Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales

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Nature provides a wide range of benefits to people. There is increasing consensus about the importance of incorporating these "ecosystem services" into resource management decisions, but quantifying the levels and values of these services has proven difficult. We use a spatially explicit modeling tool, Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST), to predict changes in ecosystem services, biodiversity conservation, and commodity production levels. We apply InVEST to stakeholder-defined scenarios of land-use/land-cover change in the Willamette Basin, Oregon. We found that scenarios that received high scores for a variety of ecosystem services also had high scores for biodiversity, suggesting there is little tradeoff between biodiversity conservation and ecosystem services. Scenarios involving more development had higher commodity production values, but lower levels of biodiversity conservation and ecosystem services. However, including payments for carbon sequestration alleviates this tradeoff. Quantifying ecosystem services in a spatially explicit manner, and analyzing tradeoffs between them, can help to make natural resource decisions more effective, efficient, and defensible.

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Ecosystems generate a range of goods and services important for human well-being, collectively called ecosystem services. Over the past decade, progress has been made in understanding how ecosystems provide services and how service provision translates into economic value (Daily 1997; MA 2005; NRC 2005). Yet, it has proven difficult to move from general pronouncements about the tremendous benefits nature provides to people to credible, quantitative estimates of ecosystem service values. Spatially explicit values of services across landscapes that might inform land-use and management decisions are still lacking (Balmford *et al.* 2002; MA 2005).

Without quantitative assessments, and some incentives for landowners to provide them, these services tend to be ignored by those making land-use and land-management decisions. Currently, there are two paradigms for generating ecosystem service assessments that are meant to influence policy decisions. Under the first paradigm, researchers use broad-scale assessments of multiple services to extrapolate a few estimates of values, based on habitat types, to entire regions or the entire planet (eg Costanza *et al.* 1997; Troy and Wilson 2006; Turner *et al.* 2007). Although simple, this "benefits transfer" approach incorrectly assumes that every hectare of a given habitat type is of equal value – regardless of its quality, rarity, spatial configuration, size, proximity to population centers, or the prevailing social practices and values. Furthermore, this approach does not allow for analyses of service provision and changes in value under new conditions. For example, if a wetland is converted to agricultural land, how will this affect the provision of clean drinking water, downstream flooding, climate regulation, and soil fertility? Without information on the impacts of land-use management practices on ecosystem services production, it is impossible to design policies or payment programs that will provide the desired ecosystem services.

In contrast, under the second paradigm for generating policy-relevant ecosystem service assessments, researchers carefully model the production of a single service in a small area with an "ecological production function" – how provision of that service depends on local ecological variables (eg Kaiser and Roumasset 2002; Ricketts *et al.* 2004). Some of these production function approaches also use market prices and non-market valuation methods to estimate the economic value of the service and how that value changes under different ecological conditions. Although these methods are superior to the habitat assessment benefits transfer approach, these studies lack both the scope (number of services) and scale (geographic and temporal) to be relevant for most policy questions.

What is needed are approaches that combine the rigor of the small-scale studies with the breadth of broad-scale assessments (see Boody *et al.* 2005; Jackson *et al.* 2005;

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Food

Antle and Stoorvogel 2006; Chan *et al.* 2006; Naidoo and Ricketts 2006; Egoh *et al.* 2008; and Nelson *et al.* 2008 for some initial attempts). Here, we present results from the application of a new, spatially explicit modeling tool, based on ecological production functions and economic valuation methods, called Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST). We apply InVEST to three plausible land-use/land-cover (LU/LC) change scenarios in the Willamette Basin, Oregon (Figure 1). We show how these different scenarios affect hydrological services (water quality and storm peak mitigation), soil conservation, carbon sequestration, biodiversity conservation, and the value of several marketed commodities (agricultural crop products, timber harvest, and rural–residential housing). We also explore the spatial patterns of ecosystem service provision across the landscape under these three scenarios, highlighting synergies and tradeoffs between multiple ecosystem services, biodiversity conservation, and market returns to landowners.

