

## CONSERVING SPECIES IN A WORKING LANDSCAPE: LAND USE WITH BIOLOGICAL AND ECONOMIC OBJECTIVES

STEPHEN POLASKY,<sup>1,2,4</sup> ERIK NELSON,<sup>1</sup> ERIC LONSDORF,<sup>2</sup> PAUL FACKLER,<sup>3</sup> AND ANTHONY STARFIELD<sup>2</sup>

<sup>1</sup>*Department of Applied Economics, University of Minnesota, 1994 Buford Avenue, St. Paul, Minnesota 55108 USA*

<sup>2</sup>*Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle,  
St. Paul, Minnesota 55108 USA*

<sup>3</sup>*Department of Agricultural and Resource Economics, Box 8109, North Carolina State University,  
Raleigh, North Carolina 27695-8109 USA*

**Abstract.** Habitat loss and fragmentation are major threats to biodiversity. Establishing formal protected areas is one means of conserving habitat, but socio-economic and political constraints limit the amount of land in such status. Addressing conservation issues on lands outside of formal protected areas is also necessary. In this paper we develop a spatially explicit model for analyzing the consequences of alternative land-use patterns on the persistence of various species and on market-oriented economic returns. The biological model uses habitat preferences, habitat area requirements, and dispersal ability for each species to predict the probability of persistence of that species given a land-use pattern. The economic model uses characteristics of the land unit and location to predict the value of commodity production given a land-use pattern. We use the combined biological and economic model to search for efficient land-use patterns in which the conservation outcome cannot be improved without lowering the value of commodity production. We illustrate our methods with an example that includes three alternative land uses, managed forestry, agriculture, and biological reserve (protected area), for a modeled landscape whose physical, biological, and economic characteristics are based on conditions found in the Willamette Basin in Oregon (USA). We find that a large fraction of conservation objectives can be achieved at little cost to the economic bottom line with thoughtful land-use planning. The degree of conflict between conservation and economic returns appears much less using our joint biological and economic modeling approach than using a reserve-site selection approach, which assumes that species survive only inside of reserves and economic activity occurs only outside of reserves.

**Key words:** *biological conservation and economic production; conserving biodiversity; economic-ecological model; efficiency frontier; integrated; land use; working landscape.*

### INTRODUCTION

Loss of habitat is perhaps the single largest factor causing the decline of biodiversity (e.g., Wilson 1988, Wilcove et al. 2000). The widespread conversion of natural habitat to human-dominated land uses has left smaller and more isolated islands of natural habitat in a growing sea of agriculture, pasture, managed forests, and urbanized areas. About half of Earth's useable land is devoted to pastoral or intensive agriculture (Tilman et al. 2001). Other lands are managed forests or developed for housing or industrial use. In response, conservation biologists have called for the establishment of a system of formal protected areas to preserve key remnants of remaining natural habitat.

While formal protected areas play a vital role, many conservation biologists and ecologists recognize the

need for conservation beyond the boundaries of protected areas (e.g., Franklin 1993, Hansen et al. 1993, Miller 1996, Reid 1996, Wear et al. 1996, Chapin et al. 1998, Daily et al. 2001, Rosenzweig 2003). Nearly 90% of land across the globe lies outside of formal protected areas (IUCN [The World Conservation Union] categories I–VI, see WRI 2003), and protected status may arise on lands for reasons other than biodiversity conservation, such as aesthetics or low economic values (Pressey 1994, UNDP et al. 2000, Scott et al. 2001). For these reasons, the consequences of land-use and land-management decisions in working landscapes outside of protected areas are vitally important. As Miller (1996: 425) stated: “. . . biodiversity will be retained to the extent that whole regions are managed cooperatively among protected areas, farmers, foresters, and other neighboring land users.”

While some land uses are clearly incompatible with some conservation goals, many elements of biodiversity can tolerate at least some level of human disturbance and alteration of the landscape (e.g., Redford

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<sup>4</sup> E-mail: spolasky@appec.umn.edu



PLATE 1. Oregon white oak trees in one of the few remnant oak savannas at the Rattlesnake Butte Preserve, Willamette Valley. Photo credit: Cathy Macdonald.

and Richter 1999, Currie 2003). A key question for conservation is whether the entire landscape, including both protected areas and areas devoted to economic uses outside of protected areas, provides a sufficient likelihood that elements of biodiversity will persist on the landscape. The flip side of this question is whether conservation plans that provide a sufficient likelihood of biodiversity persistence will be acceptable to landowners and other decision makers. Conservation planning is never done in a vacuum isolated from economic and political factors. Conservation plans that prove costly to the bottom line of landowners or other decision makers (at least in the short term) will engender more political opposition and are less likely to be implemented.

In this paper we develop a spatially explicit model for analyzing the consequences of alternative land-use patterns on the persistence of a suite of species and market-oriented economic returns. The biological model uses habitat preferences, habitat area requirements, and dispersal ability for each species to predict the probability of species persistence given a land-use pattern. The economic model uses characteristics of the land unit and location to predict the value of commodity production given a land-use pattern. We use the combined biological and economic model to search for efficient land-use patterns in which the conservation

outcome cannot be improved without lowering the value of commodity production.

We illustrate our methods with an example that includes three alternative land uses—managed forestry, agriculture, and biological reserve (protected area)—and a set of 97 terrestrial vertebrates on a modeled landscape whose physical, biological, and economic characteristics are based on conditions found in the Willamette Basin in Oregon, USA (see Plate 1). Prior work evaluating both species persistence and economic returns focused on a single or small set of species and a single economic activity such as forestry (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). Using this example, we find land-use patterns that achieve a large fraction of potentially achievable species conservation with little reduction in the value of commodity production.

We contrast our approach with a more traditional analysis of reserve-site selection in which a set of reserves is chosen to represent a target set of species in as few sites as possible (e.g., Margules et al. 1988, Sætersdal et al. 1993), or to represent as many species from the target set as possible given a constraint on the number of sites selected or the conservation budget (e.g., Church et al. 1996, Faith and Walker 1996, Ando et al. 1998). Reserve-site selection implicitly assumes

that only reserves sites contribute to conservation objectives (and only non-reserve sites contribute to economic objectives). In our model, land in managed forestry and agriculture provides some habitat value while also generating valuable commodities.

THE BIOLOGICAL AND ECONOMIC MODELS

The land-use pattern is input for both the biological and economic models. The land-use pattern is determined by land-use decisions made on each land parcel in the study area and the characteristics of those parcels. In general, parcels may be defined as irregularly shaped polygons determined by land ownership, land cover, or other criteria, or as cells in a grid. In the illustrative example developed below (see *Data and methods . . .*), land parcels are 400-ha squares. The land-use pattern and characteristics of land parcels determine habitat patterns that are used by the biological model to determine species-persistence probabilities in the study area. The land-use pattern and characteristics of land parcels are used in the economic model to determine economic returns in the study area.

*The biological model*

The biological model predicts the probability of persistence for a large suite of species given a land-use pattern. Each species' appraisal of a land-use pattern depends on three species-specific traits: the amount of land area required for a breeding pair, compatibility with habitat in the land-use pattern, and the species' ability to disperse between suitable patches of habitat.

