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Where to put things? Spatial land management to sustain biodiversity and economic returns

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ARTICLE INFO

Article history:
Received 17 August 2007
Received in revised form
3 January 2008
Accepted 16 March 2008
Available online 21 May 2008

Keywords:
Conservation planning
Efficiency frontier
Land use
Tradeoffs
Terrestrial vertebrates
Survival probability

ABSTRACT

Expanding human population and economic growth have led to large-scale conversion of natural habitat to human-dominated landscapes with consequent large-scale declines in biodiversity. Conserving biodiversity, while at the same time meeting expanding human needs, is an issue of utmost importance. In this paper we develop a spatially explicit landscape-level model for analyzing the biological and economic consequences of alternative land-use patterns. The spatially explicit biological model incorporates habitat preferences, area requirements and dispersal ability between habitat patches for terrestrial vertebrate species to predict the likely number of species that will be sustained on the landscape. The spatially explicit economic model incorporates site characteristics and location to predict economic returns for a variety of potential land uses. We apply the model to search for efficient land-use patterns that maximize biodiversity conservation objectives for given levels of economic returns, and vice versa. We apply the model to the Willamette Basin, Oregon, USA. By thinking carefully about the arrangement of activities, we find land-use

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doi:10.1016/j.biocon.2008.03.022

patterns that sustain high levels of biodiversity and economic returns. Compared to the 1990 land-use pattern, we show that both biodiversity conservation and the value of economic activity could be increased substantially.

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1. Introduction

Over the past century, human-dominated land uses have spread rapidly across landscapes around the world. Approximately 38.2% of land globally is devoted to agriculture (FAO, 2007); excluding lands without vegetative cover (e.g., desert, rock, and ice) and boreal lands, this figure rises to approximately 50% (Tilman et al., 2001). Other land is devoted to urban development, roads, and timber lands. It is estimated that over 60% of the world's temperate forests and grasslands ecosystems have been converted to human-dominated uses (MEA, 2005).

The loss of natural habitat is a primary cause of the loss of terrestrial biodiversity (Wilson, 1988; Wilcove et al., 2000; Fuller et al., 2007). As human activity has expanded, patches of natural habitat have become smaller and more fragmented. The primary response of conservation biologists to the rapid loss of natural habitat has been to push for a system of protected areas that adequately protect biodiversity (e.g., Margules and Pressey, 2000; Margules and Sarkar, 2006; Sarkar et al., 2006). Ideally, these protected areas would contain sufficient habitat to provide refuge for all species, a sort of modern day Noah's Ark. However, the amount of area protected currently is relatively limited and is insufficient to sustain all of biodiversity. Only 6.1% of land globally is designated as wilderness area, national parks, national monuments, or wildlife refuges (IUCN Categories I–V, WRI, 2007). Further, designation of protected areas has often been based on scenic beauty, recreational value, historical or cultural significance, or simply because the land has not been in high demand for human use, rather than for its biological significance (Pressey, 1994; Scott et al., 2001). To better protect biodiversity as time goes on, future protected area decision-making must explicitly consider the needs of species.

Further, successful conservation requires taking biodiversity into account on the vast domain of "working lands" beyond protected areas (Franklin, 1993; Hansen et al., 1993; Miller, 1996; Reid, 1996; Wear et al., 1996; Daily et al., 2001, 2003; Rosenzweig, 2003; Polasky et al., 2005; Pereira and Daily, 2006). There are some land uses that generate valuable economic returns that are also consistent with at least some conservation objectives. Many species can coexist with some level of human activity and human alteration of the land. The broader conservation question, beyond where are the best places to locate reserves, is whether conservation objectives can be met on a landscape that includes both human altered lands and protected lands.

Land-use decisions on working lands are based primarily on economic criteria, whether it is local people using land to make a living or corporations using land to maximize profits. While land-use decisions based solely on economic returns are often detrimental to biodiversity, securing some economic return from land need not be mutually exclusive with biodiversity conservation. By thinking carefully about the pattern, extent, and intensity of human activities across the landscape, it may be possible to achieve important biodiversity conservation objectives while also generating reasonable economic returns.

In this paper, we integrate spatially explicit biological and economic models to analyze the consequences of alternative land-use decisions for both biodiversity conservation and economic objectives. We develop a biological model that evaluates how well a set of species can be sustained on a landscape given a spatially explicit pattern of land use. For each species of interest, we use the land-use pattern, species–habitat associations, and species range information to generate a map of suitable habitat patches for the species. We combine the map of habitat patches with species–area requirements and dispersal ability to predict the number of breeding pairs that could be supported by the landscape. We use the number of breeding pairs to estimate the likelihood that the species will be sustained on the landscape. The biological "score" is the expected number of species sustained on the landscape.

On the economic side, we develop a set of models that predict the likely economic returns for each land parcel under different land uses, including agriculture, forestry and rural-residential use. We use information on a parcel's soil, slope, elevation and location to estimate yields in both agriculture and forestry. We combine commodity prices data with estimates of yields and production costs to generate economic returns for these land uses. We use information on location, such as distance to cities, and characteristics of parcels to estimate returns for rural-residential use in parcels. The economic "score" is the sum of the present value of economic returns on each parcel in its designated use.

We combine results from the biological and economic models to search for efficient land-use patterns. An efficient land-use pattern is one that generates the maximum biological score for a given economic score (and vice versa). By maximizing the biological score over the entire range of possible economic scores we can trace out an efficiency frontier for the landscape. The efficiency frontier illustrates what can be achieved in terms of biological and economic objectives by carefully arranging the spatial allocation of activities across the landscape. The efficiency frontier also demonstrates the degree of inefficiency of other land-use patterns not on frontier.

We apply our approach to biological and economic data from the Willamette Basin in Oregon, USA. The Willamette Basin has extensive forests in the Coast and Cascade Mountain Ranges with agriculture and residential development dominant on the valley floor between the two ranges. In the application of the model to the Willamette Basin, we choose from one of nine alternative land uses for each of approxi-

mately 8000 land parcels. We find land-use patterns that can simultaneously generate high biological and economic scores. For example, we find a land-use pattern that can sustain an expected value of 248.5 species, 97% of the highest biological score found for the landscape, and $25.4 billion in economic returns, 92% of the maximum economic score, from the landscape. These results indicate limited tradeoffs between biodiversity conservation and economic returns when proper attention is given to spatial management. In contrast, an estimate of the 1990 land-use pattern sustains an expected value of 238.6 species and generates $17.1 billion in economic returns, significantly lower values on both dimensions than what is feasible.

While there is a large literature on systematic conservation planning (see Margules and Sarkar, 2006, for a recent review), much of this literature focuses on efficient representation of biodiversity in reserves. This literature typically does not incorporate analysis of working lands, either in terms of the landscape's ability to sustain species or in term of economic returns. For example, the classic reserve site selection approach attempts to minimize the area needed to represent a set of species within a reserve network or maximize species represented given a constraint on area in reserves (e.g., Camm et al., 1996; Church et al., 1996; Csuti et al., 1997b). Several papers have extended the basic reserve site selection approach by incorporating land acquisition costs and management costs into conservation planning (e.g., Ando et al., 1998; Balmford et al., 2000; Polasky et al., 2001; Moore et al., 2004; Nicholson et al., 2006; Naidoo and Iwamura, 2007; Nelson, 2007; see Naidoo et al., 2006, for a recent review). Other recent work has built upon metapopulation approaches to predict species persistence for a range of species as a function of landscape configuration of habitat (Cabeza and Moilanen, 2003; Moilanen et al., 2005; Nicholson et al., 2006; Jiang et al., 2007). Almost all prior work that combines biological models of species persistence and economic models to evaluate both conservation and economic returns focus on a single species or small set of species and a single economic activity such as forestry (e.g., Montgomery et al., 1994; Haight, 1995; Hof and Bevers, 1998; Marshall et al., 2000; Calkin et al., 2002; Moilanen and Cabeza, 2002; Nalle et al., 2004; Strange et al., 2006a,b; Holzkamper and Seppelt, 2007).

The papers closest to the present paper in terms of analyzing landscape configuration for a wide range of species and economic returns are those by Montgomery et al. (1999), Lichtenstein and Montgomery (2003) and Polasky et al. (2005). Montgomery et al. (1999) analyze tradeoffs between habitat for species and economic returns considering area but not spatial pattern of habitat. Lichtenstein and Montgomery (2003) analyze forestry versus conservation and include a bonus for contiguous habitat. Polasky et al. (2005) use similar versions of the biological and economic models described in this paper but analysis is restricted to a 14×14 simulated landscape with three alternative land uses.

In the next section of the paper we describe the biological and economic models as well as the optimization algorithms used to find efficient land-use patterns. Section 3 describes the data for the application of the approach in the Willamette Basin. Section 4 contains results. We conclude with a discussion of the methods and results in Section 5.

2. Methods

We begin by partitioning the planning region into a set of distinct land parcels, $j = 1, 2, \ldots, J$. Land parcels may be delineated on the basis of ownership boundaries, dominant vegetation cover, or other variables, or by overlaying a regular hexagon or square grid pattern. In the application to the Willamette Basin, we delineate boundaries on the basis of mapped dominant vegetation cover in 1990 to create homogeneous land cover within a parcel (ORNHIC, 2000).

We select a land use for each parcel in the planning region, with land uses denoted by i, $i = 1, 2, \ldots, I$. In the Willamette Basin application we consider nine land uses: (1) orchard/vineyard agriculture, (2) grass seed agriculture (the Willamette Basin has extensive area devoted to grass seed production), (3) pasture, (4) row-crop agriculture, (5) 45-year rotation managed forestry, (6) rural-residential use, (7) conservation to create the dominant potential natural vegetation in the parcel, (8) conservation to recreate conditions at the time of EuroAmerican settlement in the parcel, or (9) conservation to maintain the 1990 land cover in the parcel. The basic approach can be readily changed to include a different set of land uses. Land uses should be included in an application if they make up a significant fraction of the landscape and have significantly different impacts in either the biological or economic dimension.

We define a land-use pattern for the landscape as a land-use choice for each land parcel in the planning region. The land-use pattern is the primary input for both the biological and economic models.

For the biological model, we convert land use into land cover. Land covers are denoted by k, $k = 1, 2, \ldots, K$. For all land uses except conservation, land use i maps directly into land cover k; $i = k$. So, for example, when land use is row-crop agriculture, the land cover is also row-crop agriculture. For conservation, however, there are multiple possible land covers that reflect the different types of natural habitat in the region. In the Willamette Basin application, we include eight potential conservation land covers: oak savanna ($k = 7$), prairie ($k = 8$), old growth conifer ($k = 9$), mixed conifer and deciduous ($k = 10$), oak and other hardwood ($k = 11$), riparian forest ($k = 12$), emergent marsh ($k = 13$), and shrub/scrub ($k = 14$). The biological model uses the spatial pattern of land cover from a particular land-use pattern, along with species-specific characteristics to determine whether a species will likely be sustained in the planning region.

