV</td>
<td>Dendroica caerulescens</td>
<td>446,221</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>BWWA</td>
<td>Verrvora pinus</td>
<td>2,879,657</td>
<td>Early successional</td>
</tr>
<tr>
<td>BOCH</td>
<td>Poecile hudsonica</td>
<td>130,474</td>
<td>Boreal forest</td>
</tr>
<tr>
<td>BERTH</td>
<td>Totostoma rufum</td>
<td>344,630</td>
<td>Edge habitat</td>
</tr>
<tr>
<td>CAWA</td>
<td>Wilsonia canadensis</td>
<td>570,187</td>
<td>Mixed conifer-deciduous forest</td>
</tr>
<tr>
<td>CEWA</td>
<td>Dendroica cerulea</td>
<td>513,537</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>CONW</td>
<td>Oporornis agilis</td>
<td>326,752</td>
<td>Boreal forest</td>
</tr>
<tr>
<td>GWWA</td>
<td>Vernivora chrysoptera</td>
<td>2,413,886</td>
<td>Early successional</td>
</tr>
<tr>
<td>LEFI</td>
<td>Empidonax minimus</td>
<td>2,425,749</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>NOSO</td>
<td>Accipiter gentilis</td>
<td>1,881,216</td>
<td>Large forest blocks</td>
</tr>
<tr>
<td>OSLE</td>
<td>Cottanus cooperi</td>
<td>261,734</td>
<td>Coniferous forest</td>
</tr>
<tr>
<td>RECR</td>
<td>Losia curvirostra</td>
<td>388,902</td>
<td>Coniferous forest</td>
</tr>
<tr>
<td>RSHA</td>
<td>Buteo lineatus</td>
<td>850,095</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>SPCR</td>
<td>Falco pennensis canadensis</td>
<td>155,527</td>
<td>Boreal forest</td>
</tr>
<tr>
<td>VEER</td>
<td>Cathares fuscescens</td>
<td>1,739,160</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>WHBP</td>
<td>Caprimulgus vociferus</td>
<td>2,394,748</td>
<td>Various forest habitat</td>
</tr>
<tr>
<td>WOTH</td>
<td>Hylocichla mustelina</td>
<td>2,638,032</td>
<td>Deciduous forest</td>
</tr>
<tr>
<td>YBCU</td>
<td>Coccothraustes americanus</td>
<td>1,721,958</td>
<td>Edge habitat</td>
</tr>
</tbody>
</table>

- See methods in Beaudry et al. (2010).
- Forest with boreal-forest associated trees such as white spruce (Picea glauca), balsam fir (Abies balsamea), and white birch (Betula papyrifera).
- Young forest often dominated by trembling aspen (Populus tremuloides), cherry (Prunus sp.), and white birch.
- 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).
- 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; Radloff 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 land capability (e.g., Least Flycatcher, Blue-winged Warbler, Wood Thrush). We correlated, for each species, proportional potential habitat loss with total amount of potential habitat (e.g., Spruce Grouse, Black-backed Woodpecker, Boreal Chickadee all with the smallest amount of potential habitat (e.g., Least Flycatcher, Blue-winged Warbler, Wood Thrush all with >2 million ha; Table 1).

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 × 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).
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
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/urban 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 (~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 exists 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...
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).

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.
We did not integrate the effects this reforestation might have on bird potential habitat, as we could not forecast the time and suc-
cessional 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 affores-
tation 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 loca-
tion of forested parcels could be arranged to provide more interior
forest, less edge, and greater connectivity with other existing for-
est. Rewarding landowners with an agglomeration bonus for con-
serving adjacent parcels is an incentive mechanism that can lead
to an effective spatial arrangement of the conserved land (Park-
hurst and Shogren, 2007), and benefits for the landowner (Grout,
2009). Novel conservation incentive systems could also be evalu-
ated and compared using the coupled economic-ecological linkage
presented here but would require more complex simulation algo-

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in
05.016.

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