We begin by calculating a suitability score for each land parcel  $j$  for each species  $s$ . The suitability score,  $Z_{sj}$ , defines the number of breeding pairs of species  $s$  that the land parcel could support given its land use,  $X_j$ :

$$Z_{sj} = \frac{A_j C_{sj}(X_j)}{AR_s} \tag{1}$$

where  $A_j$  is the area of parcel  $j$ ,  $C_{sj}(X_j)$ , is the habitat compatibility score of parcel  $j$  for species  $s$ , and  $AR_s$  is the amount of area needed by a breeding pair of species  $s$ . The habitat compatibility score,  $C_{sj}(X_j)$ , ranges from 0 to 1, where 0 represents unsuitable habitat and 1 represents prime habitat. This score scales actual area of parcel  $j$  to "effective parcel area." The habitat compatibility score for a parcel depends upon its land use,  $X_j$ ; the score may be quite different for different land uses (e.g., agricultural use vs. natural habitat). Dividing by  $AR_s$  yields the number of breeding pairs of species  $s$  that can use the effective area of parcel  $j$ .

For a given land-use pattern, we aggregate adjoining land parcels—parcels that share a common border rather than just touching at a point—that contain suitable habitat for a species into habitat patches for that species. We define "suitable habitat" for species  $s$  as those parcels that have a habitat compatibility score above a threshold value:  $C_{sj}(X_j) \geq C_s$ , for  $0 < C_s \leq 1$ . Because  $C_{sj}(X_j)$  values differ by species, each species potentially

has a uniquely defined set of habitat patches. The suitability score for habitat patch  $n_s$  for species  $s$ , is defined as the sum of the parcel suitability scores for all adjacent parcels that constitute the habitat patch:

$$Z_{sn_s} = \sum_{j \in n_s} Z_{sj} \tag{2}$$

We use the habitat-patch suitability scores and the location of habitat patches for each species to determine the landscape suitability score for that species. There are several steps in determining the landscape suitability score. We first calculate a range of possible landscape suitability scores assuming unlimited dispersal among patches (habitat as one single patch) and then assuming no dispersal among patches (complete isolation of all habitat patches). The landscape suitability score with no dispersal limitations for species  $s$  is defined as the sum of all of the habitat suitability scores for species  $s$ :

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

where  $N_s$  represents the total number of suitable habitat patches for species  $s$ . The landscape suitability score for species  $s$  where habitat patches are completely isolated and only contribute to the landscape score if they exceed some minimum threshold is defined as

$$Lmin_s = \sum_{n_s=1}^{N_s} Z_{sn_s}$$

for the set of parcels where

$$Z_{sn_s} \geq \gamma_s \tag{4}$$

where  $\gamma_s$  represents the minimum number of breeding pairs for species  $s$  that a patch must support on its own before the habitat patch contributes to the landscape score. For high values of  $\gamma_s$  the value of  $Lmin_s$  can be 0. On the other hand, as  $\gamma_s$  approaches zero,  $Lmin_s$  approaches  $Lmax_s$ . In the latter case, the landscape suitability score depends only on the total amount of effective habitat and not its spatial pattern (for an example of species persistence analysis where habitat pattern does not matter for a large group of species see Schumaker et al. [2004]).

Whether the landscape suitability score for species  $s$ ,  $LS_s$ , is closer to  $Lmin_s$  or  $Lmax_s$  depends on the connectivity of habitat patches and the species' dispersal ability. The connectivity score for each suitable habitat patch is defined as

$$P_{sn_s} = \sum_{m_s=1}^{N_s} \exp(-\alpha_s d_{m_s n_s}) Z_{sm_s} \tag{5}$$

where  $d_{m_s n_s}$  is the distance between suitable habitat patch  $m_s$  and suitable habitat patch  $n_s$ , and  $\alpha_s > 0$  represents the reciprocal of the mean dispersal ability of species  $s$ . The patch connectivity score is dependent

on the patch's own habitat suitability score and the habitat suitability scores for all other suitable habitat patches to which species  $s$  can disperse, weighted by the distance between the patches and the species dispersal ability. The effect of distance is represented by a negative exponential distribution (Vos et al. 2001). Other factors besides distance may influence dispersal ability (King and With 2002, Gardner and Gustafson 2004) but are not considered here.

We then aggregate the habitat-patch connectivity scores to compute a landscape connectivity score. In a completely connected landscape, all habitat-patch connectivity scores for species  $s$  would equal  $Lmax_s$ , and the aggregate patch score summing over all suitable habitat patches would be  $N_s Lmax_s$ . On the other hand, if all suitable habitat patches are completely isolated with no contribution from any other patch, habitat patch connectivity for patch  $n_s$  would be  $Z_{sn_s}$  and the aggregate patch score summing over all suitable habitat patches would be  $Lmax_s$ . We define the landscape connectivity score for species  $s$ ,  $LC_s$ , as the observed score relative to the possible minimum and maximum values, scaled so that its value can range between 0 and 1:

$$LC_s = \frac{\sum_{n_s=1}^{N_s} P_{sn_s} - Lmax_s}{(N_s - 1)Lmax_s}. \tag{6}$$

The landscape connectivity score for species  $s$ ,  $LC_s$ , is near zero when species  $s$  has low dispersal ability in an extremely fragmented landscape. The landscape connectivity score equals 1 for a completely connected landscape.

We use the landscape connectivity score along with  $Lmax_s$  and  $Lmin_s$  to determine the overall landscape suitability score,  $LS_s$ , for species  $s$ :

$$LS_s = (1 - LC_s)Lmin_s + LC_s Lmax_s. \tag{7}$$

For an unconnected landscape ( $LC_s = 0$ ), the landscape suitability score for species  $s$  is  $Lmin_s$ . For a completely connected landscape ( $LC_s = 1$ ), the landscape suitability score for species  $s$  is  $Lmax_s$ .

The landscape suitability score for each species,  $LS_s$ , is a measure of the expected number of breeding pairs the landscape will support. To determine the expected biodiversity score for the landscape we convert  $LS_s$  into a probability that the species will persist on this landscape,  $LP_s$ , using a saturating function:

$$LP_s = \frac{LS_s^g}{LS_s^g + k^g} \tag{8}$$

where  $k$  is the half-saturating constant (the landscape score yielding a persistence 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 or threshold value for a viable population size.

The expected number of species that persist on the landscape, i.e., the landscape biological score,  $LB$ , is

the sum of species probability scores over all the species:

$$LB = \sum_{s=1}^S LP_s. \tag{9}$$

*The economic model*

The economic model is used to predict the present value of commodity production for a given land-use pattern. We first determine the present value of commodity production for an individual parcel based on the land use and characteristics of the parcel. We then sum these values across all parcels to generate the economic score for the landscape.

We note at the outset that we focus on the value of commodity production. In principle, the economic model should include the value of all goods and services generated by the land-use pattern, including "ecosystem services," the majority of which are not bought or sold in markets (e.g., Daily 1997, Daily et al. 2000). At least in theory, the general approach of the economic model discussed below can include ecosystem goods and services. We do not do so here because of the difficulty, at present, of generating reliable estimates of ecosystem service value. Our analysis, then, illustrates the degree to which there are trade-offs between the value of commodity production and species conservation, rather than attempting to illustrate a complete set of trade-offs among all potentially valuable goods and services generated by a landscape.