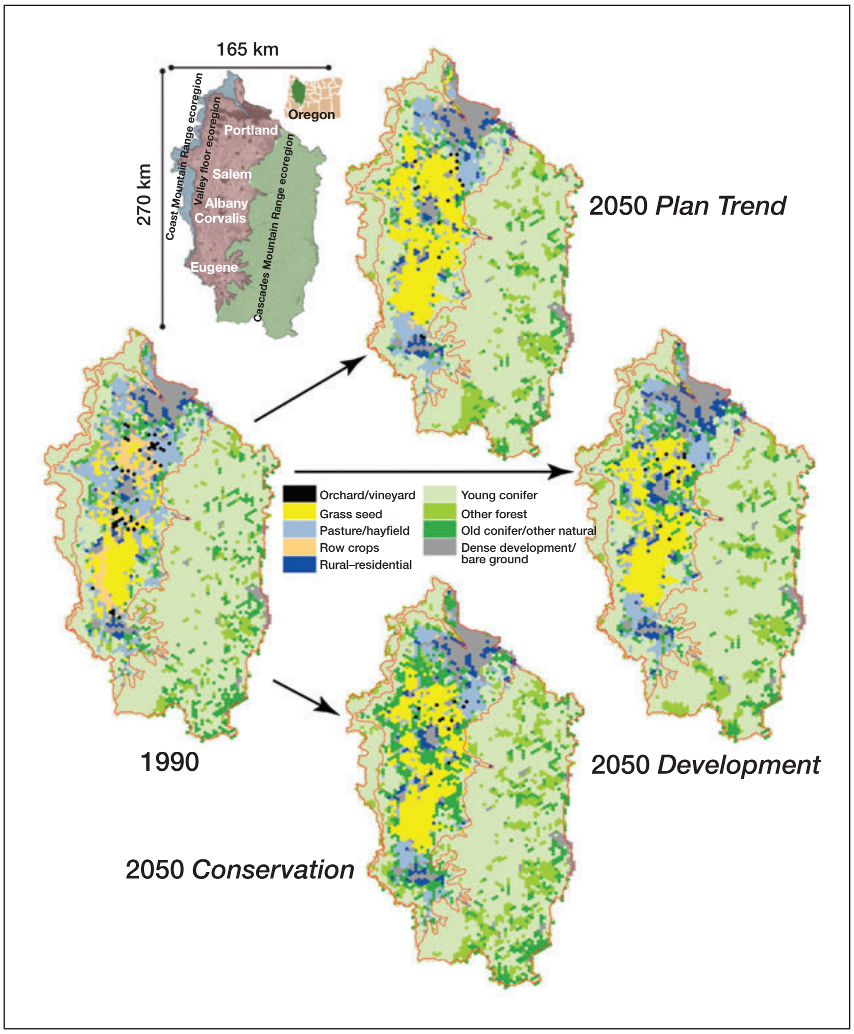

Figure 1. *Maps of the Willamette Basin and the land-use/land-cover (LU/LC) patterns for 1990 and under the three LU/LC change scenarios for 2050. A 500-ha hexagon is the spatial unit used in the LU/LC pattern maps. Each hexagon can contain more than one LU/LC. However, for illustrative purposes, we only show a hexagon's most dominant LU/LC. The light brown lines delineate the three ecoregions that intersect the Basin (Omernik 1987); from west to east, the ecoregions are the Coast Range, the Willamette Valley, and the Cascades Range. The Coast Range is a low mountain range (122–762 m) that runs the entire Oregon coast, with three of the tallest conifer species in the world supported by high annual rainfall and intensive fog during the summer. The Willamette Valley incorporates terraces and the floodplain of the Willamette River system, and most of the agricultural and urban land use in the Basin. The Cascades Range is large, steep, and high (up to 3424 m).*

Methods

InVEST consists of a suite of models that use LU/LC patterns to estimate levels and economic values of ecosystem services, biodiversity conservation, and the market value of commodities provided by the landscape. Examples of ecosystem services and commodity production that InVEST can model include water quality, water provision for irrigation and hydropower, storm peak mitigation, soil conservation, carbon sequestration, pollination, cultural and spiritual values, recreation and tourism, timber and non-timber forest products, agricultural products, and residential property values. InVEST can be run at different levels of complexity, making it sensitive to data availability and an understanding of system dynamics. Results can be reported in either biophysical or monetary terms, depending on the needs of decision makers and the availability of data. However, biodiversity conservation results are reported in biophysical terms only.

In this paper, we use a subset of the simpler InVEST models and focus largely on reporting ecosystem services in biophysical terms. We run InVEST across three different projections of LU/LC change in the Willamette Basin. Below, we briefly describe the major features and data inputs for the ecosystem services, biodiversity conservation, and commodity production value models. For greater detail, please refer to this paper's appendix, at www.naturalcapitalproject.org/pubs/NelsonetalFrontiersAppendix.pdf.

Land-use/land-cover projections in the Willamette Basin

The base map in this study was a 1990 LU/LC map for the Willamette Basin (29 728 km^2) developed by the Pacific Northwest Ecosystem Research Consortium, a multi-stake-

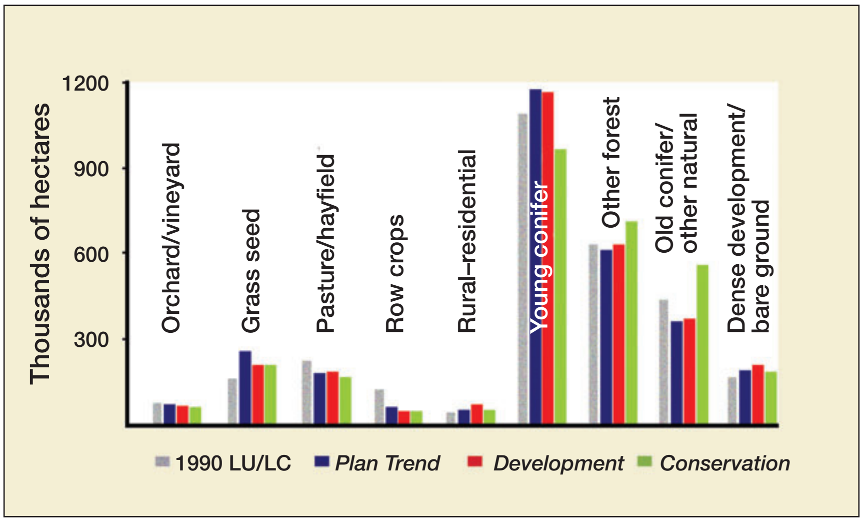

***Figure 2.** Distribution of land area under each LU/LC category for 1990 and 2050 under the three LU/LC change scenarios (see Figure 1).*

holder alliance between government agencies, non-governmental organizations, and universities (Hulse *et al.* 2002; US EPA 2002; Baker *et al.* 2004; www.fsl.orst.edu/pnwerc/wrb/access.html). This alliance facilitated the creation of three stakeholder-defined scenarios of LU/LC change, from 1990 to 2050 (Baker *et al.* 2004). Each scenario includes a set of spatially explicit raster grid LU/LC maps (30 m x 30 m grid cells) of the Basin at 10-year intervals, from 2000 to 2050 (Figures 1 and 2). The three scenarios are:

- *Plan Trend*: "the expected future landscape, should current policies be implemented as written and recent trends continue" (US EPA 2002).
- *Development*: "a loosening of current policies, to allow freer rein to market forces across all components of the landscape, but still within the range of what stakeholders considered plausible" (US EPA 2002).
- *Conservation*: placed greater emphasis on ecosystem protection and restoration; however, as with the *Development* scenario, the model still reflects "a plausible balance among ecological, social, and economic considerations, as defined by stakeholders" (US EPA 2002).

The three scenarios assume that human population in the Willamette Basin will increase from 2.0 million in 1990 to 3.9 million people in 2050 (Hulse *et al.* 2002).

Models

Ecosystem services, biodiversity conservation, and commodity production values are a function of land characteristics and the LU/LC pattern. Models were run using the 30 m x 30 m resolution data. For reporting and display purposes, we aggregated results to 500-ha hexagon units (model results are given in Figures 3, 4, and 5). In general, InVEST can be run on spatial units of any resolution.

Water service models: water quality and storm peak mitigation

In this application, we used the discharge of dissolved phosphorus into the local watershed to measure water pollution. Although this single measure ignores many other sources of water pollution, it provides a proxy for non-point-source pollution. Slope, soil depth, and surface permeability were used to define potential runoff by location. Areas with a greater potential runoff, less downhill natural vegetation for filtering, greater hydraulic connectivity to water bodies, and LU/LC associated with the export of phosphorous (ie agricultural land) have greater rates of phosphorus discharge. Areas that have the highest water quality scores export relatively little phosphorous to waterways.

The storm peak mitigation model highlights the areas on the landscape that contribute most to potential flooding after a uniform rainfall event. The model estimates the volume and timing of water flow from an area to its catchment's outlet on the Willamette River. Both the volume and timing of water flow across the landscape are affected by water retention on the land. Water retention in an area is greater if its LU/LC has a rougher surface or provides opportunities for water infiltration. In general, as water retention rates increase in a catchment, the more that flood risk at the catchment's outlet decreases. Areas in a catchment that contribute less to the storm peak at the catchment's outlet – because they export little water, deliver water at off-peak times, or both – have the highest storm peak mitigation scores.

Soil conservation

The soil conservation model uses the Universal Soil Loss Equation (Wischmeier and Smith 1978) to predict the average annual rate of soil erosion in a particular area (usually reported in tons acre^{-1} yr^{-1}; in Figure 4 we map the relative change in erosion rates across space and time). The rate of soil erosion is a function of the area's LU/LC, soil type, rainfall intensity, and topography. For this study, we assumed that rainfall intensity was homogenous across the entire landscape. In general, the model predicts greater soil losses in agricultural areas and sites with steeper slopes, and lower soil losses in forested and paved areas. regions with lower potential soil losses received higher scores.

Carbon sequestration

We tracked the carbon stored in above- and belowground biomass, soil, and harvested wood products (HWP) using standard carbon accounting methods (Adams *et al.* 1999; Plantinga *et al.* 1999; Feng 2005; Lubowski *et al.* 2006;

