Where to Put Things?
Spatial Land Management to Sustain Biodiversity and Economic Returns

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Abstract: Expanding human population and economic growth have lead 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 in a variety of potential land uses. We use the model to search for efficient land-use patterns that maximize biodiversity conservation objectives for a given level 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 patterns that sustain high biodiversity and economic returns. Compared to the current land-use pattern, we show that both biodiversity conservation and the value of economic activity could be increased substantially.

1. Introduction

Over the past century, human-dominated land uses have spread rapidly across landscapes around the world. Approximately 38% of land globally is devoted to agriculture (FAO 2004); 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. Estimates are that over 60% of the world's temperate forests and grasslands ecosystem have been converted to human dominated uses (MEA 2005).

The loss of natural habitat is a primary cause of the loss of terrestrial biodiversity (Wilcove et al. 2000, Wilson 1998). 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 protected area 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, UNEP-WCMC 2004). Further, designation of protected areas is often based on scenic beauty, recreational value, historical or cultural significance, or simply because the land is not in high demand for human use, rather than for its biological significance (Pressey 1994, Scott et al. 2001).

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 expected to be 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 residential development. We use information on soil, slope, elevation and location to estimate yields in both agriculture and forestry. We combine estimates of yield with commodity prices and estimates of production cost to generate economic returns for these land uses. We use information on location, such as distance to cities, and characteristics of the parcel to estimate returns for residential development at each site. 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 from the landscape (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 is feasible 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, U.S. The Willamette Basin has extensive forests in the Coast and Cascade 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 approximately 8,000 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 247 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, the existing landscape pattern can sustain an expected value of 236.7 species and generate $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 landscapes ability to sustain species or in term of economics 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. 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; 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). 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).

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) uses similar versions of the biological and economic models described in this paper but analysis is restricted to a 14x14 simulated landscape with three alternative land uses.

In the next section of the paper we describe the biological and economic models we use 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 specifying the planning region and partitioning the planning region into a set of distinct land parcels, $j = 1, 2, \ldots, J$. Land parcels may be delineated by overlaying a regular hexagon or square grid pattern, or on the basis of ownership boundaries, dominant vegetation cover, or other means. In the application to the Willamette Basin, we delineate boundaries on the basis of dominant vegetation cover in an attempt to have homogeneous land cover within a parcel.

We select a land use for each land parcel in the planning region. Land uses are denoted by i, $i = 1, 2, \ldots, I$. In this paper, we consider nine land uses: 1) orchard/vineyard, 2) grass seed (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 development, 7) conservation to create the dominant potential natural vegetation in the parcel, 8) conservation to recreate conditions at the time of European settlement in the parcel, or 9) conservation to maintain 1990 land cover conditions 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 uses 1 – 6), land use maps directly into land cover. So, for example, when land use is row-crop agriculture, the land cover is also row-crop agriculture. For a parcel placed in 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 land cover types for a parcel being conserved: 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. We sum across all species to determine the biological score for the planning region.

For the economic model, land use for the parcel and characteristics of the parcel determine economic returns for the parcel. For a particular land-use pattern, we sum the net present value of economic returns across parcels to determine the economic score for the planning region. Details of the biological model and the economic model are explained in the following sections.

a. The biological model

The biological model is used to predict the ability of a land-use pattern to sustain populations for a large suite of species. Because we are interested in a large suite of species rather than focusing on one or two species, we keep the biological model relatively simple. The ability of a land-use pattern to sustain a species depends on three species-specific traits: a) habitat compatibility, which includes 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 suitable patches of habitat.

We begin by calculating the number of breeding pairs for each species, $s = 1, 2, \ldots, S$, that could possibly be supported on each parcel j when the land parcel has land cover k. The number of breeding pairs of species s that parcel j can support is:

$$Z_{sj} = \frac{A_j I_{sj} C_s(k)}{AR_s} \tag{1}$$

where A_j is the area of parcel j, I_{sj} is an indicator variable that equals 1 if parcel j is potentially suitable habitat for species s, and 0 otherwise, $C_s(k)$ is the habitat compatibility score for species s with land cover k, and AR_s is the area needed by a breeding pair of species s. The numerator in equation (1) represents the effective area of habitat for species s in parcel j given land cover k, which can range from 0 to A_j. Dividing by AR_s yields the number of breeding pairs of species s

that can utilize parcel j. In the application in this paper, the habitat compatibility score, $C_s(k)$, can take on values of 0, 0.5, or 1. A habitat compatibility score of 1 means the land cover is prime habitat for breeding and feeding activities of a species. A habitat compatibility score of 0.5 means the land cover is marginally suitable for breeding and feeding activities. A habitat compatibility score of 0 means the species does not breed or feed in that land cover.

Whether parcel j is suitable habitat for species s, $I_{sj}\, C_s(k) > 0$, depends upon whether the parcel is within the potential geographic range of the species and other factors beyond land cover. 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). We also model whether there is water access for the parcel, which can be 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. To be considered habitat, a parcel must be in the geographic range of a species and be accessible to water if species s is water sensitive. The indicator variable I_{sj} is then defined as: $I_{sj} = \max\{W_s, R_j\}H_{sj}$. The 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).

The number of breeding pairs that can be supported on the landscape is a function of how many breeding pairs can be supported on parcels with suitable habitat and the connectivity of parcels containing suitable habitat. How well species utilize unconnected patches of habitat depends upon the distance between habitat patches and the species dispersal ability. To capture the effect of habitat fragmentation, we first calculate a range of possible landscape suitability scores for species *s*, from the case with no dispersal limitation among patches (species *s* views all suitable habitat as one single habitat patch), to the case with no dispersal among unconnected patches of habitat (complete isolation of all non-adjoining habitat). The measure of connectedness, described below, determines where within this range the number of breeding pairs supported by the landscape lies.