Production of commodities on a parcel is determined by the characteristics of the parcel, such as soil type and topography, and its land use. Let  $y_{jc}(X_j)$  represent the annual production of commodity  $c$  on parcel  $j$  given land use  $X_j$ ,  $p_c$  is the market price of commodity  $c$ , and  $Cost_{jc}(X_j)$  is the annual production costs of producing commodity  $c$  on parcel  $j$  associated with land use  $X_j$ . The present value of commodity production on parcel  $j$  is

$$V_j(X_j) = \sum_{t=0}^{\infty} \left\{ \sum_c [p_c y_{jc}(X_j)] - Cost_{jc}(X_j) \right\} \delta^t \tag{10}$$

where  $\delta$  is the annual discount factor ( $0 < \delta < 1$ ).

A parcel whose land use is a biological reserve does not produce a marketed commodity and thus is given an economic score of 0. Such parcels in fact generate valuable ecosystem services (apart from species conservation, which is captured in the biological model). Reserves may also have associated management costs. For both these reasons, the economic return to a biological reserve properly calculated is not zero. In principle it is easy to incorporate an economic score different from zero for a biological reserve; however, accurately estimating the score is difficult in practice.

The total landscape economic score,  $LE$ , sums the present value of commodity production of each parcel given its land use:

$$LE = \sum_j V_j(X_j). \quad (11)$$

In an important respect, the economic model is simpler than the biological model. The value of commodity production 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. Two conditions must be true for this assumption to hold. First, prices must not be significantly influenced by local supply (in other words, local production is sold into a national or global market for which it makes up a small fraction of the total supply). Second, there must not be any "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., Tyrvaainen and Miettinen 2000, Irwin 2002, Thorsnes 2002, Vossler et al. 2003) and the effect of pollinators on crop yields (e.g., Nabhan and Buchmann 1997, Allen-Wardell et al. 1998). Examples of negative externalities include pollution runoff from a parcel that lowers productivity of downstream parcels, and noise or odor from nearby industrial or agricultural operations.

#### OPTIMIZATION PROBLEM AND HEURISTIC SOLUTION METHODS

We combine the biological and economic models with optimization methods to find efficient land-use patterns for which it is not possible to increase the landscape biological (LB) score without decreasing the landscape economic (LE) score, and vice versa. In general, there will be many efficient land-use patterns. Finding the complete set of efficient land-use patterns traces out an efficiency frontier that illustrates what is feasible and the trade-offs between increasing biological returns and economic returns.

The combined biological and economic optimization problem can be written quite simply as follows:

$$\text{Max LB} \quad \text{subject to } LE \geq \bar{L} \quad (12)$$

where the maximization is taken over the choice of land use in each parcel (i.e., the maximization is taken over a land-use pattern). In words, the problem is to find a land-use pattern with the highest possible biological score that guarantees an economic return at least as large as  $\bar{L}$ . By varying the required economic threshold,  $\bar{L}$ , a whole family of solutions can be found that trace out the efficiency frontier. The frontier can also be found by maximizing the LE score subject to a constraint that the LB score meet a certain threshold.

This formulation of the problem is deceptively simple. Because the optimization problem is an integer program involving a potentially large number of parcels each with several potential land uses, and because the biological model involves nonlinear spatial considerations, finding an optimal solution to this problem can be exceedingly difficult. There are a number of heuristic algorithms that can be used to find good,

though not necessarily optimal, solutions. We use six algorithms and then combine the best solutions from these algorithms to trace out the efficiency frontier. The six heuristic algorithms are summarized in Table A1 of the Appendix. Each heuristic either starts at the land-use pattern with the maximum value of commodity production or the land-use pattern with zero commodity production (all biological reserves). Each heuristic then sequentially makes a change in land use on one parcel per step where each step maximizes the increase in the biological or economic score (or minimizes its loss), or maximizes the ratio in the gain in one score relative to the loss in the other score. Generally, heuristics that jointly consider both biological and economic scores by looking at the ratio do best, though not always. From these six heuristic solutions, we take all solutions that are not dominated, i.e., for which there is no other solution from any of the six heuristics that yields (1) a higher economic and a higher or equal biological score, or (2) a higher biological score and a higher or equal economic score. While this set of solutions is probably a good approximation of the efficiency frontier, it is not guaranteed to be identical to the true efficiency frontier because the heuristic solutions only evaluate one change at a time rather than doing a global search over all possible land-use changes.

#### DATA AND METHODS USED IN THE ILLUSTRATIVE EXAMPLE BASED ON THE WILLAMETTE BASIN

To illustrate our approach we applied our model to a simple landscape composed of 196 400-ha square parcels arranged in a  $14 \times 14$  grid with parameter values and spatial patterns similar to those found in the Willamette Basin in Oregon, USA. This illustrative example includes 97 terrestrial vertebrate species, three land uses (managed forestry, agriculture, and biological reserve), and six habitat categories (managed forestry, agriculture, shrub, hardwood, conifer, and prairie/meadow). Land use uniquely determines the habitat category except for biological-reserve land where habitat category is determined by the parcel's presettlement vegetation type.

#### *Biological model*

The 97 terrestrial vertebrate species in our study are species that live in the Willamette River Basin in Oregon and do not depend on aquatic habitat (Adamus et al. 2000, Schumaker et al. 2004). Habitat compatibility scores for each of the 97 species for each of the six habitat categories (managed forestry, agriculture, shrub, hardwood, conifer, and prairie/meadow) are based on Adamus et al. (2000). Habitat compatibility scores can take on values of 0 (unsuitable habitat), 0.5 (marginally suitable habitat), or 1.0 (prime habitat). We assume that both marginal and prime habitat count for purposes of assembling habitat patches (threshold value  $C_s = 05$ ). Parcels containing marginal or prime habitat that share a common side are combined into a hab-

itat patch (but diagonal connections are not considered). Table A2 in the appendix contains a complete list of the 97 species and their habitat compatibility scores for each of the habitat types.

There is little systematic published information on which to base values for habitat area requirement and dispersal ability for most of the 97 species used in our model, though Brown (1985), Baguette et al. (2003), Joly et al. (2003), and Lichtenstein and Montgomery (2003) contain some useful information. Habitat area requirements and dispersal-ability values are based primarily on the following assumptions: (1) area requirements scale to the size of the animal (larger animals require more habitat), (2) larger animals disperse further than smaller animals (Bowman et al. 2002), (3) birds disperse further than mammals, and (4) mammals disperse further than amphibians/reptiles. Habitat area requirements and dispersal-ability values are listed in Table A2 in the appendix. The relatively small area of our  $14 \times 14$  landscape limits distances between habitat patches, which may make our results somewhat insensitive to species' ability to disperse. Dispersal ability may be important on a large fragmented landscape where distances between patches are great.

The default values of the half saturation constant ( $k$ ) and shape coefficient ( $g$ ) in Eq. 8 were chosen to create sufficiently large differences among species' evaluations of land-use patterns. For small  $k$ , complete species persistence on the landscape results for most land-use patterns. For large  $k$ , species cannot persist on the landscape for any land-use pattern. However, because  $k$  and  $g$  are global rather than species-specific parameters they do not affect the relative ranking of species persistence scores across species.