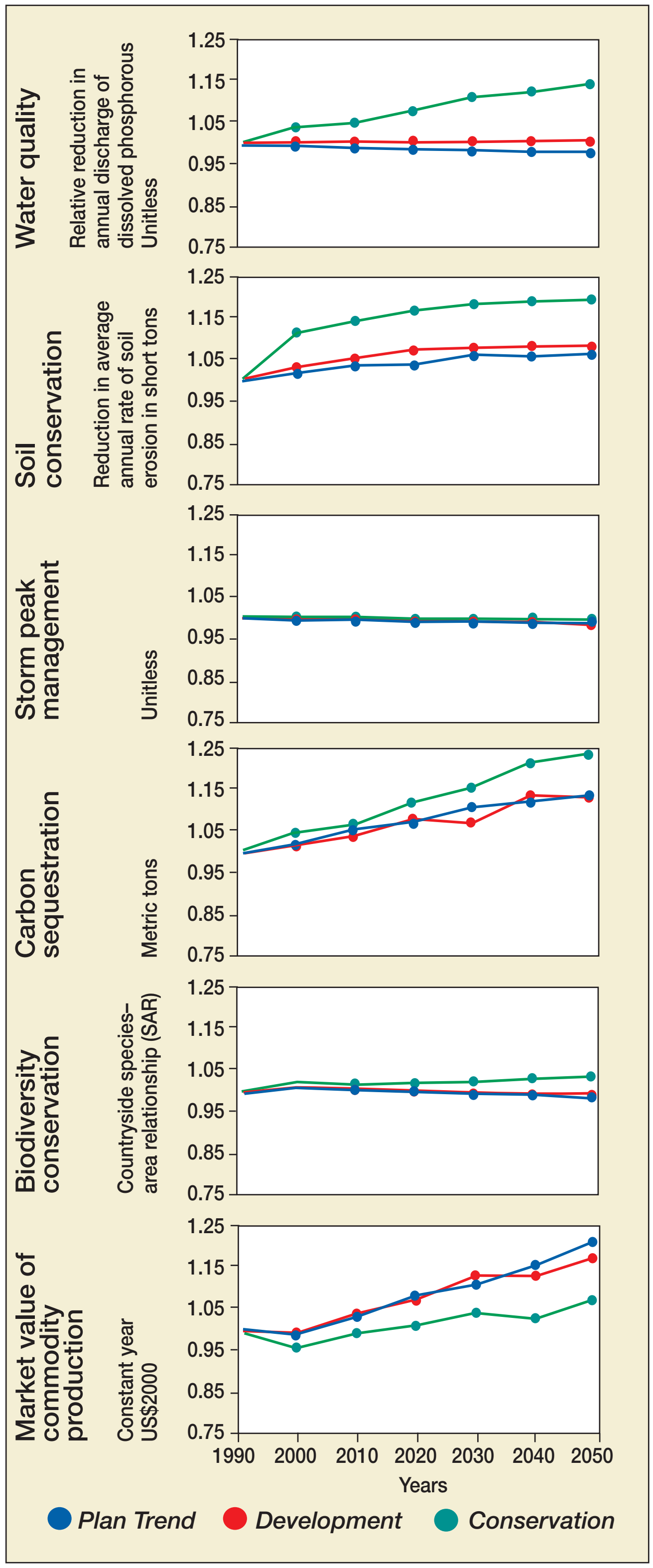

Figure 3. *Trends in normalized landscape-level ecosystem services, biodiversity conservation, and market value of commodity production for the three LU/LC change scenarios. All scores are normalized by their 1990 levels. Carbon sequestration and commodity production values are not discounted in this figure.*

Smith *et al.* 2006; Kirby and Potvin 2007; Nelson *et al.* 2008). To determine how much carbon was stored in an area, we estimated above- and belowground biomass and soil carbon pools as a function of the area's distribution of present and historic LU/LC and biomass age. We also estimated how much timber was removed from the area in previous time periods to determine the carbon that remained stored in HWP. The amount of carbon sequestered in an area across a particular time period is determined by subtracting the carbon stored in the area at the beginning of the time period from that stored in the area at the end of the time period.

In this study, we also estimated the social value of carbon sequestration (all sequestration, not just the portion of sequestration that would be eligible for trading in a carbon offset market; see Watson *et al.* 2000). We assumed a social value of $43 per Mg of carbon, which is the mean value of the social cost of carbon from Tol's (2005) survey of peer-reviewed literature. The social cost of carbon is equal to the marginal damage associated with the release of an additional metric ton of carbon into the atmosphere – or, in this case, the monetary benefit of an additional sequestered metric ton. Payments beyond 1990 were discounted to reflect the decrease in monetary value over time. We used the US Office of Management and Budget recommended rate of 7% per annum as the discount rate (US OMB 1992). In addition, we adopted the conservative assumption that the social value of carbon sequestration will decline over time (ie in the future, the social cost of carbon will *decline* at a rate of 5% per annum). Whether the social value of carbon will decrease, increase, or remain constant in the future is uncertain.

Biodiversity conservation

We used a countryside species–area relationship (SAR; Sala *et al.* 2005; Pereira and Daily 2006) to determine the capacity of each LU/LC map to support a suite of 24 vertebrate species that previous analysis found to be sensitive to LU/LC change in the Willamette Basin (Polasky *et al.* 2008). The score for each species on a given LU/LC map depended on the amount of actual and potential habitat area provided for a species. Actual habitat area for a species was equal to the amount of LU/LC in the species' geographic range that was compatible with its breeding and feeding requirements. Potential habitat area was given by a species' total mapped geographic range within the Willamette Basin. The countryside SAR score for each species was equal to the ratio of actual habitat area to potential habitat area raised to the power z ($0 < z \leq 1$). Lower z values imply less of a penalty for losing small portions of habitat and large penalties for losing the last few units of habitat. In this application, we used a z value of 0.25 for each species. We averaged across the countryside SAR scores of each species to calculate an aggregate score for each scenario.

In order to allocate biodiversity scores spatially across the landscape, we calculated a second biodiversity metric