For the economic model, land use on the parcel and characteristics of the parcel determine economic returns for the parcel. Details of the biological model and the economic model are explained in the following sections.

2.1. *The biological model*

The biological model evaluates how well a set of species can be sustained on a landscape given the pattern of land cover. We keep the biological model relatively simple because we are interested in application to a large set of species. The biological model requires three species-specific traits: (a) species–habitat compatibility (what land covers are considered habitat for the species), (b) the amount of habitat required for a breeding pair,

and (c) the ability of the species to move between patches of habitat. The model is developed for application to terrestrial vertebrate species and would be less appropriate for applications to plants or many invertebrate species. We use the following steps to combine the species-specific information with the land-cover pattern to calculate the probability that a species will be sustained on the landscape:

(i) define which parcels contain habitat for a species by using information about species–habitat compatibility and land cover;
(ii) combine all adjacent parcels containing habitat for a species into a habitat patch;
(iii) calculate upper and lower bounds for the number of breeding pairs on the landscape if all habitat patches were completely connected or completely isolated;
(iv) calculate a connectivity score for the landscape based on the distance between patches and the dispersal ability for the species;
(v) calculate the number of breeding pairs for a species on the landscape using the connectivity score to weight the upper and lower bounds;
(vi) convert the number of breeding pairs for a species on the landscape into the probability that a species will be sustained on the landscape through use of a saturating function.

Steps (i) and (ii) define habitat patches for a species. Steps (iii)–(v) take account of the spatial pattern of habitat and species dispersal ability to adjust for fragmentation. Step (vi) converts the score for each species to a common scale (measured between 0 and 1) to facilitate comparisons of land-use plans that affect multiple species.

We begin by defining what constitutes habitat for a species, which depends on both biophysical characteristics and land cover. A parcel is potentially suitable habitat for a species if it is in the species' geographic range and it provides access to water resources when necessary. Define the habitat indicator variable I_{sj} as equal to 1 if parcel j is potentially suitable habitat for species s, and 0 otherwise. Let H_{sj} equal 1 if parcel j is in the geographic range of species s and 0 otherwise. The geographic range can be defined by abiotic niche space and/or the outer envelope of a species' point locality data on the landscape (Rondinini et al., 2006). Ideally, geographic range is defined by abiotic niche space; otherwise range will be defined partly by historical patterns of habitat destruction and not entirely by the climatic and other conditions that determine where a species could persist with appropriate habitat. Water access is an important factor for many amphibians and other water sensitive species. Let W_s equal 0 if species s is a water sensitive species and 1 otherwise. Let R_j equal 1 if parcel j contains or is immediately adjacent to a water feature (e.g., stream, pond, etc.) and 0 otherwise. Therefore, potential habitat suitability for species s in parcel j is defined as

$$I_{sj} = \max\{W_s, R_j\} H_{sj}. \quad (1)$$

This indicator variable could be modified to include other important features for particular species as desired (e.g., does a parcel include interior forest habitat important for some bird species).

Whether potentially suitable habitat is actually habitat for species s also depends on land cover. Define $C_s(k_j)$, $0 \leqslant C_s(k_j) \leqslant 1$, as the habitat compatibility score for species s in parcel j with land cover k. In the application in this paper, the habitat compatibility score, $C_s(k_j)$, can take on values of 0 (non-habitat), 0.5 (marginal habitat for breeding and feeding), or 1 (prime habitat for breeding and feeding). Parcel j contains habitat for species s when $I_{sj}C_s(k_j) > 0$.

A habitat patch for species s is formed by combining all contiguous parcels that contain habitat for species s. We use habitat patches as the basic unit of analysis for the biological model. The number of breeding pairs of species s that habitat patch n_s can support ($n_s = 1, 2, \ldots, N_s$) is defined as

$$Z_{sn_s} = \sum_{j \in n_s} \frac{A_j I_{sj} C_s(k_j)}{AR_s}, \quad (2)$$

where A_j is the area of parcel j, and AR_s is the area needed by a breeding pair of species s for typical breeding and feeding activities. The numerator in Eq. (2) represents the effective area of habitat for species s in habitat patch n_s, which equals total area of the patch if $I_{sj}C_s(k_j) = 1$ for all parcels, but will be less if $C_s(k_j) = 0.5$ in some parcels that form the patch. Dividing the effective area by AR_s yields the number of breeding pairs of species s that can utilize habitat patch n_s.

The number of breeding pairs of a species that can be supported on the landscape is a function of the number of breeding pairs that habitat patches could support in isolation, the distance between habitat patches, and the species' dispersal ability. The maximum number of breeding pairs on the landscape for species s, assuming no dispersal limitations between habitat patches, is defined as the sum of the number of breeding pairs for species s across all habitat patches:

$$ZMax_s = \sum_{n_s=1}^{N_s} Z_{sn_s}. \quad (3)$$

The calculation of the maximum number of breeding pairs assumes no penalty for fragmentation, i.e., all habitat for species s is contained in a single habitat patch.

The calculation of the minimum number of breeding pairs on the landscape assumes the opposite extreme of no dispersal so that each habitat patch exists in isolation. Let γ_s represent the number of breeding pairs necessary to sustain a local population of species s in an isolated patch and let ψ_{n_s} be an indicator function that is equal to 1 if $Z_{sn_s} \geqslant \gamma_s$, and equal to 0 otherwise. The minimum number of breeding pairs on the landscape is then defined as

$$ZMin_s = \sum_{n_s=1}^{N_s} Z_{sn_s} \psi_{n_s}. \quad (4)$$

For large values of γ_s, $ZMin_s$ can be 0. On the other hand, as γ_s approaches 0, $ZMin_s$ approaches $ZMax_s$. In the latter case, the number of breeding pairs for species s will depend only on the total amount of habitat and not its spatial pattern.

The connectivity measure on the landscape for species s is derived from both the inter-patch distances and the dispersal abilities of a species and is defined as

$$D_s = \frac{\left(\sum_{n_s=1}^{N_s}\sum_{m_s=1}^{N_s} \exp(-\alpha_s d_{m_s n_s}) Z_{sm_s}\right)}{N_s ZMax_s}, \quad (5)$$

where $d_{m_s n_s}$ is the Euclidean distance between patch m_s and patch n_s, and α_s represents the reciprocal of the mean dis-

persal ability of species s. The landscape connectivity measure, D_s, is scaled to lie between 0 and 1. If there were no distance between habitat patches, the numerator would simplify to $N_s ZMax_s$, making $D_s = 1$.[1] As the ability to disperse between patches decreases the measure of connectivity falls. At the other extreme, the numerator equals zero if all patches are so far apart that the species cannot disperse between them. Ideally, $d_{m_s n_s}$ would be a function not only of distance but of the difficulty of crossing the terrain between the two patches. Constructing such a measure, however, is computationally intensive because there are many possible routes a species could take between patches and the shortest "effective" path might be indirect.

The number of breeding pairs on the landscape for species s, Z_s, uses the measure of connectivity along the maximum and minimum number of breeding pairs on the landscape, and is defined as

$$Z_s = D_s ZMax_s + (1 - D_s) ZMin_s. \quad (6)$$

In a completely connected landscape $D_s = 1$ and the number of breeding pairs equals $ZMax_s$. If all suitable habitat parcels are completely isolated $D_s = 0$, then the number of breeding pairs on the landscape equals $ZMin_s$. Increasing γ_s reduces the number of habitat patches that count in the calculation of $ZMin_s$ and widens the gap between $ZMin_s$ and $ZMax_s$, increasing the importance of connectivity. When values of γ_s are high, a landscape of disconnected patches will produce low Z_s scores.

We convert the number of breeding pairs on the landscape for species s, Z_s, into a probability that the species will be sustained on this landscape, π_s, using a saturating function:

$$\pi_s = \frac{Z_s^g}{Z_s^g + \eta^g}, \quad (7)$$

where η is the half-saturating constant (the landscape score yielding a survival probability of 0.5), and g is a constant that determines the shape of the saturating function for s. Increasing g leads to a more step-like function with a threshold value for a viable population size. In the Willamette Basin application, we set parameters η and g so there is a 50% probability of being sustained given a population of 500 breeding pairs and a 95% probability of being sustained given a population of 1000 breeding pairs: $\eta = 500$ and $g = 4.25$. Ideally, we would differentiate η and g across species; however a lack of species-specific data prevents such differentiation.

Finally, we sum the probability scores across species to determine the landscape biological score, B, which is defined as the expected number of species sustained on the landscape:

$$B = \sum_{s=1}^{S} \pi_s. \quad (8)$$

2.2. The economic model

The economic model predicts the net present value of marketed goods and services from the landscape for a given land-use pattern. The economic model is really a series of models, one for each major economic activity on the landscape. For the Willamette Basin application, we model several forms of agriculture, forestry, rural-residential use, and conservation land use.

We made two important simplifications on the economic model. First, we focus solely on the value of marketed goods and services, largely because of data availability. In principle, the economic model could be expanded to include the value of *all* goods and services generated by the land-use pattern, including non-marketed "ecosystem services" (Daily, 1997; Daily et al., 2000; NRC, 2004; MEA, 2005). We do not do so here because of the difficulty, at present, of generating reliable estimates of value for non-marketed ecosystem services. Ongoing work, however, is addressing important ecosystem services so that it may be possible to be more inclusive in the near future (e.g., Nelson et al., forthcoming-a, forthcoming-b).

Second, the economic model does not include market price effects, which can have significant impacts on local land markets (Armsworth et al., 2006). The assumption of constant prices is a reasonable assumption when commodities are sold on a national or global market in which local production makes up a small fraction of the total supply. In the Willamette Basin application, this state of affairs is at least roughly true for the agricultural and forestry commodities under consideration but does not hold for the rural-residential land market. Housing prices in an area will be a function of the supply of rural-residential housing. In principle, we should reduce rural-residential housing value as the supply of housing increases on the landscape. We did not do so here in order to keep the economic model linear in land-use choice, which greatly simplifies our computational approach to finding efficient land-use patterns (discussed in Section 2.3).