On the  $14 \times 14$  landscape the distance between parcels  $i$  and  $j$ ,  $d_{ij}$ , is given by

$$d_{ij} = \max \{ \lambda_{ij} - 2000, 0 \} \quad (13)$$

where

$$\lambda_{ij} = (|xc_i - xc_j|) + (|yc_i - yc_j|) \quad (14)$$

and  $xc_i$  and  $yc_i$  refer to the  $x$ -coordinate and  $y$ -coordinate, respectively, of a parcel  $i$ 's centroid (the  $14 \times 14$  landscape grid is measured in meters). Finally, distance between patch  $m_s$  and  $n_s$ ,  $d_{m_s, n_s}$ , is equal to the shortest distance between a parcel that is a member of patch  $n_s$  and a parcel that is a member of patch  $m_s$ .

#### Economic model

Both managed-forestry and agricultural land uses produce marketed commodities for which the model estimates a present value of returns. The present value of a parcel whose land use is managed forestry ( $X_j = x_f$ ) depends on the productivity of the parcel for growing timber ( $y_{jf}$ ), the price of timber ( $p_t$ ) and the costs of harvesting timber ( $Cost_{jf}$ ). Timber yield, measured in terms of board feet per hectare (1 board foot = 144 cubic inches, i.e., 0.00236 m<sup>3</sup> of wood), depends upon

the age of the timber stand when harvested and the parcel's forestry site index (King 1966, Curtis et al. 1981, Curtis 1992). We assumed a 45-year rotation age Douglas-fir forest (with commercial thinning at age 35), which is typical of commercial timber operations in the Willamette Basin. Douglas-fir site index information, which is based on soil, climate conditions, and other physical conditions, comes from U.S. Department of Agriculture (USDA-NRCS 2001a, b, 2003). Timber yield is multiplied by timber price per board foot (Lichtenstein and Montgomery 2003, Claire Montgomery, *personal communication*) to determine timber revenue per hectare. Timber production costs equal the sum of logging and hauling costs per board foot plus an area maintenance cost. Logging costs per board foot are a function of a parcel's average slope and tree size (Fight et al. 1984, PNW-ERC 1999b). Hauling costs per board foot are a function of a parcel's average slope and distance to the nearest processing mill (Latta and Montgomery 2004, Claire Montgomery, *personal communication*). Per unit area maintenance costs of forestry production are constant across parcels (Lichtenstein and Montgomery 2003, Claire Montgomery, *personal communication*). We assume even-aged forestry management with 45-year rotations such that 1/45th of the parcel is harvested (and thinned) each year. Given these assumptions, the present value of economic return from parcel whose land use is managed forestry is

$$V_j(x_f) = \sum_{t=0}^{\infty} \frac{A_j(p_t y_{jt}) - Cost_{jt}}{45} \delta^t \quad (15)$$

The present value of a parcel whose land use is agriculture ( $X_j = x_a$ ) depends upon the parcel's crop growing productivity ( $y_{ja}$ ), the price of agricultural produce ( $p_a$ ) and production costs ( $Cost_{ja}$ ). We modeled an agricultural operation with a typical mix of crops grown in the Willamette Basin. Agricultural crop yield per hectare depends upon the parcel's soil class and whether the parcel is irrigated (PNW-ERC 1999a, OWRD 2001, USDA-NRCS 2001a, b, 2003). The yield is multiplied by the market price for the agricultural produce,  $p_a$ , (OSU Extension Service 2002) to generate estimated revenue per hectare. Cost information ( $Cost_{ja}$ ) comes from Oregon State University's Extension Service (OSU Extension Service 2003). Assuming that agricultural activity occurs every year, the present value of economic return of a parcel whose land use is agriculture is

$$V_j(x_a) = \sum_{t=0}^{\infty} A_j(p_a y_{ja} - Cost_a) \delta^t \quad (16)$$

Because a parcel in a biological reserve ( $X_j = x_b$ ) does not produce a marketed commodity, the present value of commodity returns is zero:  $V_j(x_b) = 0$ .

#### The landscape

Each of the 196 parcels on the  $14 \times 14$  landscape was assigned a presettlement vegetation cover type

(shrub, hardwood, conifer, or prairie/meadow) and an economic return for managed forestry and agriculture. To generate reasonable values and spatial patterns for the  $14 \times 14$  landscape, we partitioned a map of the Willamette Basin (ONHP 2000) into a parcel map based on land cover (ca. 1990; *available online*)<sup>5</sup> and a constraint that no parcel be larger than 750 hectares. This parcel map was overlaid with maps of presettlement vegetation cover in the Willamette Basin as described by surveyors for the General Land Office between 1851 and 1909 (PNW-ERC 1999c), soil class index, Douglas-fir site index, and point-of-use irrigation permits. Of the 10 372 parcels on the partitioned Willamette Basin map, 6197 had a complete set of data.

Using the subset of 6197 parcels with complete data, we created a probability distribution for a parcel's presettlement vegetation type as a function of its neighbors' presettlement vegetation types. We assumed that a parcel's presettlement vegetation (shrub, hardwood, conifer, or prairie/meadow) indicates the vegetation coverage that would emerge if the parcel were a biological reserve. A presettlement vegetation pattern that mimics the Willamette Basin's presettlement vegetation pattern was generated for the  $14 \times 14$  landscape using a random-number generator and the spatially explicit presettlement vegetation probability distribution noted above.

We used more complicated techniques to generate present values for managed forestry and agriculture on the  $14 \times 14$  landscape. A forestry value for each of the 6197 parcels was found by using Eq. 15, the data sources noted in *Economic model* (above), and Willamette Basin parcel data. We used a spatial autoregressive (SAR) model (LeSage 1999) to explain a Basin parcel's present value in managed forestry as a function of its presettlement vegetation coverage and its adjacent neighbors' present value in forestry. The managed-forestry present value for each parcel on the  $14 \times 14$  landscape was generated using a random-number generator, the estimated SAR model coefficients, and the  $14 \times 14$  landscape's already-established presettlement vegetation pattern.

An agriculture value for each of the 6197 parcels was found by using Eq. 16, the data sources noted in *Economic model* (above), and Basin parcel data. We used the SAR model to estimate a Basin parcel's agricultural present value as a function of its managed-forestry present value, presettlement vegetation coverage, irrigation capability, and its adjacent neighbors' agricultural present value. The agricultural present value for each parcel on the  $14 \times 14$  landscape was generated using a random-number generator, the estimated SAR model coefficients for agriculture, modeled irrigation capability, and the  $14 \times 14$  landscape's already-established managed-forestry present value and presettlement vegetation pattern. Irrigation capability was

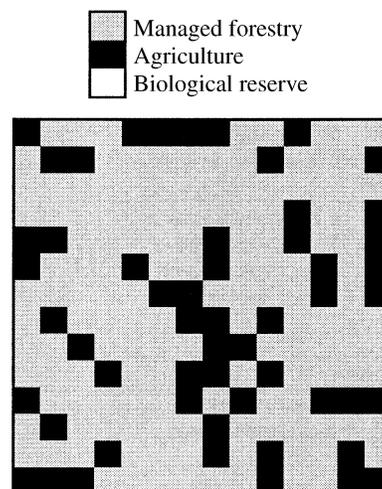


FIG. 1. A base-case land use pattern on the  $14 \times 14$  landscape where every parcel is put into its highest economic use. The landscape grid has 196 square parcels, and each parcel is 400 ha.

placed in a subset of the  $14 \times 14$  landscape's parcels such that the proportion of the modeled landscape's parcels with irrigation capability approximated the proportion of parcels in the Willamette Basin with irrigation capability.