The maximum number of breeding pairs on the landscape for species *s* assuming no dispersal limitations is defined as the sum of the number of breeding pairs for species *s* across all parcels:

$$ZMax_s = \sum_{j=1}^{J} Z_{sj} \tag{2}$$

To define the minimum number of breeding pairs on the landscape for species *s*, we need two additional definitions. Let γ_s represent the number of breeding pairs necessary to support a viable population for species *s*. Let n_s, $n_s = 1,\ldots,N_s$, index habitat patches for species *s* on the landscape, where a patch for species *s* is formed by combining all parcels *j* that are contiguous and have a positive Z_{sj} value. The number of breeding pairs of species *s* that patch n_s can support is the sum of number of breeding pairs supported by parcels that make up the patch: $Z_{sn_s} = \sum_{j \in n_s} Z_{sj}$. The minimum number of breeding pairs on the landscape is then defined as the sum of breeding pairs in habitat patches that could support a viable population in isolation:

$$ZMin_s = \sum_{n_s=1}^{N_s} Z_{sn_s} \psi_{n_s} \tag{3}$$

where $\psi_{n_s} = 1$ if $Z_{sn_s} \geq \gamma_s$, and 0 otherwise. 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 landscape suitability score for species *s* will depend only on the total amount of habitat and not its spatial pattern. In this study we set $\gamma_s = 50$ for all *s*.

The connectivity measure of a land use pattern for species *s* is derived from both the inter-patch distances and the dispersal abilities of a species and is defined as:

$$D_s = \frac{\left(\sum_{n_s=1}^{N_s} \sum_{m_s=1}^{N_s} \exp\left(-\alpha_s d_{m_s n_s}\right) Z_{sm_s} \right)}{N_s ZMax_s} \tag{4}$$

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 dispersal ability of species *s*. The landscape connectivity measure, D_s, is scaled to lie between 0 and 1. 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 intense 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:

$$Z_s = D_s ZMax_s + (1 - D_s) ZMin_s . \tag{5}$$

In a completely connected landscape $D_s = 1$ and the number of breeding pairs equals $ZMax_s$. On the other hand, if all suitable habitat parcels are completely isolated $D_s = 0$, then the number of breeding pairs on the landscape equals $ZMin_s$.

To determine the expected biodiversity score for the landscape we convert breeding pairs, Z_s, into a probability that the species will be sustained on this landscape, π_s, using a saturating function:

$$\pi_s = \frac{Z_s^g}{Z_s^g + \eta^g} \tag{6}$$

where η is the half-saturating constant (the landscape score yielding a probability of 0.5), and g is a constant that determines the shape of the saturating function. 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 $\eta = 500$ and $g = 4.25$. With these parameters there is a 50% probability of being sustained at a population of 500 breeding pairs and a 95% probability of being sustained at a population of 1000 breeding pairs.

The landscape biological score, B, is defined as the expected number of species that are expected to be sustained on the landscape:

$$B = \sum_{s=1}^{S} \pi_s\,. \tag{7}$$

b. 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 (in the Willamette Basin application this includes agriculture, forestry, residential development, and conservation).

We have made two important simplifications on the economic model. First, we focus here 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. 2007).

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 assumed to be 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 developable land. In principle, it would be possible to incorporate price effects with a downward sloping demand for residential development. We did not do so here so that we could keep the economic model linear, which greatly simplifies our computational approach to finding efficient land use patterns (discussed below in section c).

i. Agriculture

In this model we consider four types of agricultural land use: orchard/vineyard, grass-seed, pasture, and row-crop agriculture. We use a similar approach to calculate the present of economic returns for each agricultural land use. The present value of an agriculture land use on parcel *j* depends upon the type of agriculture, *i*, $i = 1, 2, 3, 4$, productivity of the agricultural land use on the parcel, the price of agricultural produce and production costs. Let y_j^i be the yield per unit area for agricultural land use *i* grown on parcel *j* where yield is a function of *j*'s soil quality distribution and whether the parcel is irrigated. The yield is multiplied by the market price of crops by agricultural land use *i*, given by p_j^i. The costs of producing crops in agricultural land use i per unit area is c_j^i. In principle, the market price and cost of production may be affected by *j*'s location on the landscape. Assuming that this crop is harvested every year, the present value of economic return from agricultural land use *i* on parcel *j* is:

$$V_j^i = \sum_{t=0}^{\infty} \frac{A_j(p_j^i y_j^i - c_j^i)}{(1+\delta)^t} = \frac{A_j(p_j^i y_j^i - c_j^i)(1+\delta)}{\delta} \qquad (8)$$

for $i = 1,2,3,4$.

ii. Managed Forestry

The present value of managed forestry 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 1,000 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 (e.g., Curtis et al. 1981). In the Willamette Basin application, timber yield includes production from commercial thinning at age 35 and final harvest at age $\tau = 45$.

Timber production in mbf per unit area is multiplied by timber price per mbf on the parcel to determine timber revenue per unit area. Timber price per mbf on parcel *j*, p_j^f, equals product price per mbf for logs delivered at the mill, p^f, minus logging and hauling costs per mbf on parcel *j*, l_j^f and h_j^f, respectively: $p_j^f = \left(p^f - l_j^f - h_j^f\right)$. Logging costs per mbf are a function of forest site index and average slope. Hauling costs per mbf are a function of distance to the nearest processing mill. Finally, we include maintenance costs of forestry production per unit area, $r^f(\tau)$, which is a function of the rotation age but not of site characteristics.