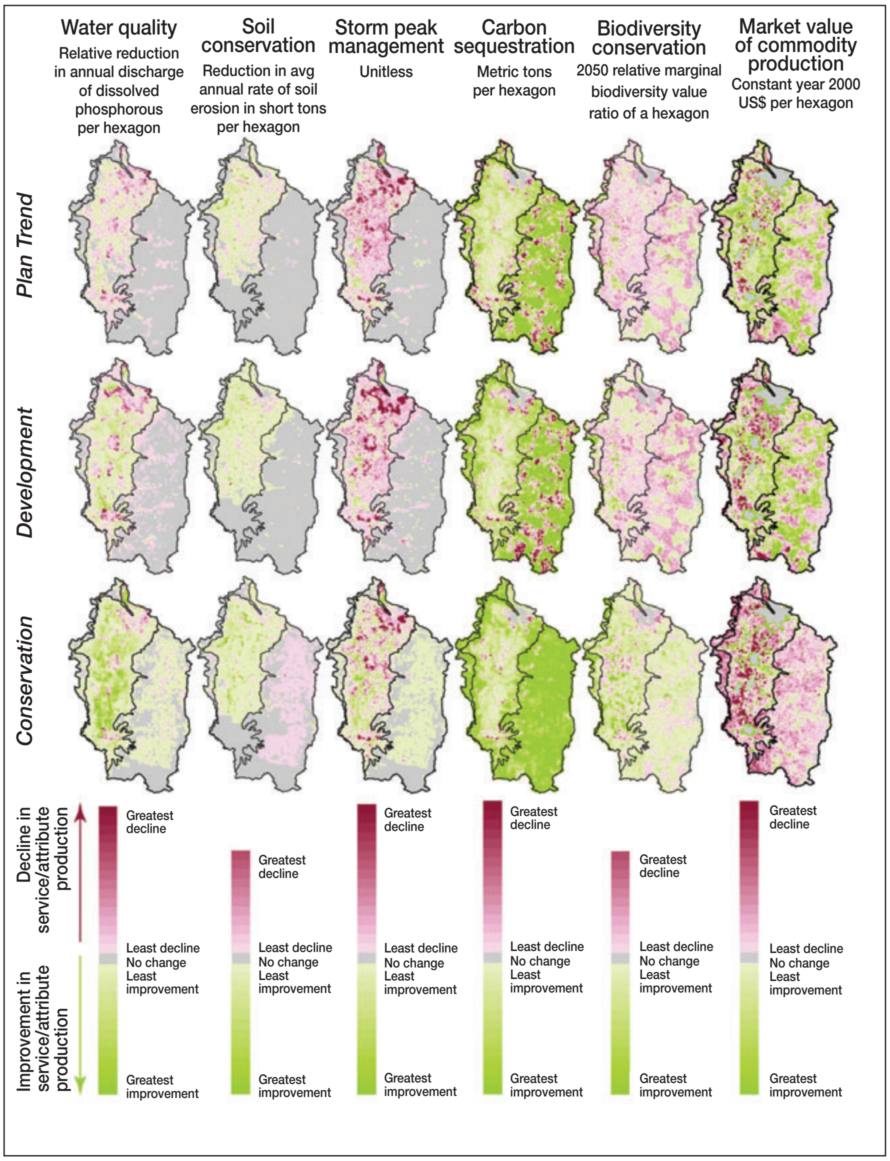

Figure 4. *Maps of change in ecosystem services, biodiversity conservation, and market value of commodity production from 1990 to 2050 for the three LU/LC change scenarios. Carbon sequestration and commodity production values are not discounted.*

that could be applied to distinct areas on the landscape (countryside SAR applies only at the landscape level). This metric estimated an area's relative contribution to the sustainability of each species. The marginal biodiversity value (MBV) of an area measures the value of habitat in the area for all species under consideration, relative to the composite value of habitat available to all species across the whole landscape. We then calculated the relative MBV (the RMBV), a modified version of MBV, to measure the change in an area's value over time, and reported the ratio of this number to the area's MBV value on the 1990 LU/LC map.

Commodity production value

In addition to the ecosystem services and biodiversity conservation, we also estimated the market value of commodities provided by an area. The market value is equal to the aggregate net present value of commodities (agricultural crops, timber, and rural–residential housing) produced in the area. The market value models were taken from Polasky *et al.* (2008). We lacked a model to value urban land use. To make fairer comparisons across scenarios, we excluded the value of commodities produced on land that was developed for urban land uses in any scenario.

The net present value of agricultural crop production in an area depends on crop type, soil productivity, irrigation, crop prices, and production costs. The net present value of timber production depends on the mix of tree species, soil productivity, forestry rotation time, timber price, and harvest cost. We used price and production cost estimates from 2000 for both agriculture and forestry. The net present value of housing in an area is a function of its proximity to urban areas (Kline *et al.* 2001) and the area's county, mean elevation, slope, lot size, and existing building density. We assumed that the annual per-hectare net return for rural residential housing in the Basin decreased by 0.75% for each 1% increase in rural residential land use in the Basin (ie elasticity of demand for rural residential housing is –0.75%) and that the value of rural residential land-use increased 2% per annum. We used a discount rate of 7% per annum to compute the net present values of commodity production across time.

Results

Of the three LU/LC change scenarios, the *Conservation* scenario produced the largest gains (or the smallest losses) in ecosystem services and biodiversity conservation (Figure 3). Under the *Conservation* scenario, carbon sequestration, water quality, and soil conservation scores increased substantially. Carbon sequestration also increased under the *Plan Trend* and *Development* scenarios, although less steeply, mainly because of sequestration losses in the lower elevations of the Cascade Mountains as a result of rural residential development and timber production (Figure 4). Water quality and potential soil conservation changed only slightly in the *Plan Trend* and *Development* scenarios, but improved under the *Conservation* scenario, because of replacement of agricultural land with forests, prairies, and other land uses on the Basin floor (Figure 1).

Storm peak mitigation scores declined slightly under all three scenarios (Figure 3), but the *Conservation* scenario exhibited the smallest reduction. Reductions in hexagon storm peak management scores (indicative of increased flood risk at the hexagon's catchment outlet on the Willamette River, all else being equal) were greatest under the *Development* scenario, which had the largest increase in impervious surface area of any of the scenarios. Outside of developing areas on the Basin floor, storm peak management scores were largely unchanged (Figure 4).