#### Simulation experiments

We performed a number of simulations using the biological and economic model applied to the  $14 \times 14$  landscape. We began with a "base case" that takes a default landscape (generated as described in *The landscape* [above]) and default parameter values for the biological model (as listed in *Biological model* [above] and Table A2 in the appendix) and the economic model (as listed in Table A3 in the appendix). In the base case, the mean value of managed forestry is  $\$9720 \pm 1195/\text{ha}$  and  $\$9250 \pm 9271/\text{ha}$  in year 2000 U.S. dollars. Agricultural values vary widely with soil quality and irrigation status. The base-case land-use pattern that generates the highest value for commodity production is shown in Fig. 1.

We compare the results obtained in the base case with a traditional reserve-site selection model, which considers only the contribution of biological-reserve parcels to the biological objective. To do this, we set all species' habitat-compatibility scores for managed forestry and agriculture lands equal to 0. We consider two variants of the reserve-site selection model, one with dispersal and one without dispersal. In the variation that drops the dispersal-ability parameter from the biology model, only reserve parcels that are contiguous contribute biological value to each other.

We also conducted a set of sensitivity analyses by changing the base-case assumptions one at a time to see how such changes affect the efficiency frontier. In the first set of sensitivity analyses we generated four

<sup>5</sup> (<http://www.fsl.orst.edu/pnwerc/wrb/access.html>)

alternative landscapes using the same methodology used to generate the base-case landscape. We also conducted sensitivity analyses by varying default parameters in the biological and economic models. We varied assumptions about: (1) the minimum amount of area needed for a breeding pair, (2) the half-saturating constant  $k$  (from Eq. 8), (3) the power constant  $g$  (from Eq. 8), and (4) changing the number of breeding pairs that a habitat patch must support on its own before the patch contributes to the landscape score. We also analyzed the model with different net present values of economic returns in managed forestry and agriculture.

## RESULTS

### *Base case*

Using the heuristic algorithms described in *Optimization problem* . . . (above) to solve the optimization problem in Eq. 12 with the base case for our  $14 \times 14$  landscape, we find the estimated efficiency frontier (Fig. 2). The most striking feature of the efficiency frontier is its L-shape, demonstrating the existence of land-use patterns that generate high scores for both biological conservation and commodity value. Relatively minor modifications of the land-use pattern that maximized the landscape economic (LE) score produced a 14.6% increase in the landscape biological (LB) score (from 74.5 to 85.3) with only a 7.1% decline in the LE score (from US \$1046 million to US \$972 million). Furthermore, the resulting LB score from this modification was near the maximum possible score, 88.5 (because the  $14 \times 14$  landscape is relatively small, not all 97 species could persist on the landscape no matter the land-use pattern). Further modifications of the land-use pattern to increase the LB score from 85.3 to the maximum score of 88.5 produced dramatic declines in the LE score (US \$972 million to US \$270 million). Note that the LB score is reasonably high even when the landscape is managed to maximize economic gain. Interestingly, the maximum LB score did not occur when all parcels were put in biological reserves.

In moving along the efficiency frontier from lower right to upper left, land-use patterns shift from maximizing commodity value to maximizing species persistence (Fig. 3A to E). The parcels most likely to be converted to biological reserves initially (Fig. 3A to C) are managed-forestry parcels with a presettlement vegetation coverage type of shrub and hardwood. Very few agricultural parcels are converted until movement is far along the efficiency frontier (Fig. 3D and E). Parcels with prairie/meadow presettlement vegetation coverage are never put into biological reserves at any of the five points along the efficiency frontier. As shown in Fig. 3A through E, land uses tend to clump together to form larger blocks of like habitat. A measure of biological reserve "connectivity," defined as the number of perimeter segments that form the conservation reserve network divided by the number of parcels in

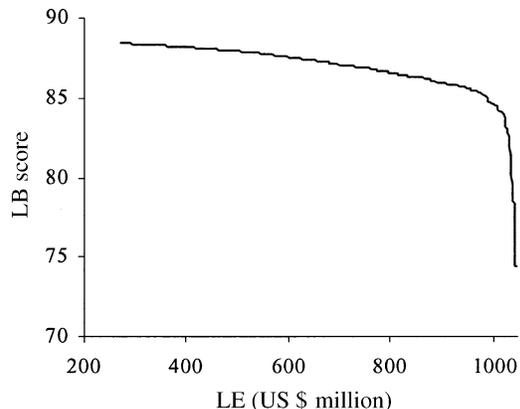


FIG. 2. The base-case landscape economic-biological score efficiency frontier. The x-axis measures the landscape economic (LE) score in millions of U.S. dollars for a given land-use pattern on the  $14 \times 14$  landscape. The y-axis measures the landscape biological (LB) score (the sum of the expected species probability scores, calculated from Eq. 9) for a given land-use pattern on the  $14 \times 14$  landscape. The land-use pattern in Fig. 1 is associated with the point that forms the right-hand terminus of the efficiency frontier. The efficiency frontier has an L-shape, indicating that it is possible to arrange the land pattern in a way that attains a high biological score and a high economic score. Trying to maximize either the biological score or the economic score results in large losses in the other score.

conservation, for various land-use patterns on the base-case efficiency frontier is given in Table 1. Smaller measures indicate more highly connected or clumped biological reserves.

### *Comparison with reserve-site selection*

The efficiency frontiers for a traditional reserve-site selection model both with and without dispersal lie well within the base-case efficiency frontier (Fig. 4). For example, at a LB score of 77, the LE score in the base case (\$1044 million) is far higher than in reserve site selection with dispersal (\$670 million) or without dispersal (\$519 million). When all land is put into managed forestry or agriculture and none into biological reserves, the LB scores for the reserve-site selection scenarios are 0; therefore, the efficiency frontiers extend to the horizontal axis. Because managed lands contribute nothing to the biological score under the reserve-site selection scenarios, increasing the amount of land in biological reserves generally increases (can never decrease) the LB scores. Therefore, the reserve-site selection efficiency frontiers extend to the vertical axis as well. The efficiency frontiers are more rounded (less L-shaped) under the reserve-site selection scenarios than under the base case. In other words, there is more apparent trade-off between biological and economic objectives under the reserve-site selection approach.