2.2.1. Agriculture

We consider four types of agricultural land use: orchard/vineyard, grass seed, pasture, and row crop ($i = 1, 2, 3, 4$). We use a similar approach to calculate the net present value of economic returns for each agricultural land use. The net present value of an agriculture land use on parcel j depends upon productivity of the agricultural land use on the parcel, the price of the agricultural product, and production costs. Let y_j^i be the annual yield per unit area for the crop associated with agricultural land-use i on parcel j where yield is a function of parcel j's soil quality distribution and whether the parcel is irrigated. Agriculture revenue per unit area is given by $p_j^i y_j^i$ where p_j^i is the observed market price of the crop grown on agricultural land-use i. Let the annual per unit area cost of producing the crop associated with agricultural land-use i be given by c_j^i. We index p_j^i and c_j^i with j because the market price and cost of production may be affected by parcel j's location on the landscape. Assuming the crop is harvested every year, the net present value of economic returns from agricultural land-use i on parcel j is

$$V_j^i = \sum_{t=0}^{\infty} \frac{A_j(p_j^i y_j^i - c_j^i)}{(1+\delta)^t} = \frac{A_j(p_j^i y_j^i - c_j^i)(1+\delta)}{\delta} \quad (9)$$

for $i = 1, 2, 3, 4$, where $t = 0, 1, 2, \ldots$, indexes years, A_j is the area of parcel j, and δ is the annual discount rate. A discount rate accounts for the opportunity cost of time so that future cost

[1] $\sum_{n_s=1}^{N_s} \sum_{m_s=1}^{N_s} e^0 Z_{sm_s} = \sum_{n_s=1}^{N_s} \sum_{m_s=1}^{N_s} Z_{sm_s} = \sum_{n_s=1}^{N_s} ZMax_s = N_s ZMax_s.$

and benefits weigh less relative to current costs and benefits. Eq. (9) takes net revenue in year t from agricultural land-use i on parcel j, discounts them back to the present ($t = 0$), and sums over all years to generate the net present value through time for the parcel. We provide details of the agricultural value estimation method in Appendix A.

2.2.2. *Managed forestry*

The net present value of managed forestry ($i = 5$) depends upon the productivity of the parcel for growing timber, the price of timber, forestry rotation time, and the costs of harvesting timber. Timber yield on parcel j, $y_j^f(\tau, q_j)$, measured in terms of 1000 board feet (mbf) per unit area, depends upon the age of the timber stand when harvested (τ) and the parcel's forestry site index (q_j), which is based on soil, climate conditions and other physical conditions on the site (Curtis et al., 1981). In the Willamette Basin application, timber yield includes production from commercial thinning at age 35 and final harvest at age $\tau = 45$. The forest-site index used in this analysis assumes that *Pseudotsuga menziesii* (Douglas fir) is the harvested tree species.

Net timber revenue per unit area is given by $p_j^f y_j^f(\tau, q_j)$ where p_j^f is the net price of a mbf of timber. The net price of a mbf of timber is equal to

$$p_j^f = (p^f - l_j^f - h_j^f), \tag{10}$$

where p^f is the price per mbf of logs delivered to a mill, l_j^f represents logging costs per mbf of timber removed from parcel j, and h_j^f gives hauling costs per mbf of timber removed from parcel j; l_j^f is a function of the forest-site index and average slope, and h_j^f is a function of the distance from parcel j to the nearest processing mill. We also include maintenance costs of forestry production per unit area, which is given by $r^f(\tau)$. Maintenance costs are a function of the rotation age but not of site characteristics.

We assume even-aged forestry management such that $1/\tau$ of each forestry parcel is harvested each year. In reality, parcels will be harvested unevenly even when the landscape as a whole is managed for even flow of timber. Assuming even flow from each parcel considerably simplifies our modeling while capturing the spirit of an even flow of timber from the landscape (Adams et al., 2002). Given these assumptions, the net present value of managed forestry on parcel j with a rotation time of τ is

$$V_j^5 = \sum_{t=0}^{\infty} \frac{A_j(p_j^f y_j^f(\tau, f_j) - r^f(\tau))}{\tau(1+\delta)^t} = \frac{A_j(p_j^f y_j^f(\tau, f_j) - r^f(\tau))(1+\delta)}{\tau\delta}. \tag{11}$$

We provide details of the managed forestry value estimation method in Appendix A.

2.2.3. *Rural-residential use*

In Oregon state law mandates that all cities and towns have an urban growth boundary (UGB) inside of which all concentrated development is supposed to occur. Outside UGBs development is limited to rural-residential use with minimum lot size requirements. The present value of land in rural-residential use per unit area is a function of location in the landscape as well as site characteristics. In the Willamette Basin application, we capture the effects of location on the value of land in rural-residential use with several variables: (a) the proximity of a parcel to urban areas using a gravity index (Kline et al., 2001), and (b) the county in which the parcel is located. Site characteristics that may influence the value of land in rural-residential use on a parcel include: (a) mean elevation, (b) slope, (c) lot size, and (d) existing building density within the parcel. Using data on undeveloped rural-residential lot sales in the Willamette Basin from 1980 to 2003 as the dependent variable we estimate a hedonic property price function that depends on the location and characteristic variables described above. We include only undeveloped lots when estimating the hedonic model; otherwise our estimated parameters would include the value of the improvements (i.e., houses) rather than just the value of land. We use the estimated hedonic property price function to predict the value of land in rural-residential use in parcel j per unit area, v_j^d, as a function of parcel j's location and site characteristics. The estimated value of parcel j in rural-residential use is then found by taking the price per unit area and multiplying by the area of the parcel:

$$V_j^6 = A_j v_j^d. \tag{12}$$

We provide details on the hedonic estimation method and the estimated hedonic property price function in Appendix A.

2.2.4. *Conservation use*

We assume there are no economic returns generated on land used for conservation. As mentioned above, in principle one could include the value of recreation and ecosystem services, such as providing clean water, from conserved land. In the Willamette Basin application, however, we lacked spatially explicit data to include such benefits. Conservation may require active management to maintain a particular land cover and we include conservation management costs. Therefore economic returns to conservation use can be negative. Let the annual per unit area management cost of land-use conservation type i on parcel j be u_{ij}. The present value of economic returns for conservation of land-use i in parcel j is

$$V_j^i = -\sum_{t=0}^{\infty} \frac{A_j u_{ij}}{(1+\delta)^t} = -\frac{A_j u_{ij}(1+\delta)}{\delta} \tag{13}$$

for $i = 7, 8, 9$. We provide details of the conservation land-use value estimation method in Appendix A.

2.2.5. *Total landscape economic score*

The total landscape economic score, E, sums the present value of land use on each parcel. Define $w_j^i = 1$ if parcel j is in land-use i and 0 otherwise. The landscape economic score for a given land-use pattern is

$$E = \sum_{j=1}^{J} \sum_{i=1}^{I} w_j^i V_j^i. \tag{14}$$

2.3. *Optimization problem and solution methods*

The goal of the analysis is to find land-use patterns that maximize the landscape biological score (B from Eq. (8)) for a given landscape economic score (E from Eq. (14)), and vice versa. By finding the maximum biological score for a fixed economic score, and then varying the economic score over its entire

potential range, we trace out the efficiency frontier (also called a production possibility frontier). The efficiency frontier illustrates what is feasible to attain from the landscape in terms of the biological and economic objectives, and the necessary tradeoffs between the biological and economic objectives on the landscape. The efficiency frontier also illustrates the degree of inefficiency of other land-use patterns not on the frontier, showing the amount by which the biological score and/or economic score could be increased.

Because the optimization problem in this model is an integer program involving a large number of parcels, each with a number of potential land uses, the discrete choice space is very large. With J parcels that can be put into I different land uses there are I^J potential land-use patterns to choose from. Further, the biological model described in Section 2.1 involves non-linear spatial considerations. Therefore, finding an optimal solution using the biological model described in Section 2.1 is exceedingly difficult.

In this paper, we use heuristic methods to find good solutions to this problem. First, we find optimal solutions (i.e., land-use patterns) using three simple biological models that are linear in land use, described below, that approximate the full biological model described in Section 2.1. Because the economic models are linear in land-use choice we can use the full economic models described above.

Because we are maximizing approximate biological scores using simple linear biological models we are not guaranteed to find points on the efficiency frontier. Therefore, we use a local search heuristic to see if any improvements can be made on the solutions found using the simple linear biological models. Next, we calculate the biological score for each land-use pattern generated in the first two steps using the full biological model described in Section 2.1. This step gives us a set of $\{B,E\}$ pairs. Finally, we approximate the efficiency frontier by taking the outer envelope of the set of $\{B,E\}$ pairs.

The first step in this process involves finding a land-use pattern that maximizes a simplified linear biological model scores for a given economic score. In the first simple biological model we choose a land-use pattern that maximizes the total amount of effective habitat summed across all species:

$$B_1 = \sum_{s=1}^{S} \sum_{j=1}^{J} A_j I_{sj} C_s(k_j) \tag{15}$$

subject to meeting a given economic score, E. We solve for the maximum B_1 for levels of E that range from −$1 billion to $28 billion in steps of $0.2 billion.

In the second simple linear biological model, the objective is to choose a land-use pattern that maximizes the number of breeding pairs summed across all species up to a limit number of breeding pairs Γ. Breeding pairs beyond Γ do not contribute to the model's biological score. In this model we choose a land-use pattern that maximizes

$$B_2 = \sum_{s=1}^{S} \mathrm{Min}\left(\Gamma, \sum_{j=1}^{J} \frac{A_j I_{sj} C_s(k_j)}{\mathrm{AR}_s}\right) \tag{16}$$

subject to meeting a given economic score, E. The advantage of the second model over the first is that it does not credit increases in habitat for species that are already relatively secure. We solved this model using values of 1000, 2000, and 4000 for Γ. For each value of Γ we solve Eq. (16) using levels of E that range from −$1 billion to $28 billion in steps of $0.2 billion.

These first two simple linear biological models use information about habitat but ignore the spatial pattern of habitat. In the third simple linear biological model we use a modified version of Eq. (16) that incorporates a penalty for dispersed habitat patches. In this model we choose a land-use pattern that maximizes

$$B_3 = \sum_{s=1}^{S} \mathrm{Min}\left(\Gamma, \sum_{j=1}^{J} \frac{\sum_{z=1}^{J} A_z I_{sz} C_s(k_z) P_{sjz}}{\mathrm{AR}_s}\right) \tag{17}$$

subject to meeting a given economic score, E, where $P_{sjz} = 1$ if parcels j and z are adjacent and declines toward 0 as parcels j and z get further apart. How quickly P_{sjz} approaches 0 as distance between patches increase is a function of the reciprocal of the mean dispersal ability of species $s(\alpha_s)$.

After generating candidate solutions with the three simple linear biological models, we use a local search algorithm to see if we could improve upon these solutions. Starting from a land-use pattern generated by optimizing B_1, B_2, or B_3, we consider all one-parcel land-use changes that improve the economic score. Of these, the algorithm selects the one-parcel land-use change that maximizes the score for a biological model that is identical to the biological model in Section 2.1 with two exceptions: (a) there are no dispersal limits ($D_s = 1$ for all species), and (b) the probability of survival for species is set to zero if the number of breeding pairs for a species on the landscape is less than γ_s.