We assume even-aged forestry management with rotations of τ years 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 the computations while capturing the spirit of an even flow of timber from the landscape. Given these assumptions, the present value of economic return from managed forestry with a rotation time of τ is

$$V_j^i = \sum_{t=0}^{\infty} \frac{A_j(p_j^f y_j^f(\tau, f_j) - r^f(\tau))}{\tau(1+\delta)^t} = \frac{A_j(p_j^f y_j^f(\tau, f_j) - r^f(\tau))(1+\delta)}{\tau\delta} \qquad (9)$$

for $i = 5$, where δ is the annual discount rate.

iii. Rural-Residential Development

The present value of rural-residential development per unit area is a function of location as well as site characteristics. In the Willamette Basin application, we capture the effects of location on the value of rural-residential development per unit area using several variables: a) the proximity of a parcel to urban areas using a gravity index (Kline et al. 2001), b) the county in which the parcel is located, and c) whether or not any portion of the parcel is inside an "urban growth boundary." In Oregon, all cities and towns have been mandated to have an urban growth boundary inside of which all concentrated development is supposed to occur, though a recently passed voter initiative seems likely to change this planning requirement. Outside urban growth boundaries development is limited to rural-residential development with minimum lot size requirements. Site characteristics that may influence the value of rural-residential development on a parcel include: a) mean elevation, b) slope, c) housing density on the parcel, and d) building density within a certain radius of the parcel. Using data on rural-residential home sales in the Willamette Basin as the dependent variable we estimate a hedonic property price function that depends on the location and site characteristic variables described above. We then use the estimated hedonic property price function to predict the value of rural-residential development in parcel j per unit area, v_j^d, as a function of the location and the characteristics of the parcel. The estimated value of parcel *j* in rural-residential development is then found by taking the price per unit area and multiplying by the area of the parcel:

$$V_j^i = A_j v_j^d \tag{10}$$

for $i = 6$. We provide details of the hedonic estimation method in the appendix.

iv. Conservation

We assume there are no economic returns generated on conservation land. In general, it should be possible to include the value of recreation and other benefits, such as providing clean water, from conservation land. In the Willamette Basin application, however, we lacked spatially-explicit data to include such benefits. We do include conservation management costs so that economic returns are not in general zero. Conservation may require active management to maintain a particular land cover. Let the annual management cost of preserving land cover in *j* be $u_j(k)$. The present value of economic returns for conservation of land cover *k* in parcel *j* is:

$$V_j^i = -\sum_{t=0}^{\infty} \frac{A_j u_j(k)}{(1+\delta)^t} \tag{11}$$

for $i = 7, 8, 9$.

v. Total landscape 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 zero otherwise. Then the landscape economic score for a given land-use pattern is

$$E = \sum_{j=1}^{J} \sum_{i=1}^{I} w_j^i V_j^i \,. \tag{12}$$

c. Optimization problem and solution methods

The goal of the analysis is to find land-use patterns that maximize the biological score for a given economic score, and vice versa. By finding the maximum biological score for a fixed economic score, and then varying the economic score over its entire range, we can 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 that the landscape can provide. The efficiency frontier also illustrates the degree of inefficiency of other land-use patterns, 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 (I^J potential land-use patterns). Further, the biological model involves non-linear spatial considerations so that finding an optimal solution to this problem is exceedingly difficult.

In this paper, we use heuristic methods to find good solutions to this problem. We begin by finding optimal solutions for simpler biological models. We evaluate these solutions in the biological model described in section (a). We then use a simple local search heuristic around these solutions to see if there are any improvements that can be made. We then approximate the efficiency frontier by taking the outer envelope of the solutions found in these steps using the biology model from section (a) to generate biology scores.

The first step in this process involves finding land use plans that optimize a simplified biological score for a given economic score using models that are (relatively) quick to solve. Doing so enables us to generate many potential solutions that may be on or near the efficiency frontier. In simple model 1, the objective is to choose a land-use pattern that maximizes the total amount of effective habitat summed across all species:

$$B_1 = \sum_{s=1}^{S}\sum_{j=1}^{J} A_j I_{sj} C_s(k), \tag{13}$$

subject to meeting a given economic score, E. This optimization problem can be solved rapidly because this objective is linear in the choice of land use (which affects land cover k). In simple model 2, we modify the objective given in (13) to maximize the number of breeding pairs summed across all species up to 2,000 breeding pairs per species, with no credit beyond 2,000 breeding pairs. We maximize this objective subject to meeting a given economic score, E. We also ran simple model 2 assuming that no species is credited for more than 1,000 breeding pairs or 4,000 breeding pairs. The advantage of model 2 over model 1 is to put added weight on getting species to a threshold amount of habitat while ignoring added habitat for species that appear relatively secure. Simple models 1 and 2 assume no dispersal limitation among patches.

In simple model 3 we add the condition that dispersal on the landscape is limited. A bonus is given to land-use patterns that tend to clump like habitat together.

In step 2 we determine the landscape biological score *B* for each simple model-produced land-use pattern using the biology model described in section (a).

In step 3 we take a land-use pattern produced as a solution from one of the simple models described above. We then change land use on parcels one at a time and find the change that minimizes the increase in the economic score relative to the increase in the biological score:

$$\frac{\left(E_1 - E_0\right)}{\left(\sum_{s=1}^{S}\sum_{j=1}^{J} A_j I_{sj} C_s\left(k_1\right)\right) - \left(\sum_{s=1}^{S}\sum_{j=1}^{J} A_j I_{sj} C_s\left(k_0\right)\right)},$$

where E_1 is the landscape economic score after a one-parcel change, E_0 is the landscape economic score before the one-parcel change, k_1 is the land cover after a one-parcel change, k_0 is the land cover before the one-parcel change, given that $\left(\sum_{s=1}^{S}\sum_{j=1}^{J} A_j I_{sj} C_s\left(k_j\left(i_1\right)\right)\right) > \left(\sum_{s=1}^{S}\sum_{j=1}^{J} A_j I_{sj} C_s\left(k_j\left(i_0\right)\right)\right)$ and $E_1 \geq E_0$. We continue making one-parcel land-use changes until no additional single change generates an improvement in the biological score while keeping the economic score as high as it was before. This local search process is conducted over all of the solutions generated by the simple models. Once we find a solution that cannot be improved upon we determine the landscape biological score *B* using the biology model described in section (a).