There are major differences in land-use patterns generated by reserve-site selection and the base case. To

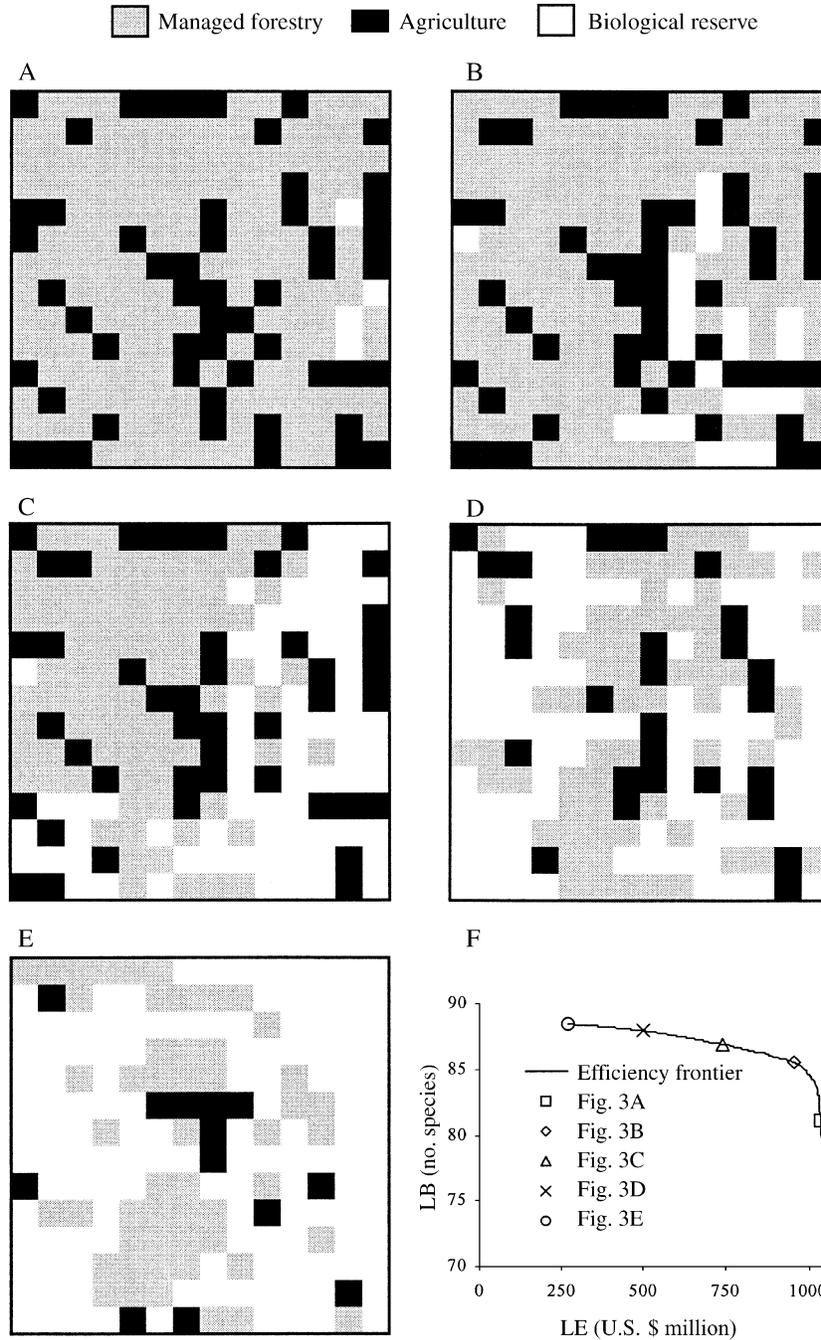


FIG. 3. Various base-case land-use patterns for points that lie on the base-case efficiency frontier (see Fig. 2). Beginning from the right-hand terminus of the efficiency frontier, land-use patterns are shown that are (A) 10% along the efficiency frontier, (B) 25% along the efficiency frontier, (C) 50% along the efficiency frontier, (D) 75% along the efficiency frontier, and (E) at the left-hand terminus of the efficiency frontier. (F) The coordinate positions of the land-use patterns shown in (A)–(E).

illustrate the differences consider the efficient land-use pattern for each scenario at an LB score of 77 (Fig. 5A–C). Under the base case, 77 species can be sustained mainly through having large blocks of managed forest. There is only one parcel put into biological reserve. In the reserve-site selection model with dispersal, 95 parcels need to be put into biological re-

serves to sustain 77 species, while 101 parcels are needed in the reserve site selection case without dispersal.

*Sensitivity analyses*

Comparing the efficiency frontiers for alternative landscapes shows that the efficiency frontier is largely unchanged in terms of shape or location (Fig. 6). The

TABLE 1. Summary of various base-case land-use patterns (as presented in Fig. 3A–E) that have landscape economic (LE) and biological (LB) score combinations that lie on the efficiency frontier.

Land-use pattern	Landscape score		No. parcels in land use			No. parcels in initial base case converted to biological reserve†		
	Economic, LE (US \$ × 10 <sup>6</sup> )	Biological, LB (No. species persisting)	Agriculture ( $X_j = x_a$ )	Managed forestry ( $X_j = x_r$ )	Biological reserve ( $X_j = x_b$ )	Agriculture ( $X_j = x_a$ )	Managed forestry ( $X_j = x_r$ )	Biological reserve “connectivity”‡
Fig. 3A	1034	81.09	54	138	4	0	4	3.50
Fig. 3B	954	85.55	53	121	22	4	18	2.82
Fig. 3C	740	86.91	45	81	70	10	60	1.80
Fig. 3D	498	87.93	28	65	103	26	77	1.67
Fig. 3E	270	88.48	13	52	131	35	96	1.25

† See Fig. 1.

‡ The number of perimeter segments that form the conservation reserve network divided by the number of parcels in conservation.

only noticeable difference among landscapes comes when more randomly drawn high-value managed forestry and agricultural lands are included, which shifts the efficiency frontier a bit to the right. These results indicate that it was not the particular random draw of landscape that generates our results.

Making changes in default biological or economic parameters shifts the efficiency frontier but does not change its basic shape (Fig. 7A–C). Favorable changes in biological parameters (decreasing the minimum area required for a breeding pair, reducing the half-saturation coefficient, increasing the power coefficient in the saturation function, or lowering the threshold value on the number of breeding pairs that a habitat patch must support on its own before the patch contributes to the landscape score) shift the efficiency frontier upwards. Unfavorable changes in biological parameters shift the efficiency frontier downward. Favorable changes in economic parameters (increasing the value of agricultural or timber production) shifts the efficiency frontier to the right. In general, changes in biological or economic parameters shift the efficiency frontier but do not change its L-shape. (Other changes in default assumptions, including the size and shapes of the parcels, did not change the efficiency frontier’s L-shape).

#### DISCUSSION

Rather than facing a stark trade-off between conserving biodiversity and production of high-valued commodities, we find that a large fraction of conservation objectives can be achieved at little cost to the economic bottom line with thoughtful land-use planning. In our example landscape, based on conditions in the Willamette Basin (Oregon, USA), there is a land-use pattern that simultaneously generates 96% of the maximum landscape biological (LB) score (85.3 out of 88.5) and 93% of the maximum landscape economic (LE) score (US \$972 million out of US \$1046 million). Many species are able to persist in a landscape largely devoted to economic use because they view managed forests or agricultural land as suitable habitat. The

number of species that persist on the landscape can be increased by adjusting the spatial pattern of economic activity to create large blocks of forest (or agriculture), often at little economic cost. Further increases in species persistence can be achieved at relatively low cost by strategically placing biological reserves in areas with natural habitats required by some species but low economic value.

More evidence of the limited trade-offs between conservation and economic returns in the  $14 \times 14$  landscape example (a  $14 \times 14$  square grid of 196 parcels; each parcel is 400 ha) is shown by the fact that the efficiency frontier under the base case does not extend to either the horizontal or vertical axis (Fig. 2). The efficiency frontier starts above the horizontal axis because many species are able to persist even when the landscape is managed to maximize economic gain because they view managed forest and/or agricultural land as suitable habitat and there are relatively large contiguous blocks of both. The efficiency frontier does not extend to the vertical axis because the maximum landscape biological score does not occur where all parcels are reserves. This initially counterintuitive outcome occurs because a few of the 97 species depend solely on managed-forestry lands or agricultural lands for habitat. A landscape comprised entirely of conservation with no economic activity, while clearly best for some species, is not the best land-use pattern for maximizing the sum total of persistence for all species. Others studies have found that biodiversity can be higher in slightly disturbed areas vs. in natural undisturbed areas (e.g., Yazvenko and Rapport 1996, Johnson et al. 1998).