Landscape-level biodiversity conservation scores also showed only small changes through time under each of the three scenarios. The 24-species countryside SAR showed a small increase under the *Conservation* scenario, but declined slightly under both the *Plan Trend* and *Development* scenarios (Figure 3). The areas immediately surrounding urban areas saw the greatest biodiversity losses, as measured by RMBV ratios. Some of the greatest increases in RMBV ratios occurred in the Coast Mountain Range and toward the southern end of the valley floor (Figure 4). Despite widespread declines in RMBV ratios across the landscape in the *Plan Trend* and *Development* scenarios, the declines were not great enough to greatly reduce the 24-species countryside SAR score under either scenario. The use of a higher z value in the countryside SAR calculation would result in greater biodiversity conservation score declines in the *Plan Trend* and *Development* scenarios.

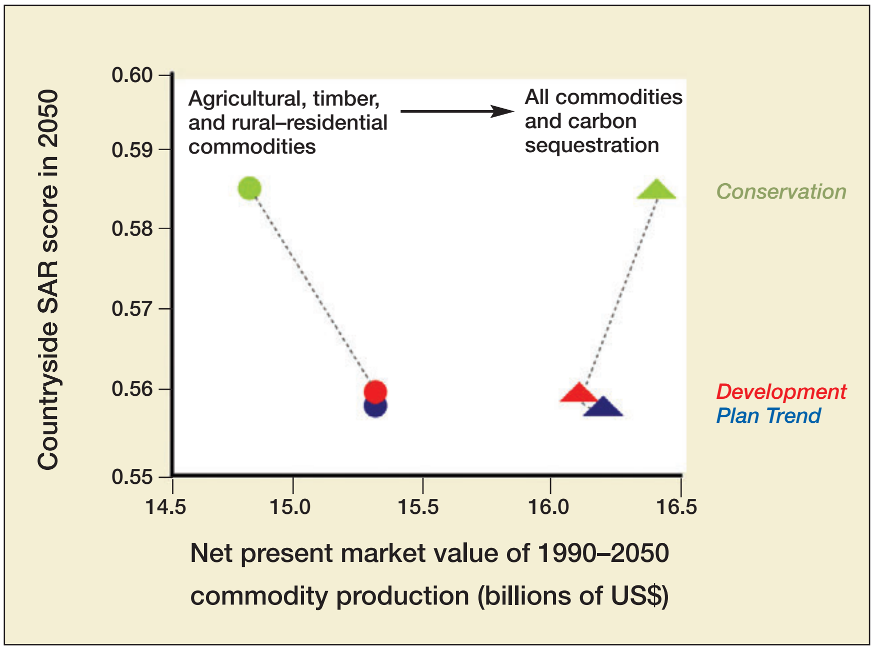

Figure 5. *Tradeoffs between market values of commodity production and biodiversity conservation on the landscape between 1990 and 2050, excluding (circles) and including (triangles) the market value of carbon sequestration (we assume that the social value of carbon is equal to the market value of sequestered carbon). The x axis measures the total discounted value of commodities, whereas the y axis measures the biodiversity (ie countryside SAR) score for 2050.*

The aggregate market value of commodities produced on the landscape was the only measure where the *Conservation* scenario did not outperform the *Plan Trend* and *Development* scenarios (Figure 3). The market value of commodity production increased in many areas under the Plan Trend and Development scenarios, as a result of both increased residential development and more intensive timber harvesting (Baker *et al.* 2004; Figure 4). Although the market value of commodity production declined in a majority of areas under the *Conservation* scenario (4143 out of 6214 hexagons), aggregate market value of commodity production summed over the whole region increased, because the high value of rural residential development near cities more than compensated for losses elsewhere.

Given the emerging interest in carbon markets, we calculated the aggregate market value of carbon sequestration under the three scenarios. We assumed the market value of carbon sequestration was equal to its social value of \$43 Mg^{-1} of sequestered carbon (this may be an underestimate, since carbon prices on the European carbon market were \$133–162 Mg^{-1} of sequestered carbon, at an exchange rate of US\$1.58–€1 in July 2008, and \$88–112 Mg^{-1} of sequestered carbon, at an exchange rate of US\$1.33–€1 in October 2008). The total present value of carbon sequestration on the landscape from 1990 to 2050 was \$1.6 billion, \$0.9 billion, and \$0.8 billion, under the *Conservation*, *Plan Trend*, and *Development* scenarios, respectively (and \$1.5 billion, \$0.8 billion and \$0.7 billion, respectively, if we only applied a market value to 50% of HWP carbon sequestration on the landscape). If these carbon sequestration values are added to aggregate market value of commodities for each scenario, then *Conservation* generates more monetary value than *Plan Trend* and *Development* (\$16.38 versus \$16.16 or \$16.07 billion [Figure 5]; or \$16.27 versus \$16.05 or \$15.96 billion, if we only applied a market value to 50% of HWP carbon sequestration on the landscape). If payments were made for the other ecosystem services, the value of the *Conservation* scenario would increase even further relative to the other two scenarios.

Discussion

We applied the InVEST model to predict the provision of ecosystem services, biodiversity conservation, and the market value of commodities across space and time for three contrasting scenarios of future LU/LC change. This research contributes to an emerging literature that attempts to quantify the value of multiple ecosystem services at a broad scale (geographic and temporal) by way of ecological production functions and economic valuation methods. Analyzing how ecosystem service provision and value change under alternative realistic scenarios distinguishes our approach from the well known maps of "total" value (ie benefits transfer) that can be produced for a site (Troy and Wilson 2006), a state (Costanza *et al.* 2006), or the world (Costanza *et al.* 1997).