In step 4 we approximate the efficiency frontier by taking the outer envelope of all the $\{B,E\}$-combinations produced in steps 1 and 2, and all the $\{B,E\}$-combinations produced in step 3. For a solution with scores of $\{B_0, E_0\}$ to be on the outer envelope, there must not be another solution with scores $\{B_1, E_1\}$ such that $B_1 \geq B_0$ and $E_1 \geq E_0$ with at least one strict inequality.

The appendix contains a more complete description of the simple biological models, the search methods and the method to find the outer envelope of solutions that we used in steps 1 – 4.

3. Data

a. The planning region – Willamette Basin

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

The parcel map we use is based on a 30x30 meter raster grid map of land cover in the Basin (ORNHIC 2000). The raster grid map indicates the land cover type on each grid cell in 1990. We combined adjacent cells of the same land cover type to form larger land parcels. The smallest parcel we allowed was 900 square meters (4 contiguous cells). Isolated land cover fragments of smaller than this size were merged into adjoining land covers. The maximum parcel size was limited to 750 hectares. We exclude parcels that were densely developed (e.g., industrial, high density housing, etc.) or were exclusively water. After excluding these parcels our planning region map includes 10,372 parcels.

There were 2,196 parcels within urban growth boundaries 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 economic value of parcels inside of urban growth boundaries differs significantly from 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 8,176 parcels on which we consider the full suite of land use options. However, we included the 2,196 non-densely developed parcels inside the urban growth boundaries in the biology model because these parcels contain habitat that can be utilized by species. We also ran the biological model excluding these parcels and found similar results (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 in Table 1.

b. Application of the biology model in the Willamette Basin

We used a data set on 267 terrestrial vertebrate species culled from a set of 279 terrestrial vertebrate species that breed or feed in the Willamette River Basin 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 (Verts and Carraway 1998, Adamus et al. 2001, St. John 2002, and Marshall et al. 2003). Based on information in Adamus et al. 2000, each species in our database was given a habitat compatibility score for each of the 14 land cover categories used in our model.

Other species-specific parameters in the biological model are abiotic niche space and/or geographic range (H_{sj}), water sensitive species (W_s), the minimum amount of area needed for a breeding pair (AR_s), and dispersal ability (α_s). Adamus et al. (2000) contains information on the abiotic niche space and/or geographic ranges of nearly all 267 species (see the Appendix for geographic range maps of several of the modeled 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 that gave both AR_s and α_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. See the Appendix for $C_s(k)$, W_s , AR_s, and α_s values for all 267 species. The matrix of H_{sj} values is available upon request from the authors.

c. 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 equation (8), with data on soil class, irrigation permit data, parcel area and elevation. Crop yield as a function of soil type, irrigation, and county came from USDA-NRCS (2001). We used information from the Oregon State University Extension Services (OSUES 2002, 2003) to determine agricultural production costs in the Willamette Basin for each crop. We assumed that any parcel with at least one irrigation permit grew irrigated crops. See the Appendix for more details on the calculation of parcel-specific agricultural net present value.

In the Willamette Basin, standard commercial timber rotation is 45 years. A 45-year rotation managed forestry value for each parcel on the Basin map was found by using equation (9), 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. See the

Appendix for more details on the calculation of parcel-specific managed forestry net present value.

The rural-residential land use value for each parcel in the Willamette Basin was found by estimating a hedonic property price equation using the natural log of sale price for rural-residential homes sold from 1980 to 2003 in the Basin as the dependent variable, location and site specific characteristics, along with a dummy variable for each year from 1980 to 2002 as independent variables. We measured proximity to urban areas using distances to the major cities in the Willamette Basin: Portland, Salem, Eugene, Albany, and Corvallis. We assumed that housing density in parcels would be one house per five acres.

The present value of conservation depends on the land cover chosen. Management costs, $u_j(k)$ in equation (11), are set equal to 0 if the land cover chosen is the parcel's dominant potential natural vegetation. Management costs are set equal to \$61.75 per hectare per year when the land cover is to maintain 1990 land cover conditions or to recreate conditions at the time of European settlement (personal communication with Ed Alverson).

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

4. Results

Using the methods described in section 2 for the Willamette Basin data described in section 3, we find an efficiency frontier (shown in figure 2). Starting from the land-use pattern that generates the maximum economic return, labeled as point A in figure 2, we find a number of land-use changes that can increase the biological score markedly while having minimal impact on the economic score. Moving from point A to point B in figure 2, increases the biological score from 228.0 to 241.6, which is more than 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 in trying to increase the biological score for least cost to the economic score are to restore wetlands, primarily along the main stem of the Willamette in the heart of the valley and a small increase in old growth conifer forests (see table 3 and figures 3 and 4). The increase in these relatively rare land cover types greatly 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 out of managed forestry, rural residential development, 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 241.6 to 247.0, while still keeping reductions in the economic score relatively modest. The main land use change from B to D involves taking a large block of relatively high elevation forest in the Cascade Range out of managed forest and putting it 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 development into conserved land status. 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 6.2%, oak savanna 2.6%, emergent marsh 2.6% at point H). The shift to dominance of land in conserved status increases the biological score from

247.0 to 254.5 but comes at a steep economic cost. The economic returns fall to zero for the land-use pattern at point H.