Even the limited trade-offs between conservation and economic objectives shown in the example may be something of an overstatement. In this example we did not consider the economic value of ecosystem services, such as the provision of clean water, nutrient filtration, climate regulation, and ecotourism (Daily 1997). Including the value of ecosystem services in economic returns would tend to increase the value of conserving

TABLE 1. Extended.

No. biological reserve parcels ( $X_j = x_b$ ), by habitat type			
Shrub	Hardwood	Prairie/meadow	Conifer
1	1	0	2
9	10	0	3
12	27	0	31
20	29	0	54
23	46	0	62

land in biological reserves relative to other land uses, thereby reducing apparent trade-offs between conservation objectives and economic returns.

Even so, there remains at least some degree of conflict between conservation and the value of commodity production. In the  $14 \times 14$  landscape example, obtaining the final 4% of the conservation objective (moving the landscape biological score from 85.3 to 88.5) requires a drop in commodity value of over 70% (\$972 million to \$270 million). Similarly, pushing for maximum economic returns (moving from \$972 million to \$1,046 million) generates significant biological losses (from 85.3 to 74.5). Other studies have found a similar pattern in trade-offs between conservation and economic objectives, namely that many conservation objectives can be achieved at very low cost but that full protection is often very expensive (Montgomery et al. 1994, 1999, Ando et al. 1998, Polasky et al. 2001). In general, difficult trade-offs occur when the habitat of a species with limited range overlaps and is inconsistent with economically valuable land uses. Still, even in this case, costs can be reduced by careful consid-

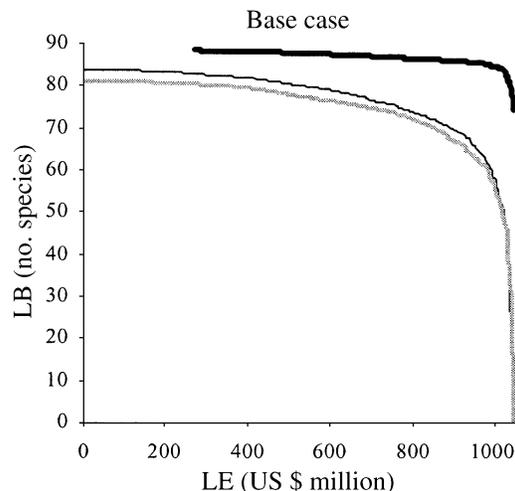


FIG. 4. The efficiency frontiers from two reserve-site selection scenarios simulated on the default  $14 \times 14$  landscape. For comparison purposes, the base-case efficiency frontier is also presented. The gray line denotes the efficiency frontier of the reserve-site selection scenario without dispersal. The thin black line denotes the efficiency frontier of the reserve-site selection scenario with dispersal. The efficiency frontiers from the reserve-site selection scenarios lie well within the efficiency frontier of the base case. The efficiency frontiers associated with the reserve-site selection scenarios are more rounded (less L-shaped), indicating more continuous trade-offs between biological (LB) and economic (LE) objectives.

eration of the type and location of economic activities that can coexist with survival of the species.

The degree of conflict between conservation and economic returns appears much greater using the reserve-site selection approach than using our joint biological and economic modeling approach. Assuming no biological value in lands used for economic purposes and

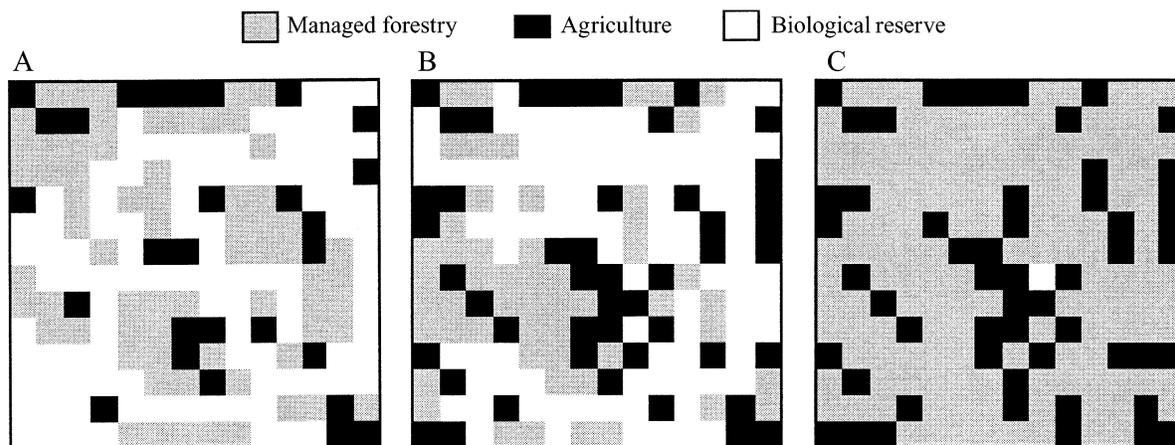


FIG. 5. Land-use patterns on the default  $14 \times 14$  landscape that have landscape biological (LB) scores of  $\sim 77$  for the reserve-site selection scenarios and the base case. (A) The land-use pattern for reserve-site selection without dispersal scenario. (B) The land-use pattern for reserve-site selection with dispersal scenario. (C) The land-use pattern for the base case. A single contiguous biological reserve is chosen in the scenario for reserve-site selection without dispersal. With dispersal, not all biological reserves are connected. In the base case, only one parcel is put into a biological reserve.

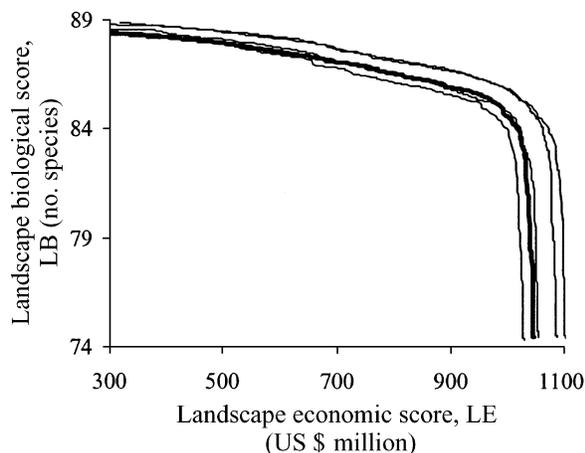


FIG. 6. Efficiency frontiers associated with alternative  $14 \times 14$  landscapes. The alternative landscapes were created using the same methodology that was used to create the default  $14 \times 14$  landscape. The thick black line represents the base-case efficiency frontier. All efficiency frontiers have the same basic shape. The right-hand terminus of the efficiency frontier is shifted right when the landscape has higher present values for commodity production.

no economic value in lands used for biological purposes makes some degree of conflict inevitable between economic and biological objectives. A major theme of this paper is to incorporate the biological value of lands outside of formal protected areas. Further work to incorporate the economic value of ecosystem services generated by formal protected areas is also needed.