We then determine the landscape biological score B using the biology model described in Section 2.1 for each of the land-use patterns generated maximizing Eqs. (15)–(17) and those found using the local search algorithm. Each land-use pattern's biological score (B) was then matched with its economic score (E) giving a $\{B,E\}$ combination. Finally, we approximate the efficiency frontier by taking the outer envelope of all the $\{B,E\}$ combinations. For a solution with the scores $\{B_0,E_0\}$ to be on the outer envelope, there must not be another set of scores $\{B_1,E_1\}$ such that $B_1 \geqslant B_0$ and $E_1 \geqslant E_0$ with at least one strict inequality. Appendix A contains a more complete description of the simple linear biological models, the local search heuristics, and the optimization methods used.

3. Data

3.1. *The planning region – Willamette Basin*

The planning region used in this paper is the Willamette Basin, Oregon, USA (Fig. 1). The Willamette Basin is defined as the Willamette River watershed, bordered on the east by the crest of the Cascade Mountain Range and on the west by the crest of the Coast Mountain Range.

Our parcel map was delineated using a 30 × 30 m raster grid map of 1990 land cover in the Basin (ORNHIC, 2000). When possible, we combined adjacent raster cells of the same or similar 1990 land-cover type to form larger land parcels. The smallest parcel on our map was 900 m^2. The maximum parcel size was limited to 750 ha. Our parcel map excludes parcels that were densely developed in 1990 (e.g., industrial, high density

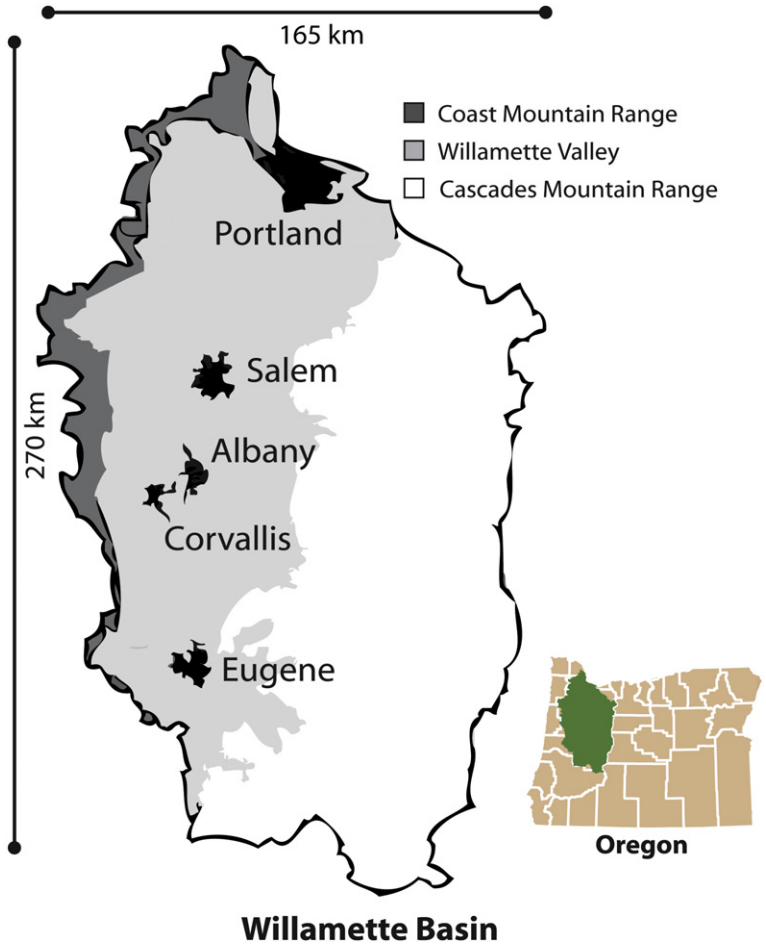


Fig. 1 – *Willamette Basin Map* showing the major biophysical regions of the Coast Mountain Range, Willamette Valley and the Cascade Mountain Range and the location of the Basin within the State of Oregon (*Source*: Willamette Restoration Initiative, 1999).

housing, etc.) or were exclusively water. After excluding these parcels our planning region map includes 10,372 parcels.

In 1990 there were 2196 parcels within UGBs that were not densely developed or exclusively water. Some of these parcels represent parks or natural areas within urban areas while other parcels are likely to be densely developed in the near future. These parcels tended to be fairly small and fragmented. Because the underlying determinants of economic values in parcels inside UGBs differs significantly from those in parcels outside the boundaries, we did not model land-use changes or predict the economic value of these parcels in alternative land uses. As a result, there are a total of 8176 parcels on which we consider the full suite of land-use options (i.e., 10,372 − 2196 = 8176). However, we included the 2196 non-densely developed UGB parcels in calculating scores from the biological model because these parcels may contain habitat that can be utilized by species. To measure the impact of this inclusion decision we also generated scores excluding these parcels and found similar results to those reported below (in all likelihood their impact was minimal because these parcels tended to be small and fragmented).

We collected extensive parcel-level data for use in both the biological and economics models. We summarize the parcel-level data and their sources in Table 1.

3.2. *Application of the biological model in the Willamette Basin*

We used a data set on 267 terrestrial vertebrate species. These species were culled from a set of 279 terrestrial vertebrate species that breed or feed in the Willamette River Basin as reported in Adamus et al. (2000). Twenty-one of the 279 species were dropped from the data set either because the species is an exotic whose natural home range does not include the Basin (e.g., House Mouse, Nutria, Rock Dove), or the species has been extirpated from the Basin (e.g., Yellow-Billed Cuckoo, Gray Wolf, Grizzly Bear). In addition, we added nine species not identified in Adamus et al. (2000) to our database that were determined to have natural home ranges that extend into the Basin (Csuti et al., 1997a; Verts and Carraway, 1998; Adamus et al., 2001; St. John, 2002; Marshall et al., 2003). Based on information in Adamus et al. (2000) and on the professional judgment of several co-authors (Csuti, White, Kagan, Starfield and Lonsdorf), each species in our database was given a habitat compatibility score for each of the 14 land-cover categories ($k = 1, 2, \ldots, 14$) used in our model.

Other species-specific parameters in the biological model are geographic range (H_{sj}), water sensitive species (W_s), the minimum amount of area needed for a breeding pair (AR_s),

Table 1 – Parcel-level data and data sources

Data	Source
Land-cover type in 1990	ORNHIC (2000)
Agriculture soil capability class distribution	PNW-ERC (1999c)
Irrigation point-of-use permits in 2000	OWRD (2001)
50-year Douglas fir forestry site index distribution	USDA-NRCS (2001)
Distance to the nearest processing mill	Author Montgomery
Average elevation	PNW-ERC (1999a)
Average slope	PNW-ERC (1999d)
Dominant potential natural vegetation	ORNHIC (2003b)
Land-cover type at the time of European settlement	PNW-ERC (1999e)
County location	OGEO (1998a)
Urban growth boundaries	OGEO (1998b)
Number of buildings within 350 m of parcel centroid	Hulse et al. (2002)
Location of perennial streams	ORNHIC (2003a)

dispersal ability (α_s), and minimum number of breeding pairs for an isolated population (γ_s). Adamus et al. (2000) contain information on geographic ranges of nearly all 267 species. Modifications to several Adamus et al. (2000) geographic range maps were made using the professional judgment of two co-authors (Csuti and Kagan). See Appendix A for geographic range maps for 37 of the species. The designation of W_s was based on the professional judgment of several co-authors (Csuti, White, Kagan, Starfield and Lonsdorf). We found few resources giving values for AR_s, α_s, and γ_s for the species used in our model. A few guidelines for AR_s and α_s values were found in Brown (1985) and Adamus et al. (2000). Most of the values used for AR_s and α_s are based primarily on the following assumptions: (a) area requirements scale to the size of the animal, (b) larger animals disperse further than smaller animals, (c) birds disperse further than mammals, and (d) mammals disperse further than amphibians/reptiles. Because we lacked data on species-specific values for γ_s, we set $\gamma_s = 50$ for all s. See Appendix A for $C_s(k)$, W_s, AR_s, and α_s values for all 267 species.

3.3. *Application of the economic model in the Willamette Basin*

The values for the four agricultural land uses (orchard/vineyard, grass seed, pasture, row crops) for each parcel on the Basin map were found by using Eq. (9) with data on soil capability class, irrigation permit data, parcel area, and elevation. Crop yield as a function of soil capability class, irrigation, and county came from USDA-NRCS (2001). We used information from the Oregon State University Extension Services (OSUES, 2002) to determine crop prices in each parcel j for each crop type (product prices varied across counties and thus prices in j are a function of the county it is in). We used information from the Oregon State University Extension Services (OSUES, 2003) to determine production costs for each crop type. We assumed that any parcel with at least one irrigation permit grew an irrigated crop type.

In the Willamette Basin, standard commercial timber rotation is 45 years ($\tau = 45$; Adams et al., 2002). A 45-year rotation Douglas fir managed forestry value for each parcel on the Basin map was found by using Eq. (11) with information found in Curtis (1992), Curtis et al. (1981), Fight et al. (1984), King (1966), Latta and Montgomery (2004), and relevant parcel data, including 50-year Douglas fir site index data, average slope, area, and distance to the nearest processing mill.

Rural-residential land-use value in the Willamette Basin was found by estimating a hedonic property price equation using the natural log of sale price for unimproved rural-residential lots with rural-residential zoning classification sold from 1980 to 2003 in the Basin as the dependent variable. Lot location and site specific characteristics, along with a dummy variable to indicate the year of the sale, were the independent variables in the hedonic property price model. We measured a lot's proximity to urban areas with a gravity statistic that summarizes parcel distance to Portland, Salem, Eugene, Albany, and Corvallis (Kline et al., 2001). After the property price equation was estimated, parcel-level location and site specific characteristics were used to estimate the rural-residential use value of each parcel j assuming 5 acre lot sizes.

The present value of conservation depends on the land cover chosen. Management costs, u_{ij} in Eq. (13), are set equal to \$61.75 per hectare per year when the land on j is actively managed to maintain 1990 land-cover conditions or to recreate conditions at the time of EuroAmerican settlement (personal communication with Ed Alverson). Management costs are set equal to 0 if the conserved land cover is parcel j's dominant potential natural vegetation. This latter assumption is a simplification. Even though there may not be active management needed to create the dominant potential natural vegetation there will be costs associated with such things as patrolling boundaries and preventing anthropogenic disturbances.