Even though increases in biological benefits entails some economic costs, it is interesting to note that the economic score at point D exceeds the economic score from the current landscape, shown as point I in figure 2, by a substantial amount. The land-use pattern at point D generates a biological score that is 97% 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 biodiversity 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 highly economically desirable places like the valley floor (see figures 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 228. Nearly 40 species of the 267 that currently exist in the Willamette Basin would not be expected to be sustained under land-use patterns for the landscape at point A. At the other extreme, increasing the biological score towards its maximum drives economic returns down to zero, as shown at point H in figure 2. To maximize the number of species sustained in the Willamette Basin requires that large amounts of land be put into conservation (see figures 3 and 4). There are a few species that have large area requirements and only do well in natural habitat (e.g., spotted owl). Land in conservation does not generate economic rents in this model and may require annual management costs to maintain land cover other than the dominant potential natural vegetation. We also note that some species require agricultural lands in order to be sustained. At point H, some land is maintained in agriculture, but this agriculture is highly unprofitable, generating economic losses of nearly $1.5 billion.

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 Ranges, is managed forest, which provides adequate habitat for a large proportion of species.

The current landscape, point I in figure 2, does not do particularly well on either the biological or the economic objective. The current landscape generates estimated economic returns of $17.1 billion, which is lower than points A - F on the efficiency frontier. The current landscape is able to sustain an expected value of 236.7 species, which is lower than all of the highlighted points on the efficiency frontier except point A. The current landscape does 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 development, 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 land use pattern that maximizes economic returns versus the current landscape, for example, shows a large increase in the amount of rural-residential development and a contraction in agriculture. The controversies surrounding the spotted owl and timber policy in the 1990s tilted public land management towards 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 resulted in an inefficient spatial pattern of land use in the Willamette Basin (Lichtenstein and Montgomery 2003, Nalle et al. 2004).

A part of the apparent inefficiency of the current land-use pattern may occur because we use land cover from 1990 while data on agricultural, forestry and rural-residential development is from 2000 to 2005. There has, in fact, been some change in land-use patterns during the 1990s. The amount of land-use change, however, could explain only a small portion of the inefficiency of the current land-use pattern relative to the frontier.

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 5). Larger animals fare less well regardless of taxonomic group (table 6) 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 7). Greater ability to disperse should help species. This effect, however, appears to be dominated by the correlated need for large blocks of habitat. Not surprisingly, imperiled and critically imperiled species fare less well than other species (table 8). 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 above 1. 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).

5. Discussion

In this paper, we used biological and economic models that take as input land use and land cover to explore the joint biological and economic impacts of land use decisions at a regional scale. Our results point to several conclusions. First, in the Willamette Basin application we found that it is possible to maintain a high level of biodiversity and generate large economic returns by careful spatial management of land use. We found land-use patterns that generated high scores both for sustaining a large fraction of species on the landscape and economic returns from marketed commodities. These land-use patterns exceeded the biological and economic scores for the current landscape by large margins, indicating that there are large improvements that potentially can be realized.

Second, it is important to incorporate the biological benefits of working landscapes, including how species utilize agricultural lands and 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).

Third, 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., Calkins et al. 2003, Nalle et al. 2004) or a conservation cost function (e.g., Montgomery et al. 1994, 1999, Ando et al. 1998, and Polasky et al. 2001). 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 endangered species 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 urban growth boundaries, 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 into 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 this investment to sustain biodiversity at a regional scale. This amount could be financed through a combination of a government bond issue for public purchases 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. Details of particular parcels may preclude certain uses even though the analysis here indicates those uses are beneficial. Further, missing details for specific species 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 guide conservation planning in the Willamette Basin.

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 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.

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 market price and economies of scale effects, where changes in the supply of land for given use could change economic returns through changes in market prices or production costs, respectively. The supply effect is 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 for adjacency to biological reserves or open space (e.g., Tryvainen and Miettenen 2000, Schulz and King 2001, Thorsnes 2002,) and the effect of pollinators on crop yields (e.g., Nabman and Buchmann 1997, Allen-Wardell et al. 1998, Ricketts et al. 2004, Greenleaf and Kremen 2006). Examples of negative externalities include pollution runoff from a parcel that lowers productivity of downstream parcels.

Including spatial patterns in the biological model considerably complicates the analysis. 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. Ignoring spatial considerations would considerably simplify the biological model and allow for much faster search for efficient solutions.

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. 2006) and papers analyzing tradeoffs between conservation and forestry uses (e.g., Calkin et al. 200, 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. Beside 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. In addition, human population changes and shifts in market prices will alter the economic returns of various alternative land-uses through time. Future work should include analysis of these important dynamics and transitions.

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Figure Legends

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

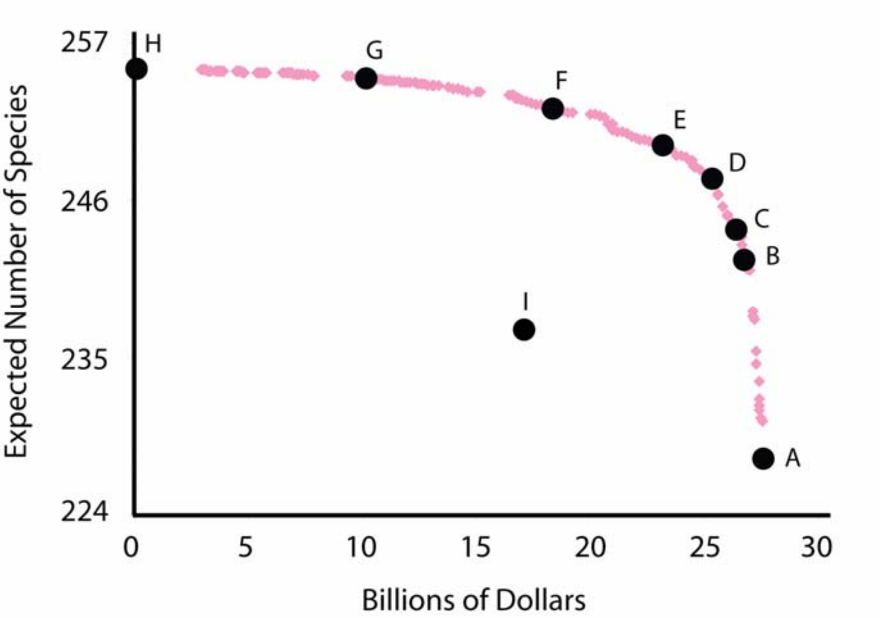
Figure 2: Efficiency frontier. The present value of economic activity generated by a land-use pattern is shown on the horizontal axis. The number of species expected to be sustained by a land-use pattern is shown on the vertical axis. The efficiency frontier is outlined by solutions shown by diamonds. 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. Point I represents the biological and economic scores for the current landscape.