The reserve-site selection approach has also been criticized on the grounds that it targets current representation of species in a reserve network rather than the long-term persistence of those species (e.g., Cowling et al. 1999, Williams and Araujo 2000, Calkin et al. 2002, Moilanen and Cabeza 2002, Cabeza and Moilanen 2003). Modeling persistence requires incorporating spatial population modeling into conservation planning (Cabeza and Moilanen 2003). In this paper we model species persistence as a function of the landscape's capacity to support species, which depends upon the extent and spatial pattern of habitat, the area requirements of the species, and species' dispersal ability. Hansen et al. (1993) and Schumaker et al. (2004) represent similar efforts to model persistence of a large number of species on a landscape.

The biological model developed in this paper is relatively simple so that it could be applied to a large set of species. Additional features could be added to increase biological realism of the model and to make the predictions richer and more robust. In our model, dispersal is a function of distance between habitat patches. Prior work emphasizes the important of distance between habitat patches but other factors such as the availability of prey, predation risk, and dispersal barriers (e.g., highways) are also important factors in explaining dispersal (e.g., Hanski and Ovaskainen 2000,

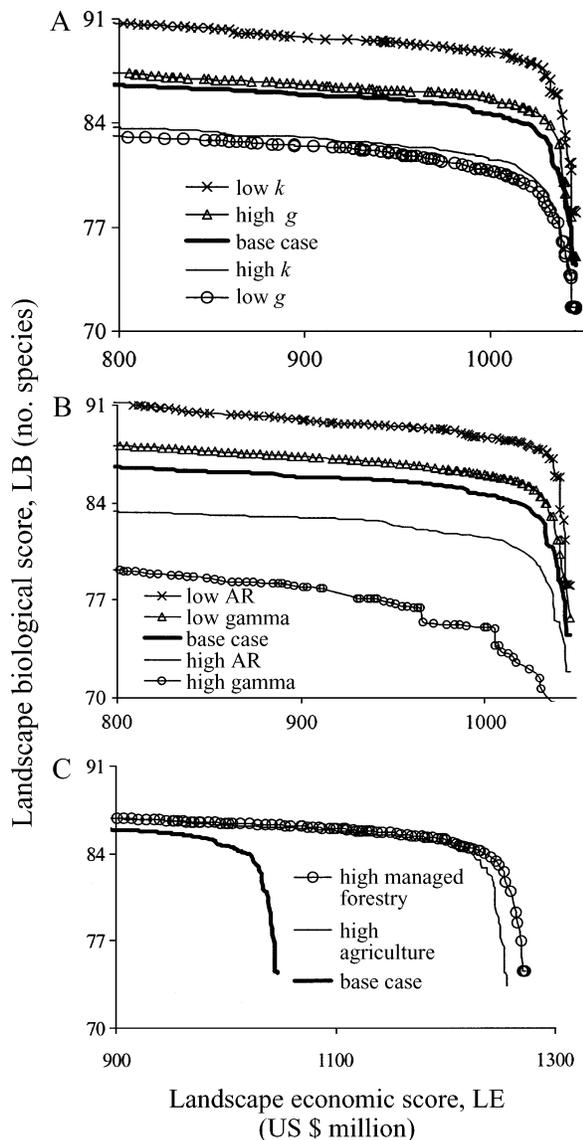


FIG. 7. Efficiency frontiers for various sensitivity analyses on the default  $14 \times 14$  landscape. (A) Efficiency frontiers for simulations with a 50% increase and a 50% decrease from default parameter values for  $g$ , the constant that determines the shape of the species-persistence probability function, and  $k$ , the half-saturating constant in the species-persistence probability function (see Eq. 8). (B) Efficiency frontiers for simulations with a 50% increase and a 50% decrease in default parameter values for  $AR_s$ , the number of hectares needed by a breeding pair of species  $s$  (see Eq. 1), and changes in the default value of  $\gamma_s$  (low  $\gamma_s = 0$ , high  $\gamma_s = 50$ ), the minimum number of breeding pairs of species  $s$  that a patch must support on its own before the patch contributes to the minimum landscape biological (LB) score (see Eq. 4). (C) Efficiency frontiers for simulations with a 40% increase in the default economic value of agriculture (high agriculture) or in the default economic value of managed forestry (high managed forestry). A thick black line in each figure represents the base-case efficiency frontier. Changes in biological parameters shift the efficiency frontier vertically (A and B); changes in economic parameters shift the efficiency frontier horizontally (C). The L-shape of the efficiency frontier remains unchanged.

Goodwin and Fahrig 2002, Baguette et al. 2003, Gardner and Gustafson 2004). Inclusion of the probability of patch colonization is another promising direction for model improvement (e.g., Gustafson and Gardner 1996). We included only a subset of terrestrial vertebrates, in particular, terrestrial vertebrates not dependent on aquatic habitats. The model used in the example also does not consider different habitat needs for breeding and feeding, or edge effects. We also ignored boundary effects from the landscape outside of the study area. Incorporating different breeding and feeding needs, edge effects, or boundary effects could be included with relatively minor extensions to the existing model. Incorporating interactions among species (e.g., competition, predator–prey interactions) would require more fundamental changes to the model.

We use the expected number of species persisting on the landscape as the biological score for the model. Other metrics could be used instead. For example, instead of giving equal weight to all species, greater weight could be given to endemic or endangered species. One could also base the landscape biological score on phylogenetic diversity, ecological diversity, ecosystem productivity, stability, resilience, ecosystem services, or other measures; all one needs is a way of modeling how the desired metric changes under alternative land-use patterns.

On the economic side, a broader set of economic activities such as recreation or residential and commercial land use could be included. Modeling recreation and residential development would necessitate incorporating price effects and spatial externalities in which neighboring land use may affect economic values on a parcel. Additionally, the economic model could be expanded to include positive returns from species persistence (e.g., birdwatching) or negative returns (e.g., crop damage).

The model we developed in *The biological and economic models and Optimization problem . . .*, above, is general in the sense that it can be applied to different sets of species, different economic activities, and different definitions of land parcels (e.g., polygons or grid cells). How best to define land parcels presents some challenges. Ideally, parcel boundaries would match land-use decision-making units (e.g., private property boundaries) and parcels would be relatively homogeneous within their boundaries. In practice, there is no perfect way to define parcels when including species with different range sizes and dispersal abilities, different economic activities, and land-ownership patterns. There are trade-offs between including increasingly finer-scale resolution and computational limits. However, the choice of scale is not innocuous. In the reserve-site selection literature, the size of parcels can influence the choice of which parcels to include in a reserve network (Stoms 1994, Pressey and Logan 1998, Warman et al. 2004). In our case, the choice of which parcels to put in which land use can be affected by

scale of analysis but the general conclusion about the shape of the trade-off curve between biological and economic objectives is not dependent on scale.

Another important extension would be to explicitly include dynamics. Changing existing land-use patterns entails transition costs that would change the economic returns. Species populations also respond over time to habitat changes. If dispersal is limited, species may have difficulty in colonizing new habitat patches that become available. With a dynamic approach, effects of climate change and stochastic events, such as fire, drought, or disease outbreaks, could also be considered.

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