We assumed a discount rate of 7% ($\delta = 0.07$) for purposes of calculating net present values.

4. Results

Using the methods described in Section 2 with the Willamette Basin data described in Section 3, we find an efficiency frontier for terrestrial vertebrate conservation and economic returns in the Basin (shown in Fig. 2). Starting from the land-use pattern that generates the maximum economic return, labeled as point A in Fig. 2, we find land-use changes that increase the biological score markedly while having minimal impact on the economic score. Moving from point A to point B in Fig. 2, increases the biological score from 229.3 to 242.9, which is 50% of the total possible increase in the biological score, while reducing the economic score by less than 3% (see Table 2 for biological and economic scores for selected points on the efficiency frontier). Among the first changes made to increase the biological score for least cost starting from point A are to restore wetlands, primarily along the main stem of the Willamette River in the heart of the valley, and to add a small amount of old growth conifer forest area (see Table 3 and Figs. 3 and 4). The increase in these relatively rare land-cover types benefits species that rely on these land-cover types for habitat. To accomplish this expansion of natural habitat types, a small amount of land is taken

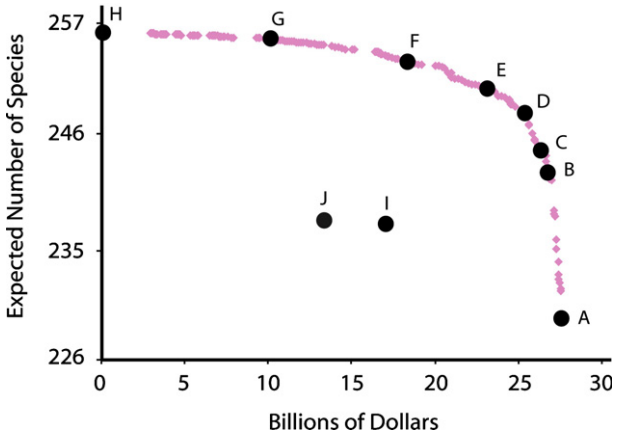


Fig. 2 – *Efficiency frontier.* The present value of economic activity generated by a land-use pattern is shown on the horizontal axis. The number of species expected to be sustained by a land-use pattern is shown on the vertical axis. The efficiency frontier is outlined by solutions shown by diamonds. The lettered circles represent specific land-use patterns along the frontier. Point A represents the maximum economic returns possible. Point H represents the highest biological score found for zero economic returns. Points I and J represent different estimates for the biological and economic scores for the 1990 land-use pattern (ORNHIC, 2000; Hulse et al., 2002; PNW-ERC, 1999b; see Appendix A for details). There is uncertainty in 1990 land-use pattern because the 1990 base maps provide land-cover information (e.g., closed conifer) but often not land-use and land-management information (i.e., is the closed-conifer forest managed for timber production or not). Points I and J represent reasonable bounds on the 1990 land-use pattern's economic score.

out of managed forestry, rural-residential use, orchard/vineyard and row-crop agriculture.

Moving further up the frontier from point B to point D, results in a further increase in the biological score from 242.9 to 248.5, while still keeping reductions in the economic score relatively modest. The main land use change from B to D involves placing a large block of managed forest parcels at high elevations in the Cascade Mountain Range into conserved conifer forest. There is also some increase in other relatively rare natural habitat types, such as prairie. Because relatively more land is shifted out of economic uses to conservation, the economic costs are higher in moving from B to D than from A to B.

Moving still further around the efficiency frontier from point D to point H requires increasingly shifting lands from human uses in agriculture, managed forestry and rural-residential use into conserved land use. Much of this conserved land becomes old growth conifer forests (60.9% of land in the land-use pattern at point H), with other natural habitat types also expanding (e.g., prairie constitutes 6.2% of the Basin's land area, oak savanna constitutes 2.6% of the Basin's land area, and emergent marsh constitutes 2.6% of the Basin's land area at point H). The shift to dominance of land in conserved status increases the biological score from 248.5 to 256.5 but comes at a steep economic cost. The economic returns fall to zero for the land-use pattern at point H. We show the species with the greatest increases in probability of survival as we move along the efficiency frontier from A to B, B to D, D to F and F to H in Table 4.

The maximum biological score of 256.5 falls short of 267 that would represent full protection for entire set species in the database. Five species in the data set have almost no habitat range within the basin (*Anas acuta*, *Anas clypeata*, *Chondestes grammacus*, *Lynx lynx*, *Melanerpes lewis*) and two others (*Aquila chrysateos*, *Nycticorax nycticorax*) have limited habitat range within the basin and large area requirements. Considering only land within the Willamette Basin, these seven species have zero or nearly zero probability of survival even if all habitat for the species within the Basin is preserved. At point H, two species have survival probabilities between 0.01 and 0.5 (*Elanus leucurus*, *Buteo lineatus*), three species have survival probabilities between 0.5 and 0.8 (*Gulo gulo*, *Odocoileus virginianus*, *Phalaropus tricolor*), and eight species have survival probabilities between 0.8 and 0.99 (*Circus cyaneus*, *Crotalus viridis*, *Haliaeetus leucocephalus*, *Loxia curvirostra*, *Martes pennanti*, *Melanerpes formicivorus*, *Oxyura jamaicensis*, *Strix occidentalis*).

Even though increases in biological benefits entail some economic costs, the economic score at point D exceeds the

Table 2 – Biological and economic scores for selected points along the efficiency frontier and the 1990 landscape

Land-use pattern	Present value of economic returns on the landscape (billion $)	Percentage of maximum economic score	Expected number of species to be sustained on the landscape	Percentage of maximum biological score
Efficiency frontier				
A	27.6	100.0	229.3	89.4
B	26.8	97.1	242.9	94.7
C	26.4	95.7	245.0	95.5
D	25.4	92.0	248.5	96.9
E	23.2	84.1	251.0	97.8
F	18.4	66.7	253.6	98.9
G	10.2	37.0	255.9	99.8
H	0.1	0.4	256.5	100.0
1990 Land-use patterns				
I	17.1	62.0	238.6	93.0
J	13.4	48.5	239.0	93.2

Table 3 – Rank (and fraction) of area in each land-cover type for selected points along the efficiency frontier and the 1990 landscape

Rank	I	J	A	B	C	D	E	F	G	H
1	Managed forestry (0.415)	Managed forestry (0.415)	Managed forestry (0.603)	Managed forestry (0.587)	Managed forestry (0.570)	Managed forestry (0.527)	Managed forestry (0.420)	Managed forestry (0.335)	Old growth conifer (0.479)	Old growth conifer (0.609)
2	Old growth conifer. (0.154)	Old growth conifer (0.154)	Rural residential (0.201)	Rural residential (0.195)	Rural residential (0.193)	Rural residential (0.197)	Rural residential (0.225)	Old growth conifer (0.251)	Rural residential (0.154)	Prairie (0.062)
3	Mixed con. and dec. (0.138)	Mixed con. and dec. (0.138)	Orchard/ vineyard (0.104)	Orchard/ vineyard (0.097)	Orchard/ vineyard (0.096)	Orchard/ vineyard (0.096)	Old growth conifer (0.142)	Rural residential (0.152)	Managed forestry (0.135)	Pasture (0.053)
4	Orchard/ vineyard (0.123)	Pasture (0.086)	Row crops (0.020)	Grass seed (0.025)	Grass seed (0.027)	Old growth conifer (0.079)	Orchard/ vineyard (0.091)	Orchard/ vineyard (0.075)	Orchard/ vineyard (0.042)	Grass seed (0.051)
5	Grass seed (0.05)	Grass seed (0.06)	Grass seed (0.018)	Emergent marsh (0.020)	Old growth conifer (0.024)	Row crops (0.019)	Row crops (0.020)	Prairie (0.037)	Prairie (0.038)	Rural residential (0.049)
6	Rural residential (0.037)	Row crops (0.047)	Mixed con. and dec. (0.018)	Mixed con. and dec. (0.018)	Emergent marsh (0.021)	Mixed con. and dec. (0.018)	Grass seed (0.019)	Mixed con. and dec. (0.032)	Mixed con. and dec. (0.029)	Mixed con. and dec. (0.032)
7	Row crops (0.032)	Rural residential (0.037)	Pasture (0.012)	Row crops (0.018)	Mixed con. and dec. (0.018)	Grass seed (0.017)	Mixed con. and dec. (0.018)	Pasture (0.023)	Emergent marsh (0.025)	Oak savanna (0.026)
8	Pasture (0.018)	Orchard/ vineyard (0.029)	Prairie (0.009)	Pasture (0.012)	Row crops (0.018)	Prairie (0.016)	Pasture (0.017)	Emergent marsh (0.023)	Pasture (0.023)	Managed forestry (0.026)
9	Prairie (0.011)	Prairie (0.011)	Riparian forest (0.005)	Prairie (0.009)	Pasture (0.012)	Pasture (0.012)	Emergent marsh (0.017)	Row crops (0.019)	Row crops (0.018)	Emergent marsh (0.026)
10	Shrub/ scrub (0.008)	Shrub/ scrub (0.008)	Shrub/ scrub (0.004)	Old growth conifer (0.008)	Prairie (0.009)	Emergent marsh (0.009)	Prairie (0.016)	Oak savanna (0.015)	Grass seed (0.017)	Row crops (0.018)
11	Oak and other hardwood (0.008)	Oak and other hardwood (0.008)	Oak and other hardwood (0.002)	Riparian forest (0.005)	Riparian forest (0.005)	Riparian forest (0.005)	Riparian forest (0.011)	Grass seed (0.013)	Riparian forest (0.013)	Orchard/ vineyard (0.015)
12	Riparian forest (0.006)	Riparian forest (0.006)	Old growth conifer (0.002)	Shrub/ scrub (0.004)	Shrub/ scrub (0.004)	Shrub/ scrub (0.004)	Shrub/ scrub (0.004)	Riparian forest (0.012)	Shrub/ scrub (0.011)	Riparian forest (0.013)
13	Emergent marsh (0.001)	Emergent marsh (0.001)	Emergent marsh (0.001)	Oak and other hardwood (0.002)	Oak and other hardwood (0.002)	Oak and other hardwood (0.002)	Oak and other hardwood (0.002)	Oak and other hardwood (0.006)	Oak savanna (0.008)	Shrub/scrub (0.011)
14	Oak savanna (0.000)	Oak savanna (0.000)	Oak savanna (0.000)	Oak savanna (0.000)	Oak savanna (0.000)	Oak savanna (0.000)	Oak savanna (0.000)	Shrub/ scrub (0.006)	Oak and other hardwood (0.007)	Oak and other hardwood (0.010)