Combining multiple outputs under different LU/LC scenarios demonstrates the extent of the synergies or tradeoffs among these outputs. In the Willamette Basin application, we found little evidence of tradeoffs between ecosystem services and biodiversity conservation: scenarios that enhance biodiversity conservation also enhance the production of ecosystem services. Fears that a focus on ecosystem services will fail to help us achieve biodiversity conservation goals (eg Terborgh 1999; McCauley 2006) were not borne out in this case. A negative correlation between commodity production values and (1) ecosystem services and (2) biodiversity conservation is the one clear tradeoff we found. These results indicate that when landowner decisions are based solely on market returns (without payments for ecosystem services), they will tend to generate LU/LC patterns with lower provision of ecosystem services and biodiversity conservation.

Even this tradeoff, however, can be modified by policy interventions. If markets for carbon sequestration emerge, payments for sequestered carbon may make it more profitable for landowners to choose LU/LC favoring conservation. In this application, payments for carbon sequestration cause the aggregate market value of the *Conservation* scenario to be greater than the aggregate market value of the *Development* and *Plan Trend* scenarios (Figure 5). This result doesn't necessarily mean that the *Conservation* scenario would emerge if payments for carbon sequestration were made. The actual LU/LC pattern that emerges under a carbon market will depend on the prices paid for sequestration, which carbon pools are eligible for payment, and the individual preferences of landowners. However, it is more likely that land-use choices with carbon payments, especially in rural areas, would generate a spatial pattern more like the *Conservation* scenario than those of the *Development* and *Plan Trend* scenarios. Payments for water quality, soil conservation, and storm peak mitigation would strengthen the likelihood that LU/LC patterns similar to those described in the *Conservation* scenario would emerge.

Before payments for these ecosystem services are instituted, however, clear links need to be made between their biophysical provision and their ultimate use by people. Other than carbon sequestration, we have only modeled biophysical production of ecosystem services. The crucial second step is to determine how much of this production is actually of value to people and where that value is captured. In this study, we have done this with carbon sequestration (we assumed that all sequestration provides value to all people in the world). For other services, use values will be determined by local patterns of land use and population density. For example, in a flooding-prone watershed in which few people or farms occur, flood mitigation services will provide relatively little benefit to people.

Another important caveat to our analysis is that we did not include the market value of commodities generated in urbanized areas in any scenario (this was done to keep the base land area in the market value model equal across all scenarios). Because market returns on urban land tend to be higher than returns for other land uses, we probably underestimated the aggregate value of marketed commodities for scenarios that experience greater urbanization (ie the *Development* scenario). In general, for land-use decisions involving a choice between intensive urban development and conservation, development values might very well overwhelm the ecosystem services values that could be generated by conserving the land. We should not expect existing markets or market valuation of ecosystem services inevitably to favor conservation, especially in high-value urban areas. The kinds of analyses we show here, however, make transparent the tradeoffs between ecosystem services, biodiversity conservation, and market returns, and that transparency alone is desirable in engaging stakeholders and decision makers.

Another intriguing outcome of our analyses was that the scenarios did not produce more marked differences in the provision of ecosystem services and biodiversity conservation. This may be a reflection of the relatively modest LU/LC change under the scenarios considered here: "The stakeholder advisory group, which oversaw design of the future scenarios, did not consider…drastic landscape alterations plausible, given Oregon's history of resource protection, social behaviors, and land-ownership patterns" (Baker *et al.* 2004). Indeed, using more complex habitat–species relationship data, Schumaker *et al.* (2004) also found little change in a biodiversity status measure (essentially a countryside SAR score with 279 species and a z value of 1) from 1990 to 2050 across the three scenarios. The Willamette Basin has large tracts of contiguous forests in the Cascade and Coastal Mountain Ranges that remained relatively unchanged cross all three scenarios. Most of these areas are not suitable for agriculture or urban development. They probably act as a buffer for maintaining provision of ecosystem services and biodiversity, no matter how great the changes on the Basin floor (Figures 1, 2, and 4). We expect the modeling and valuation approach illustrated here to reveal more striking tradeoffs between conservation and development in rapidly developing regions.

Although the structure of the models presented here can, in principle, include drivers besides land-use change (eg climate change), we have not included these in the analysis to date. Furthermore, there may be important feedback effects, such as the amenity value of conserved land, that increases development pressure on land near conserved areas. Including changes in climate, technology, market prices, human population, and feedback effects – all of which are likely to drive the ecological, social, and economic relationships that determine the value of ecosystem services in the future – is an essential next step in the application of InVEST.

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References

Adams DM, Alig RJ, McCarl BA, *et al.* 1999. Minimum cost strategies for sequestering carbon in forests. *Land Econ* **75**: 360–74.

Antle JM and Stoorvogel JJ. 2006. Predicting the supply of ecosystem services from agriculture. *Am J Agr Econ* **88**: 1174–80.

Baker JP, Hulse DW, Gregory SV, *et al.* 2004. Alternative futures for the Willamette River Basin, Oregon. *Ecol Appl* **14**: 313–24.

Balmford A, Bruner A, Cooper P, *et al.* 2002. Economic reasons for conserving wild nature. *Science* **297**: 950–53.