Figure 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 development. There is a shift from predominantly managed forest toward conservation land as the biological objective is emphasized more relative to the economic objective.

Figure 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. A land-use change that increases the biological score greatly per dollar of lost economic value is to conserve land in a corridor along the Willamette River just north of Eugene up to around the Corvallis-Albany area. The conserved land increases relatively rare types of natural habitat, particularly wetlands. The decline the amount of land devoted to agriculture and expansion of rural-residential development relative to the current landscape is also readily apparent in this area.


Portland
Coast Range
Willamette Valley
Cascades
TUALATIN R
YAMHILL R
SOUTH YAMHILL R
PUDDING R
MOLALLA R
CLACKAMAS R
Salem
LITTLE N SANTIAM R
N SANTIAM R
Corvallis
Albany
MIDDLE SANTIAM R
S SANTIAM R
CALAPOOIA R
WILLAMETTE R
Eugene
MCKENZIE R
COAST F. WILLAMETTE R
M F WILLAMETTE R
Cottage Grove
10
0
10
20
30
40
50
Miles
Willamette Basin
Oregon

Figure 1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235
224
Expected Number of Species
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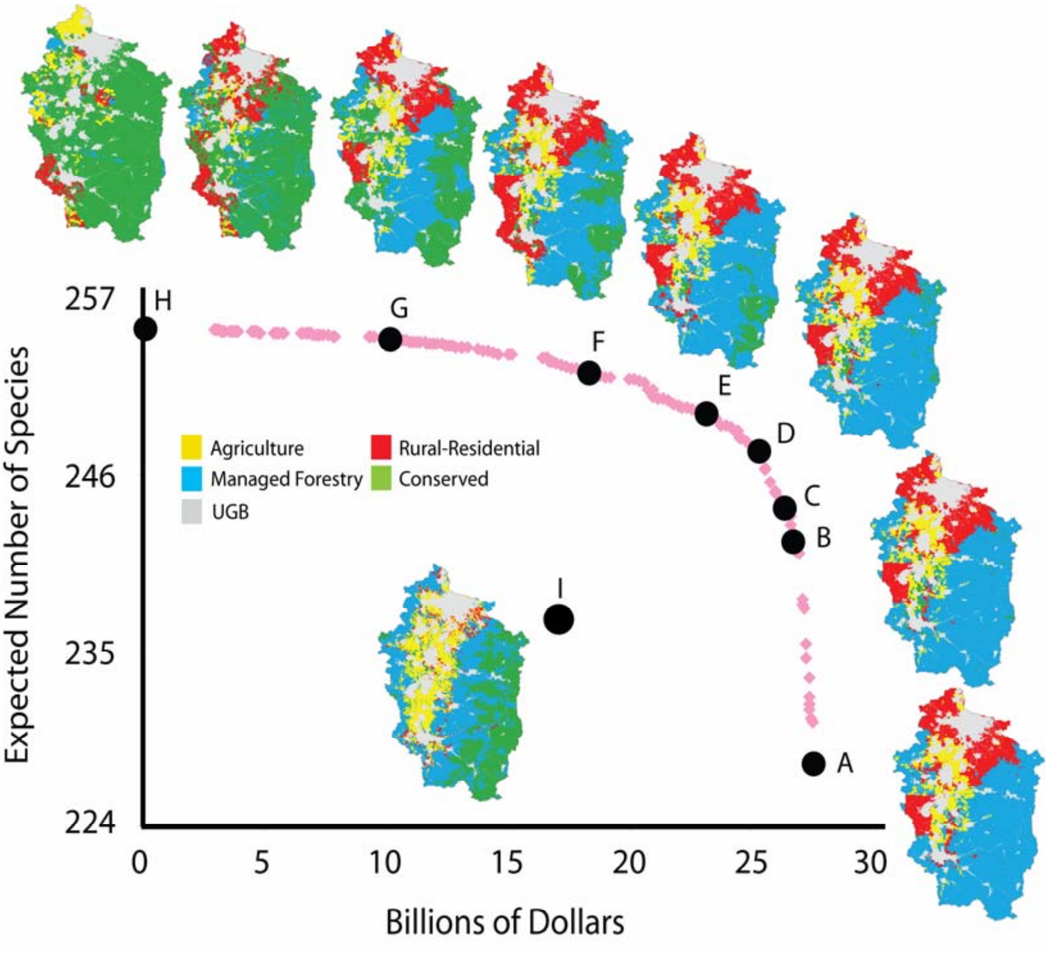
Billions of Dollars