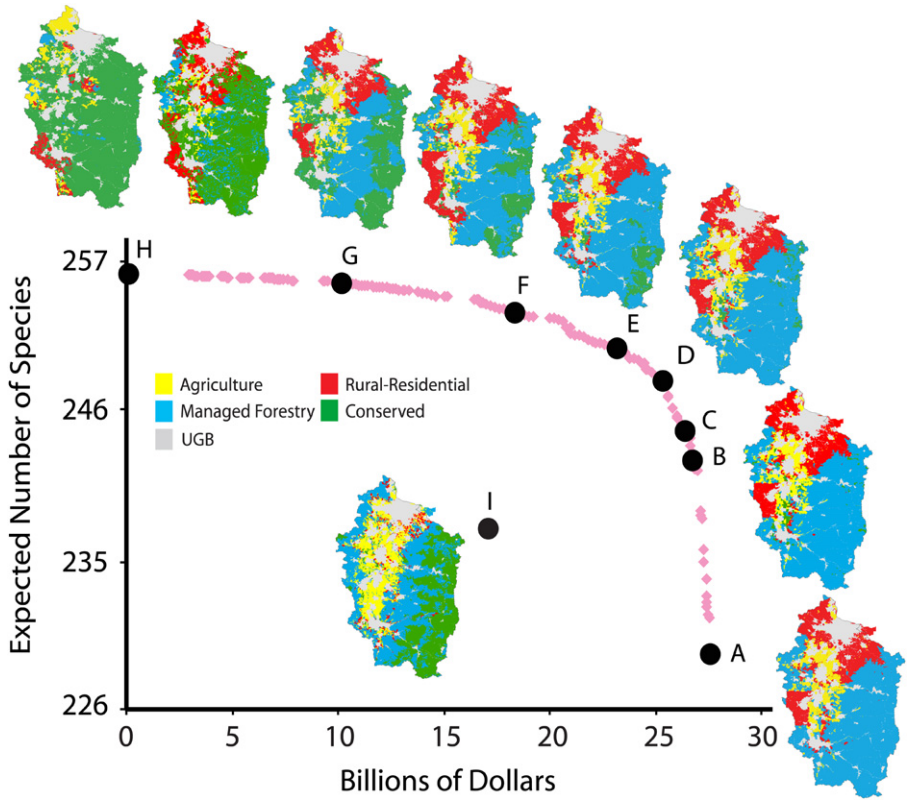


Fig. 3 – *Land-use patterns associated with specific points along the efficiency frontier and the current landscape.* Each land-use pattern shown outside of the efficiency frontier corresponds to a lettered point on the frontier. The current land-use pattern is also shown. Compared to the current landscape, points on the efficiency frontier have less agriculture and more rural-residential use. There is a shift from predominantly managed forest toward conservation land as the biological objective is emphasized more relative to the economic objective.

economic score from an estimate of the 1990 land-use pattern, shown as point I in Fig. 2, by a substantial amount (ORNHIC, 2000, 2005; Hulse et al., 2002). The land-use pattern at point D generates a biological score that is 96.9% of the highest biological score found for the landscape, and generates $25.4 billion in economic returns, 92% of the maximum economic score from the landscape. These results show that for the Willamette Basin it is possible to maintain a high level of species conservation and generate large economic returns by paying careful attention to spatial land management.

While it is possible to find land-use patterns that generate high scores for both the biological and economic objectives, insisting on maximizing either the biological objective or the economic objective requires large sacrifices in the other objective. Maximizing the economic score results in virtually no natural habitat remaining on the landscape, especially in economically desirable places like the valley floor (see Figs. 3 and 4). At point A, economic returns rise to $27.6 billion but the expected number of species that can be sustained on the landscape falls to 229.3. Approximately 37 of the 267 species modeled would not be expected to be sustained in the Basin exclusively under land-use patterns for the landscape at point A. At the other extreme, increasing the biological score toward its maximum drives economic returns down to zero, as shown at point H in Fig. 2. To maximize the number of species sustained in the Willamette Basin requires that large amounts of land be put into conservation (see Figs. 3 and 4) because there are a few species that have large area requirements and only do well in natural habitat (e.g., spotted owl, *Strix occidentalis*). At point H, some land is maintained in agriculture because some species use agricultural land as habitat, but this agriculture is highly unprofitable, generating economic losses of nearly $1.5 billion (Table 5). These economic loses at point H are balanced by a small area of high-value rural-residential land use on the landscape.

In contrast to the relatively few species that require specific land covers, the vast majority of the 267 species in the Willamette Basin database are generalists. These species can be sustained in the Willamette Basin without large amounts of land dedicated to conservation, or really without any specific actions being taken on their behalf. Many species utilize both managed and natural land covers as habitat. The most profitable land use for large blocks of land in the Willamette Basin, especially in the Cascade and Coast Mountain Ranges, is managed forest, which provides adequate habitat for a large proportion of species.

Two estimates of the 1990 land-use pattern, points I and J in Fig. 2, do not do particularly well on either the biological or the economic objective. For example, the 1990 landscape associated with point I generates estimated economic returns of $17.1 billion, which is lower than points A–F on the efficiency frontier. The 1990 landscape associated with point I

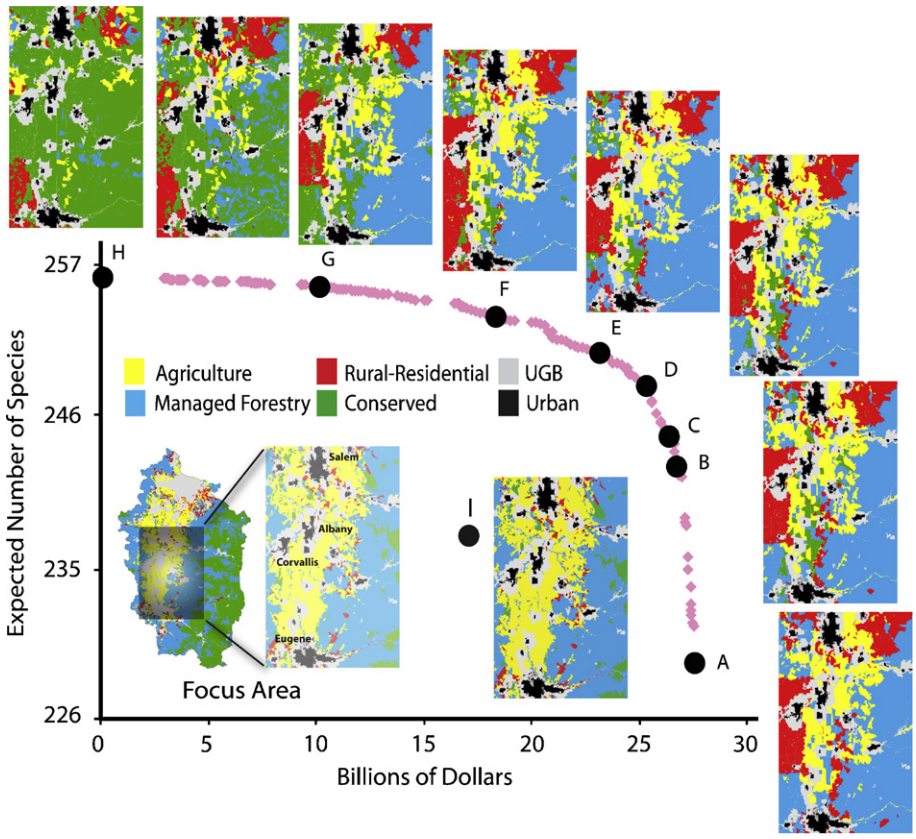


Fig. 4 – *A more detailed view of land-use patterns associated with specific points along the efficiency frontier and the current landscape for a portion of the Willamette Basin.* The portion of the Basin highlighted extends from Salem in the north to Eugene-Springfield in the south and includes a large part of the valley floor extending into the foothills of the Cascade Range on the east and the Coast Range on the west. Conserving land along the Willamette River just north of Eugene up to the Corvallis-Albany area increases the biological score greatly per dollar of lost economic value. The conserved land increases relatively rare types of natural habitat, particularly wetlands. The decline in the amount of land devoted to agriculture and the expansion of rural-residential land use relative to the current landscape is also readily apparent in this area.

Table 4 – The change in biological score along the efficiency frontier for the five species that experience the greatest gain in survival probability

A to B		B to D		D to F		F to H	
Efficiency frontier points (see Fig. 2)							
Clemmys marmorata	0.99	*Marmota flaviventris*	1.00	*Pandion haliaetus*	0.91	*Haliaeetus leucocephalus*	0.86
Ceryle alcyon	0.99	*Phenacomys longicaudus*	0.99	*Gulo gulo*	0.61	*Strix occidentalis*	0.79
Botaurus lentiginosus	0.98	*Accipiter gentilis*	0.84	*Ammodramus savannarum*	0.34	*Branta canadensis*	0.32
Anas crecca	0.98	*Falco peregrinus anatum*	0.83	*Loxia curvirostra*	0.30	*Odocoileus virginianus*	0.20
Anas cyanoptera	0.98	*Strix varia*	0.82	*Branta canadensis*	0.25	*Elanus leucurus*	0.16

is able to sustain an expected value of 238.7 species, which is lower than all of the highlighted points on the efficiency frontier except point A. The species that experience the greatest gain and the greatest loss in survival probability in moving from the 1990 landscape associated with point I to various points along the efficiency frontier is shown in Table 6. The estimated 1990 land-use patterns do relatively poorly in large part because: (a) much of the land on the valley floor is allocated to relatively low-value agriculture (though private landowners may find it profitable to stay in agriculture because of subsidies), (b) not much land on the valley floor is allocated to relatively high-value rural-residential use, (c) not much land on the valley floor is allocated to the conservation of relatively rare land covers (oak savanna, prairie, riparian forest, wetlands), and (d) land use reflects management differences between public and private lands that may not be efficient. Comparing the land use pattern that maximizes economic returns (point A on the efficiency frontier) versus the 1990 land-use pattern associated with point I, for example, shows a large increase in the amount of rural-residential use and a contraction in agriculture (Fig. 3). The controversies surrounding the spotted owl and timber policy in the 1990s tilted

Table 5 – Economic value by activity for selected points along the efficiency frontier and the 1990 landscape

Land-use pattern	Agricultural value (billion $)	Managed forestry value (billion $)	Rural-residential value (billion $)	Total economic value (billion $)
Efficiency frontier				
A	4.886	14.891	7.814	27.6
B	4.706	14.481	7.663	26.8
C	4.715	14.139	7.600	26.4
D	4.519	13.234	7.687	25.4
E	4.382	10.657	8.237	23.2
F	3.591	8.795	6.252	18.4
G	1.745	3.539	5.152	10.2
H	−1.496	0.738	1.260	0.10
1990 Land-use patterns				
I	5.654	10.619	1.175	17.1
J	1.948	10.619	1.175	13.4