Boody GB, Vondracek D, Andow M, *et al.* 2005. Multifunctional agriculture in the United States. *BioScience* **55**: 27–38.

Chan KMA, Shaw MR, Cameron DR, *et al.* 2006. Conservation planning for ecosystem services. *PLoS Biology* **4**: 2138–52.

Costanza R, Wilson M, Troy A, *et al.* 2006. The value of New Jersey's ecosystem services and natural capital. Burlington, VT: Gund Institute for Ecological Economics, University of Vermont. www.state.nj.us/dep/dsr/naturalcap/nat-cap-2.pdf. Viewed 14 Nov 2008.

Costanza R, d'Arge R, de Groot R, *et al.* 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**: 253–60.

Daily GC (Ed). 1997. Nature's services: societal dependence on natural ecosystems. Washington, DC: Island Press.

Egoh B, Reyers B, Rouget M, *et al.* 2008. Mapping ecosystem services for planning and management. *Agri Ecosyst Environ* **127**: 135–40.

Feng H. 2005. The dynamics of carbon sequestration and alternative carbon accounting, with an application to the Upper Mississippi River Basin. *Ecol Econ* **54**: 23–35.

Hulse D, Gregory S, and Baker J (Eds). 2002. Willamette River Basin planning atlas: trajectories of environmental and ecological change. Corvallis, OR: Oregon State University Press.

Jackson RB, Jobbagy EG, Avissar R, *et al.* 2005. Trading water for carbon with biological carbon sequestration. *Science* **310**: 19–47.

Kaiser B and Roumasset J. 2002. Valuing indirect ecosystem services: the case of tropical watersheds. *Environ Dev Econ* **7**: 701–14.

Kirby KR and Potvin C. 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. *Forest Ecol Manag* **246**: 208–21.

Kline JD, Moses A, and Alig RJ. 2001. Integrating urbanization into landscape-level ecological assessments. *Ecosystems* **4**: 3–18.

Lubowski RN, Plantinga AJ, and Stavins RN. 2006. Land-use change and carbon sinks: econometric estimation of the carbon sequestration supply function. *J Environ Econ Manag* **51**: 135–52.

MA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being. Synthesis. Washington, DC: Island Press.

McCauley D. 2006. Selling out on nature. *Nature* **443**: 26–27.

Naidoo R and Ricketts TH. 2006. Mapping the economic costs and benefits of conservation. *PLoS Biol* **4**: 2153–64.

NRC (National Research Council). 2005. Valuing ecosystem service: towards better environmental decision-making. Washington, DC: National Academies Press.

Nelson E, Polasky S, Lewis D, *et al.* 2008. Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *P Natl Acad Sci USA* **105**: 9471-9476.

Omernik JM 1987. 2008. Ecoregions of the conterminous United States. Map (scale 1:7 500 000). *Ann Assoc Am Geogr* **77**: 118–25.

Pereira HM and Daily GC. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* **87**: 1877–85.

Plantinga AJ, Mauldin T, and Miller DJ. 1999. An econometric analysis of the costs of sequestering carbon in forests. *Am J Agr Econ* **81**: 812–24.

Polasky S, Nelson E, Camm J, *et al.* 2008. Where to put things: spatial land management to sustain biodiversity and economic returns. *Biol Conserv* **141**: 1505–24.

Ricketts, TH, Daily GC, Ehrlich PR, *et al.* 2004. Economic value of tropical forest to coffee production. *P Natl Acad Sci USA* **101**: 12579–82.

Sala OE, Vuuren DV, Pereira HM, *et al.* 2005. Biodiversity across scenarios. In: Carpenter SR, Pingali PL, Bennett EM, *et al.* (Eds). Ecosystems and human well-being: vol 2. Scenarios: findings of the Scenarios Working Group. Washington, DC: Island Press.

Schumaker NH, Ernst T, White D, *et al.* 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. *Ecol Appl* **14**: 381–400.

Smith JE, Heath LS, Skog KE, *et al.* 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station.

Terborgh J. 1999. Requiem for nature. Covelo, CA: Island Press.

Tol RSJ. 2005. The marginal damage costs of carbon dioxide emissions: an assessment of the uncertainties. *Energ Policy* **33**: 2064–74.

Troy A and Wilson MA. 2006. Mapping ecosystem services: practical challenges and opportunities in linking GIS and value transfer. *Ecol Econ* **60**: 435–49.

Turner WR, Brandon T, Brooks M, *et al.* 2007. Global conservation of biodiversity and ecosystem services. *BioScience* **57**: 868–73.

US EPA (US Environmental Protection Agency). 2002. Willamette Basin alternative futures analysis. Environmental assessment approach that facilitates consensus building. Washington, DC: US Environmental Protection Agency, Office of Research and Development.

US OMB (US Office of Management and Budget). 1992. Guidelines and discount rates for benefit–cost analysis of Federal programs. Washington, DC: US Office of Management and Budget.

Watson RT, Noble IR, Bolin B, *et al.* 2000. Project-based activities. In: Watson RT, Noble IR, Bolin B, *et al.* (Eds). IPCC special report on land use, land-use change and forestry. Cambridge, UK: Cambridge University Press.

Wischmeier WH and Smith DD. 1978. Predicting rainfall erosion losses – a guide to conservation planning. Washington, DC: US Department of Agriculture.

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