Figure 2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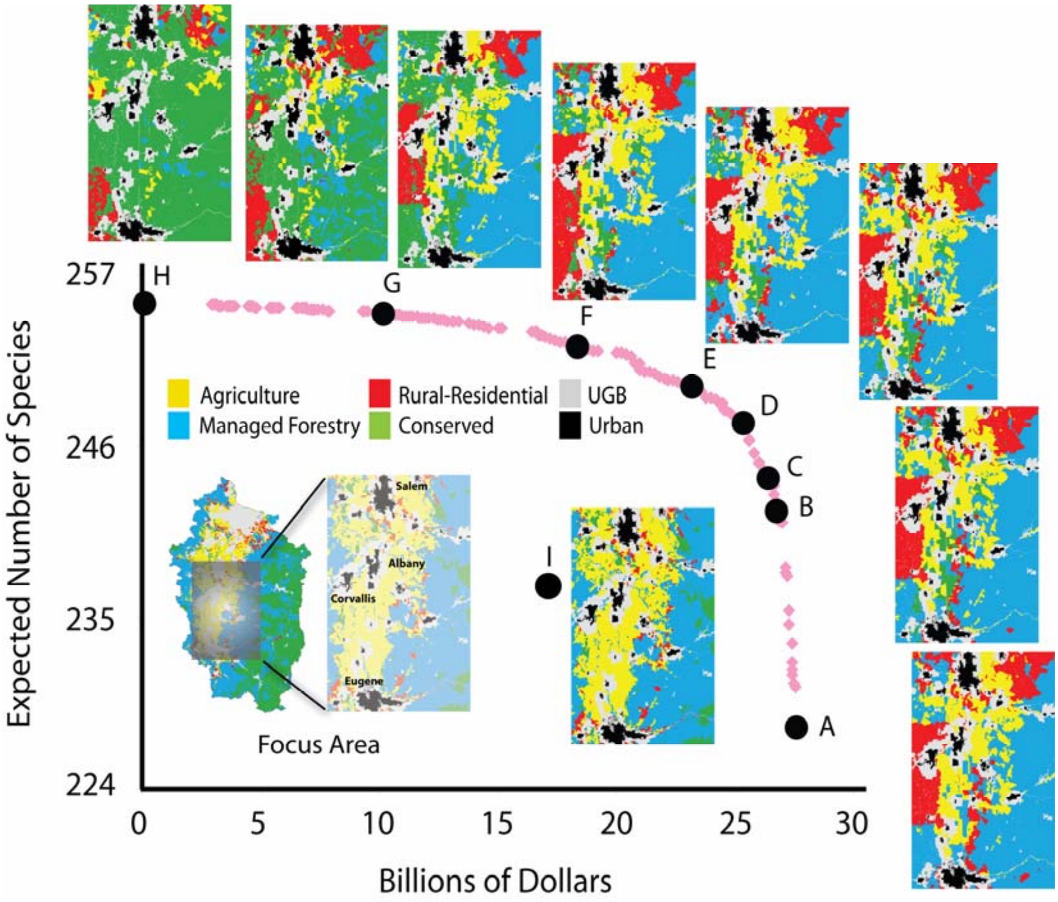
Agriculture
Rural-Residential
Managed Forestry
Conserved
UGB

Figure 3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Agriculture
Managed Forestry
Rural-Residential
Conserved
UGB
Urban
Salem
Albany
Corvallis
Eugene
Focus Area

Figure 4

Table 1: Parcel-Level Data and Data Sources

Data	Source
Land cover type in 1990	ORNHIC 2000
Agriculture soil class distribution	PNW-ERC 1999a
Irrigation point-of-use permits in 2000	OWRD 2001
50-year Douglas fir forestry site index distribution	USDA-NRCS 2001b
Distance to the nearest processing mill	Montgomery
Average elevation	PNW-ERC 1999b
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
Building density within one mile radius of a rural-residential house sale (date?)	
Number of buildings within 350 meters of parcel centroid (date?)	
Location of perennial streams	ORNHIC 2003a

Table 2: Biological and Economic Scores for Selected Points along the Efficiency Frontier and the Current 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	228.0	89.6
B	26.8	97.1	241.6	94.9
C	26.4	95.7	243.6	95.7
D	25.4	92.0	247.0	97.0
E	23.2	84.1	249.3	98.0
F	18.4	66.7	251.8	98.9
G	10.2	37.0	253.9	99.8
H	0.1	0.4	254.5	100.0
Current land-use pattern				
I	17.1	62.0	236.7	93.0

Table 3: Rank (and Fraction) of Area in Each Land-Cover Type for Selected Points along the Efficiency Frontier and the Current Landscape

Rank	I	A	B	C	D	E	F	G	H
1	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)	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)	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)	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 (0.018)	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)	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)	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)	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)	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 (0.004)	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 (0.002)	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)	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)	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)	shrub / scrub (0.006)	oak and other hardwood (0.007)	oak and other hardwood (0.010)

Table 4: Economic Value by Activity for Selected Points along the Efficiency Frontier and the Current Landscape

Formattato

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
Current land-use pattern				
I	5.654	10.619	1.175	17.1

Table 5: 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%)	69.12 (89.8%)	13.53 (84.6%)	228.0 (85.4%)
B	17.00 (100%)	138.54 (88.2%)	70.10 (91.0%)	15.94 (99.6%)	241.6 (90.5%)
C	17.00 (100%)	139.11 (88.6%)	71.57 (93.0%)	15.95 (99.7%)	243.6 (91.2%)
D	17.00 (100%)	142.36 (90.7%)	71.96 (93.5%)	15.70 (98.1%)	247.0 (92.5%)
E	17.00 (100%)	143.68 (91.5%)	72.72 (94.4%)	15.91 (99.4%)	249.3 (93.4%)
F	17.00 (100%)	146.04 (93.0%)	72.73 (94.5%)	15.99 (99.9%)	251.8 (94.3%)
G	17.00 (100%)	147.97 (94.3%)	72.95 (94.7%)	15.99 (99.9%)	253.9 (95.1%)
H	17.00 (100%)	148.59 (94.6%)	72.96 (94.8%)	15.99 (99.9%)	254.5 (95.3%)
Current land-use pattern					
I	17.00 (100%)	134.72 (85.8%)	71.03 (92.3%)	14.00 (87.5%)	236.7 (88.7%)