Table 6 – The change in biological score between the 1990 landscape (point I) and points on the efficiency frontier for the species that experience the greatest gain or loss in survival probability

I to A		I to B		I to D		I to F		I to H	
Greatest gain									
Odocoileus virginianus	0.18	*Clemmys marmorata*	0.99	*Asio flammeus*	0.96	*Clemmys marmorata*	1.00	*Clemmys marmorata*	1.00
Martes pennanti	0.10	*Ceryle alcyon*	0.99	*Clemmys marmorata*	0.93	*Brachyramphus marmoratus*	1.00	*Brachyramphus marmoratus*	1.00
Branta canadensis	0.04	*Botaurus lentiginosus*	0.98	*Ceryle alcyon*	0.83	*Chrysemys picta*	1.00	*Chrysemys picta*	1.00
Greatest loss									
Phenacomys longicaudus	−1.00	*Strix varia*	−1.00	*Loxia curvirostra*	−0.35	*Loxia curvirostra*	−0.06	*Melanerpes formicivorus*	−0.06
Marmota flaviventris	−1.00	*Marmota flaviventris*	−1.00	*Lutra canadensis*	−0.29	*Crotalus viridis*	-2.0×10^{-3}	*Crotalus viridis*	−0.01
Strix varia	−1.00	*Phenacomys longicaudus*	−1.00	*Strix varia*	−0.18	*Melanerpes formicivorus*	-1.8×10^{-3}	*Falco sparverius*	-2.0×10^{-4}

public land management toward conservation. Because of decreased supply of timber from public lands, there was increased demand for timber harvesting on other land including private lands in the Pacific Northwest, as well as timber lands outside the region (Murray and Wear, 1998). Relying on public lands for the bulk of conservation and private lands for the bulk of economic activity may have resulted in an inefficient spatial pattern of land use in the Willamette Basin (Lichtenstein and Montgomery, 2003; Nalle et al., 2004).

We analyzed how well certain classes of species do on the landscape at various points along the efficiency frontier and on the current landscape. Birds and mammals tend to do less well than amphibians and reptiles because there are a number of bird and mammal species that need large blocks of natural habitat (see Table 7). Larger animals fare less well regardless of taxonomic group (Table 8) for a similar reason, as do species that are modeled to require large areas for a breeding territory but also have large dispersal ability (Table 9). Not surprisingly, imperiled and critically imperiled species fare less well than other species (Table 10). Only 1 of 3 critically imperiled species can be sustained in the Willamette Basin except for heavily conservation-oriented landscapes (e.g., points G and H) where the expected number of critically imperiled species sustained rises just slightly. Imperiled species, however, show far more responsiveness to conservation actions, rising from less than 50% sustained under the maximum economic orientation (point A), to almost 95% sustained under the maximum conservation orientation (point H) (see Table 10).

5. Discussion

In this paper, we used biological and economic models that utilize land-use and land-cover pattern to explore the joint biological and economic impacts of land-use decisions at a regional landscape scale. Our general modeling approach is widely applicable, though it would need to be tailored for specific economic activities and biodiversity concerns relevant to different regions.

Considering the joint effects on biological and economic consequences of land-use decisions in the Willamette Basin application, we found that it is possible to maintain a high level of biodiversity and generate large economic returns through careful spatial management of land use. It is important to incorporate the biological benefits of working landscapes, including how species utilize agricultural lands and

Table 7 – Number (and percentage) of species expected to be sustained by taxonomic category for selected points along the efficiency frontier and the current landscape

Land-use pattern	Amphibians	Birds	Mammals	Reptiles	All
Total number of species					
	17	157	77	16	267
Efficiency frontier					
A	16.98 (99.9%)	128.40 (81.8%)	70.42 (91.5%)	13.53 (84.6%)	229.33 (85.9%)
B	17.00 (100%)	138.54 (88.2%)	71.43 (92.8%)	15.94 (99.6%)	242.91 (91.0%)
C	17.00 (100%)	139.11 (88.6%)	72.91 (94.7%)	15.95 (99.7%)	244.97 (91.7%)
D	17.00 (100%)	142.36 (90.7%)	73.48 (95.4%)	15.70 (98.1%)	248.54 (93.1%)
E	17.00 (100%)	143.68 (91.5%)	74.40 (96.6%)	15.91 (99.4%)	250.99 (94.0%)
F	17.00 (100%)	146.04 (93.0%)	74.58 (96.9%)	15.99 (99.9%)	253.61 (95.0%)
G	17.00 (100%)	147.97 (94.3%)	74.91 (97.3%)	15.99 (99.9%)	255.87 (95.8%)
H	17.00 (100%)	148.59 (94.6%)	74.94 (97.3%)	15.99 (99.9%)	256.52 (96.1%)
1990 Land-use patterns					
I	17.00 (100%)	134.72 (85.8%)	72.83 (94.6%)	14.00 (87.5%)	238.55 (89.3%)
J	17.00 (100%)	135.23 (86.1%)	72.84 (94.6%)	13.99 (87.5%)	238.96 (89.5%)

Table 8 – Number (and percentage) of species expected to be sustained by animal size category for selected points along the efficiency frontier and the 1990 landscape

Land-use pattern	4–14 cm	14–20.5 cm	20.5–41 cm	41–213 cm	Unknown	All
Total number of species						
	75	56	67	64	5	267
Efficiency frontier						
A	73.49 (98.0%)	50.62 (90.4%)	56.19 (83.9%)	45.04 (70.4%)	4.00 (80.0%)	229.33 (85.9%)
B	74.00 (98.7%)	53.40 (95.4%)	63.05 (94.1%)	48.45 (75.7%)	4.00 (80.0%)	242.91 (91.0%)
C	74.00 (98.7%)	54.50 (97.3%)	63.39 (94.6%)	49.08 (76.7%)	4.00 (80.0%)	244.97 (91.7%)
D	74.66 (99.5%)	54.29 (96.9%)	63.63 (95.0%)	51.96 (81.2%)	4.00 (80.0%)	248.54 (93.1%)
E	74.72 (99.6%)	54.64 (97.6%)	64.06 (95.6%)	53.43 (83.5%)	4.12 (82.4%)	250.99 (94.0%)
F	75.00 (100%)	54.88 (98.0%)	64.49 (96.3%)	55.25 (86.3%)	4.00 (80.0%)	253.61 (95.0%)
G	75.00 (100%)	54.97 (98.2%)	64.69 (96.6%)	57.10 (89.2%)	4.12 (82.4%)	255.87 (95.8%)
H	75.00 (100%)	54.98 (98.2%)	64.69 (96.6%)	57.71 (90.2%)	4.12 (82.4%)	256.52 (96.1%)
1990 Land-use patterns						
I	74.01 (98.7%)	52.87 (94.4%)	57.85 (86.3%)	49.82 (77.8%)	4.00 (80.0%)	238.55 (89.3%)
J	74.16 (98.9%)	52.87 (94.4%)	57.94 (86.5%)	49.99 (78.1%)	4.00 (80.0%)	238.96 (89.5%)

Notes: Animal size is given by NatureServe. See http://www.natureserve.org/ for details.

managed forests, rather than having an exclusive conservation focus on protected areas. Doing so gives a more realistic picture of how well species are likely to do on landscapes and lessens the apparent conflict between conservation and economic objectives (Polasky et al., 2005).

The largely positive findings for the Willamette Basin, where certain land-use patterns can jointly generate high biological and economic scores, occurs because many species in the Basin are generalists and can be sustained on lands managed to generate high economic returns. The fact that the highest value economic activity for large blocks of land in the Basin is managed forestry, which provides good habitat for many species, is also important in limiting the degree of conflict between biological and economic objectives. In other regions, where the most economically profitable land uses are intensive agriculture or urban development, there will likely be much greater conflict between conservation objectives and economic returns. Even in the Willamette Basin, if heavier weights are given to more highly threatened species there will be more apparent tradeoff between biological and economic objectives. For example, in moving from point D to point H in Fig. 2, imperiled species increase by 19.8%, vulnerable species increase by 9.1%, and abundant species increase by only 1.4% (based on results in Table 10).

In this application we found that biological and economic scores for land-use patterns on the efficiency frontier exceeded those for the 1990 landscape by large margins, indicating that there are large improvements that potentially can be realized by better spatial management. For example, point D on the efficiency frontier had economic returns $8.3 billion higher than the 1990 land-use pattern represented by point I, while the biological score (expected number of species surviving on the landscape) increased by 9.9. Both of these increases cover the majority of the gap between the point I 1990 land-use pattern and the maximum score found for each objective. A part of the apparent inefficiency of the 1990 land-use pattern may be due to data issues: data on agricultural, forestry and rural-residential use is from 2000 to 2005. There has, in fact, been some change in land-use patterns since 1990. The amount of land-use change, however, can explain only a small portion of the inefficiency of the 1990 land-use pattern relative to the frontier. In addition, there may be some

Table 9 – Number (and percentage) of species expected to persist by breeding territory size (AR_s in m^2) and dispersal ability (α_s in m) for selected points along the efficiency frontier and the current landscape

Land-use pattern	AR_s = 10,000, α_s = 1/800	AR_s = 250,000, α_s = 1/3200	AR_s = 2,000,000, α_s = 1/8000	AR_s = 10,000,000, α_s = 1/32,000	All
Total number of species	150	78	27	12	267
Efficiency frontier					
A	146.33 (97.6%)	58.32 (74.8%)	18.09 (67.0%)	6.59 (54.9%)	229.33 (85.9%)
B	149.69 (99.8%)	68.31 (87.6%)	18.30 (67.8%)	6.61 (55.1%)	242.91 (91.0%)
C	149.69 (99.8%)	70.13 (89.9%)	18.43 (68.3%)	6.71 (55.9%)	244.97 (91.7%)
D	149.69 (99.8%)	70.91 (90.9%)	21.00 (77.8%)	6.93 (57.8%)	248.54 (93.1%)
E	149.69 (99.8%)	71.93 (92.2%)	22.14 (82.0%)	7.22 (60.2%)	250.99 (94.0%)
F	149.69 (99.8%)	72.78 (93.3%)	23.30 (86.3%)	7.85 (65.4%)	253.61 (95.0%)
G	149.69 (99.8%)	72.81 (93.3%)	23.87 (88.4%)	9.49 (79.1%)	255.87 (95.8%)
H	149.69 (99.8%)	72.81 (93.3%)	24.28 (89.9%)	9.73 (81.1%)	256.52 (96.1%)
1990 Land-use patterns					
I	148.89 (99.3%)	61.88 (79.3%)	20.30 (75.2%)	7.47 (62.3%)	238.55 (89.3%)
J	148.89 (99.3%)	62.11 (79.6%)	20.48 (75.8%)	7.48 (62.3%)	238.96 (89.5%)

errors in our estimations of the 1990 land-use patterns but these errors are also likely to explain only a small portion of the gap between the current landscape and the efficiency frontier.