Table 6: Number (and Percentage) of Species Expected to be Sustained by Animal Size Category for Selected Points along the Efficiency Frontier and the Current 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%)	43.74 (68.3%)	4.00 (80.0%)	228.0 (85.4%)
B	74.00 (98.7%)	53.40 (95.4%)	63.05 (94.1%)	47.12 (73.6%)	4.00 (80.0%)	241.6 (90.5%)
C	74.00 (98.7%)	54.50 (97.3%)	63.39 (94.6%)	47.74 (74.6%)	4.00 (80.0%)	243.6 (91.2%)
D	74.66 (99.5%)	54.29 (96.9%)	63.63 (95.0%)	50.44 (78.8%)	4.00 (80.0%)	247.0 (92.5%)
E	74.72 (99.6%)	54.64 (97.6%)	64.06 (95.6%)	51.75 (80.9%)	4.12 (82.4%)	249.3 (93.4%)
F	75.00 (100%)	54.88 (98.0%)	64.49 (96.3%)	53.40 (83.4%)	4.00 (80.0%)	251.8 (94.3%)
G	75.00 (100%)	54.97 (98.2%)	64.69 (96.6%)	55.14 (86.2%)	4.12 (82.4%)	253.9 (95.1%)
H	75.00 (100%)	54.98 (98.2%)	64.69 (96.6%)	55.73 (87.1%)	4.12 (82.4%)	254.5 (95.3%)
Current landscape						
I	74.01 (98.7%)	52.87 (94.4%)	57.85 (86.3%)	48.02 (75.0%)	4.00 (80.0%)	236.7 (88.7%)

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

Table 7: Number (and Percentage) of Species Expected to Persist by Breeding Territory Size (AR_s) and Dispersal Ability (α_s) for Selected Points along the Efficiency Frontier and the Current Landscape

Land-use pattern	$AR_s = 10{,}000$ $\alpha_s = 800$	$AR_s = 250{,}000$ $\alpha_s = 3{,}200$	$AR_s = 2{,}000{,}000$ $\alpha_s = 8{,}000$	$AR_s = 10{,}000{,}000$ $\alpha_s = 32{,}000$	All
Total number of species					
	150	78	27	12	267
Efficiency frontier					
A	146.33 (97.6%)	58.32 (74.8%)	17.09 (63.3%)	6.29 (52.4%)	228.0 (85.4%)
B	149.69 (99.8%)	68.31 (87.6%)	17.30 (64.1%)	6.28 (52.3%)	241.6 (90.5%)
C	149.69 (99.8%)	70.13 (89.9%)	17.43 (64.6%)	6.37 (53.1%)	243.6 (91.2%)
D	149.69 (99.8%)	70.91 (90.9%)	20.00 (74.1%)	6.41 (53.4%)	247.0 (92.5%)
E	149.69 (99.8%)	71.93 (92.2%)	21.14 (78.3%)	6.54 (54.5%)	249.3 (93.4%)
F	149.69 (99.8%)	72.78 (93.3%)	22.30 (82.6%)	7.00 (58.3%)	251.8 (94.3%)
G	149.69 (99.8%)	72.81 (93.3%)	22.87 (84.7%)	8.53 (71.1%)	253.9 (95.1%)
H	149.69 (99.8%)	72.81 (93.3%)	23.28 (86.2%)	8.75 (72.9%)	254.5 (95.3%)
Current landscape					
I	148.89 (99.3%)	61.88 (79.3%)	19.30 (71.5%)	6.67 (55.6%)	236.7 (88.7%)

Table 8: Number (and Percentage) of Species Expected to be Sustained by Subnational Conservation Status for Selected Points along the Efficiency Frontier and the Current 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%)	114.39 (86.7%)	80.91 (91.9%)	4.30 (71.7%)	228.0 (85.4%)
B	1.00 (33.3%)	5.81 (58.1%)	23.92 (85.4%)	122.45 (92.8%)	84.10 (95.6%)	4.30 (71.7%)	241.6 (90.5%)
C	1.00 (33.3%)	5.84 (58.4%)	23.94 (85.5%)	124.33 (94.2%)	84.22 (95.7%)	4.30 (71.7%)	243.6 (91.2%)
D	1.00 (33.3%)	7.91 (79.1%)	24.75 (88.4%)	124.60 (94.4%)	83.63 (95.0%)	5.12 (85.3%)	247.0 (92.5%)
E	1.00 (33.3%)	8.80 (88.0%)	25.06 (89.5%)	124.98 (94.7%)	84.09 (95.6%)	5.36 (89.3%)	249.3 (93.4%)
F	1.00 (33.3%)	9.45 (94.5%)	25.30 (90.4%)	126.29 (95.7%)	84.44 (96.0%)	5.30 (88.3%)	251.8 (94.3%)
G	1.15 (38.3%)	9.47 (94.7%)	26.80 (95.7%)	126.55 (95.9%)	84.44 (96.0%)	5.50 (91.7%)	253.9 (95.1%)
H	1.16 (38.7%)	9.48 (94.8%)	27.00 (96.4%)	126.56 (95.9%)	84.83 (96.4%)	5.50 (91.7%)	254.5 (95.3%)
Current land-use pattern							
I	1.00 (33.3%)	5.84 (58.4%)	23.14 (82.6%)	120.69 (91.4%)	80.95 (92%)	5.12 (85.3%)	236.7 (88.7%)

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.