The results also show that insisting on "getting it all" by maximizing either the economic or biological score imposes large losses on the other objective. The efficiency frontier shows that at points close to the economic maximum, further small increases in the economic score impose large declines in the biological score. At the other end of the efficiency frontier, when the landscape is close to the biological maximum, further small increases in the biological score come at the expense of large declines in the economic score. Our results in this regard are similar to other studies that have combined biological and economic models in terms of an efficiency frontier (e.g., Calkin et al., 2002; Nalle et al., 2004) or a conservation cost function (e.g., Montgomery et al., 1994, 1999; Ando et al., 1998; Polasky et al., 2001; Nelson, 2007). These papers have generally found that a large portion of conservation benefits can be achieved at relatively low cost but that obtaining the final few increments of a conservation objective are extremely expensive. For example, Ando et al. (1998) found that representing 50% of species listed under the U.S. Endangered Species Act required 2% of the total cost required to represent all 100% of endangered species, with most of the costs being incurred to represent the final few species.

Because we modeled the present value of land use for the entire Willamette Basin, excluding the lands inside of UGBs, the total value of economic returns was high (maximum of $27.6 billion). Even a reduction of 3% in economic returns, which is what was needed to raise the percentage of species sustained on the landscape to 94.9% of the maximum attainable, is a substantial sum of money ($828 million). This figure, however, is the present value of all lost economic value in perpetuity. At a discount rate of 7%, the annual costs for making this conservation investment are $54.2 million. It is not unreasonable to think of making an investment of this size to sustain biodiversity at a regional scale. This amount could be financed through a combination of a government bond issue for public purchases of land or conservation easements along with purchases by non-governmental conservation organizations.

The results in this paper should be viewed as suggestive rather than being prescriptive about particular land use for particular parcels or conservation plans for particular species. Details of particular parcels may preclude certain uses or make certain uses undesirable even though the analysis here indicates those uses are beneficial. Lack of detailed species-specific information may make this model inappropriate for designing species-specific conservation plans. However, the overall pattern of tradeoffs between conservation objectives and economic returns, and the general characteristics of land use and land cover that will benefit large classes of species should be robust and could help guide conservation planning.

In the application we treated the Willamette Basin as an island ignoring geographic range lying outside of the basin. Seven species included in the analysis had very little geographic range in the Basin and zero or near zero probabilities of survival exclusively within the Basin even if all area within a species' geographic range is conserved. Expanding the

Table 10 – Number (and percentage) of species expected to be sustained by subnational conservation status for selected points along the efficiency frontier and the 1990 landscape

Land-use pattern	Critically imperiled	Imperiled	Vulnerable	Apparently secure	Abundant	Unranked	All
Total number of species							
	3	10	28	132	88	6	267
Efficiency frontier							
A	1.00 (33.3%)	4.85 (48.5%)	22.59 (80.7%)	114.69 (86.9%)	81.91 (93.1%)	4.30 (71.7%)	229.33 (85.9%)
B	1.00 (33.3%)	5.81 (58.1%)	23.92 (85.4%)	122.78 (93.0%)	85.10 (96.7%)	4.30 (71.7%)	242.91 (91.0%)
C	1.00 (33.3%)	5.84 (58.4%)	23.94 (85.5%)	124.67 (94.4%)	85.22 (96.8%)	4.30 (71.7%)	244.97 (91.7%)
D	1.00 (33.3%)	7.91 (79.1%)	24.75 (88.4%)	125.12 (94.8%)	84.63 (96.2%)	5.12 (85.3%)	248.54 (93.1%)
E	1.00 (33.3%)	8.80 (88.0%)	25.06 (89.5%)	125.66 (95.2%)	85.09 (96.7%)	5.36 (89.3%)	250.99 (94.0%)
F	1.00 (33.3%)	9.45 (94.5%)	25.30 (90.4%)	127.14 (96.3%)	85.44 (97.1%)	5.30 (88.3%)	253.61 (95.0%)
G	1.15 (38.3%)	9.47 (94.7%)	26.80 (95.7%)	127.51 (96.6%)	85.44 (97.1%)	5.50 (91.7%)	255.87 (95.8%)
H	1.16 (38.7%)	9.48 (94.8%)	27.00 (96.4%)	127.54 (96.6%)	85.83 (97.5%)	5.50 (91.7%)	256.52 (96.1%)
1990 Land-use patterns							
I	1.00 (33.3%)	5.84 (58.4%)	23.14 (82.6%)	121.49 (92.0%)	81.95 (93.1%)	5.12 (85.3%)	238.55 (89.3%)
J	1.00 (33.3%)	5.99 (59.9%)	22.14 (79.1%)	122.58 (92.9%)	82.12 (93.3%)	5.12 (85.4%)	238.96 (89.5%)

Notes: 'Subnational Conservation Status' is based on NatureServe's subnational Conservation Status ranking for each species in the Pacific Northwest as of 2004. Unranked species are due to a lack of information or to substantially conflicting information about status or trends. See http://www.natureserve.org/explorer/ranking.htm for more details.

analysis beyond the Willamette Basin would be necessary to craft conservation plans for these species. In general, habitat links to other regions will be important in conservation planning at anything less than a continental scale. Considering the broader conservation context will also be important for knowing which species are important to conserve within the conservation planning region and which species could best be conserved elsewhere.

In an important respect, the economic model used in this paper is simpler than the biological model. The value of economic returns on a parcel is solely a function of the parcel's characteristics. Nearby or adjoining parcels do not influence the economic score for a parcel. In doing so, we ignore changes in market prices (Armsworth et al., 2006) or effects of economies of scale from changes in land-use decisions. Changes in market price are likely to be most significant for rural-residential development. We also do not include "externalities" from adjacent land uses. Examples of positive externalities include a premium for housing values adjacent to biological reserves or open space (e.g., Tyrvainen and Miettinen, 2000; Shultz and King, 2001; Thorsnes, 2002) and the effect of pollinators on crop yields (e.g., Nabman and Buchman, 1997; Allen-Wardell et al., 1998; Ricketts et al., 2004; Greenleaf and Kremen, 2006). Examples of negative externalities include pesticide and nutrient runoff from agricultural parcels, along with odor, noise or congestion from neighboring land uses.

The biological model also contains several important simplifications that deserve mention. We were constrained in the Willamette Basin application by lack of species-specific data for dispersal ability and parameters of the saturating function that translates from number of breeding pairs to probability of survival on the landscape. More detailed information about species would improve the reliability of model predictions. In particular, in assuming the same parameter values for all species in the saturating function we tend to over-estimate the probability of survival as a function of number of breeding pairs for highly variable populations and under-estimate the probability of survival for relatively stable populations.

There are few prior examples of multi-species conservation planning that integrate a formal mathematical basis with principles of decision theory (McCarthy et al., 2006), so most of the complexity in the biological model comes from a relatively novel attempt to incorporate spatial patterns of habitat. Many prior studies addressing multiple species have avoided this by simply considering the amount of habitat or by arbitrarily rewarding compactness or contiguity clumping of habitat (e.g., Nalle et al., 2002). Including spatial patterns considerably complicates the analysis because it is then not just a matter of thinking about characteristics of parcels themselves but of the relationship among parcels. Thus, we applied an ecologically scaled landscape index as a proxy (Vos et al., 2001) and metapopulation capacity (Hanski and Ovaskainen, 2000), rather than run intensive simulations for every species. Our specific approach follows earlier work by Polasky et al. (2005) and is consistent with another recent application of metapopulation theory to multi-species conservation planning by Nicholson et al. (2006) that used area requirement (AR) and dispersal (α) to determine effective area and similarly converted area to an extinction probability using a non-linear saturating function.

Due to constraints of computational feasibility, modeling consequences of spatially explicit patterns of habitat for persistence of multiple species required us to make simplifying assumptions that are not completely satisfactory. For example, in calculating the minimum number of breeding pairs on the landscape ($ZMin_s$) we assumed that only habitat patches above a threshold number contribute to this score. In reality, patches just below the threshold contribute only marginally less than patches just above the threshold. Also, if all habitat patches satisfy the constraint, then the minimum and the maximum score are equal so connectivity does not influence the calculation of the number of breeding pairs on the landscape. For highly fragmented landscapes how these issues are modeled can make a substantive difference.

We plan to further investigate how much the spatial pattern of habitat and connectivity matter for biodiversity

conservation. If there is not much difference between choosing land use based solely on the amount of habitat and the more complicated approach that takes account of the spatial pattern, then simpler approaches focusing on total habitat area could be used (Nelson et al., forthcoming-b). Ignoring spatial considerations would considerably simplify the biological model and allow for much faster search for efficient solutions. If the way in which spatial pattern is modeled affects results in important ways, then further work on spatial modeling will be required.

Probably the most important set of issues not addressed in this paper are related to land-use change and dynamics. The vast majority of work in conservation planning to date has been static. Notable exceptions to this rule include papers analyzing a sequence of conservation decisions (e.g. Meir et al., 2004; Costello and Polasky, 2004; Strange et al., 2006b; Wilson et al., 2006) and papers analyzing tradeoffs between conservation and forestry uses (e.g., Calkin et al., 2002; Nalle et al., 2004; Lichtenstein and Montgomery, 2003). In this paper, we analyzed the "steady-state" consequences of a landscape in terms of the biological and economic objectives. In reality, however, there is an existing landscape and changes will take time to occur. For example, if the current land use is agriculture but the desired land-use is managed forest or conserved forest, it will take decades for the trees to grow to maturity so that there will be a significant delay between the land-use change and the onset of forestry activities or obtaining the biological benefits of a mature forest. Besides the time it takes to make intentional transition between different land covers, there may be unintentional transitions caused by disturbances such as fire or pest outbreaks, or more long-term fundamental changes brought on by climate change. Species populations also take time to adjust. The presence of some species in a region may be a function of habitat conditions in the past but they may be unable to continue to persist if current land-use continues (an example of an extinction debt; Tilman et al., 2002; see also Nicholson et al., 2006). On the other hand, some species may not be currently present but might be reintroduced and persist if suitable restoration of habitat occurs. In addition, human population changes and shifts in market prices will alter the economic returns of various alternative land-uses through time resulting in pressures for land-use change. Future work should include analysis of these important dynamics and transitions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.03.022.

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