Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape

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We develop an integrated model to predict private land-use decisions in response to policy incentives designed to increase the provision of carbon sequestration and species conservation across heterogeneous landscapes. Using data from the Willamette Basin, Oregon, we compare the provision of carbon sequestration and species conservation under five simple policies that offer payments for conservation. We evaluate policy performance compared with the maximum feasible combinations of carbon sequestration and species conservation on the landscape for various conservation budgets. None of the conservation payment policies produce increases in carbon sequestration and species conservation that approach the maximum potential gains on the landscape. Our results show that policies aimed at increasing the provision of carbon sequestration do not necessarily increase species conservation and that highly targeted policies do not necessarily do as well as more general policies.

conservation payments | ecosystem services | landscape modeling | private landowners | land-use change

Ecosystems provide a wide array of goods and services of value to people, as well as support for biodiversity. Human activities, particularly regarding land use and land management, have altered ecosystems in fundamental ways with broad-ranging consequences for human well-being and the survival of other species. However, the effects of land-use and land-management decisions on ecosystem services and biodiversity often are not incorporated into decision-making, resulting in outcomes that reduce the provision of ecosystem services and biodiversity conservation in ways that harm both human well-being and biodiversity.

One important step in improving decision-making is to provide information about the effects of human decisions on ecosystem services and biodiversity. Although models exist that project the effects of land-use and land-management decisions (hereafter referred to simply as land-use decisions) on individual ecosystem services or specific taxonomic groups (e.g., refs. 1–3), few landscape-scale assessments of multiple ecosystem services and biodiversity have been conducted (exceptions include refs. 4 and 5). Managing landscapes to deliver ecosystem services and species conservation requires the integration of spatially explicit data and models from ecology, economics, and other disciplines.

Information about ecosystem services and biodiversity conservation, although necessary, is not sufficient to generate socially beneficial landscape-level management. Providing incentives to make decisions that reflect the value of ecosystem services and biodiversity conservation is also important. Land-use decisions are typically made by a large number of private landowners and public entities. Private landowners typically lack the incentive to manage land to provide ecosystem service and biodiveristy conservation benefits because many of the benefits produced on their land accrue to others (i.e., the benefits are public goods). For example, carbon sequestration provides a global benefit by reducing atmospheric CO_2 levels, while water purification services help those downstream. In addition, the provision of ecosystem services may depend on the spatial pattern of land use, requiring coordinated effort across multiple landowners (6). Incentives for provision of ecosystem services and biodiversity conservation can be supplied by government programs such as the U.S. Department of Agriculture's Conservation Reserve Program (CRP), which pays farmers to take land out of production and establish perennial plant cover to improve habitat, reduce erosion, and supply other environmental benefits. Currently the CRP pays farmers >$1.8 billion annually to enroll 36 million acres in the program (7). Land trusts and conservation organizations are another important avenue for providing ecosystem services and biodiversity conservation by securing conservation easements or buying land outright.

Here we develop an integrated model that (*i*) predicts landowner decisions as a function of existing market conditions and incentive-based conservation payments and (*ii*) predicts the impact of land-use changes on ecosystem services and biodiversity conservation. Our approach integrates the effect of policy on land-use decisions and the resulting consequences for the joint provision of ecosystem services and biodiversity conservation across a landscape.

We use National Resources Inventory (8) data over several time periods to estimate a model of land-use change on private land. Landowners choose to allocate land among various uses based on current land use, predicted economic net returns to each land use, land quality, and specific characteristics of the landowner (e.g., preferences or skill level). The empirical model yields transition probabilities expressed as functions of net returns and starting land use. This approach has the advantage of being based on observed land-use decisions, and, because transition probabilities depend on net returns, the effect of incentive-based policies on landowner decisions can be simulated by modifying net returns. Distributions of future land-use patterns in the Willamette Basin under alternative land conser-

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vation payment schemes, including a baseline with no conservation payments, are generated by running repeated simulations, with each simulation generating a land-use pattern consistent with the transition probabilities and the given conservation payment scenario. This approach explicitly accounts for the uncertainty about individual landowner decisions. Further details on our land-use change model are presented in *Materials and Methods*.

The policy-generated and baseline land-use patterns are then used as inputs into models that predict the provision of ecosystem services and biodiversity conservation. Modeling these factors often involves the use of sophisticated models that require extensive data inputs, which makes them inapplicable in some situations. An important question we address is the degree to which policy recommendations are robust to changes in data input requirements and model sophistication. We use models with different levels of complexity and detail to explore this question. The first level of models uses readily available data and simple relationships to link land use to ecosystem services and biodiversity. The second level requires more detailed, site-specific information and incorporates more complex relationships.

To demonstrate the potential tradeoffs and synergies between ecosystem services and biodiversity conservation on a landscape, we focus on carbon sequestration and terrestrial vertebrate species conservation. Carbon sequestration is an important ecosystem service for which data and models are readily available and for which markets for payment are emerging. Terrestrial vertebrate species conservation is an important objective of policy and is the main objective of many conservation organizations. Details on the models we used to predict carbon sequestration and species conservation are presented in *Materials and Methods*.

We use these models to compare efficient land-use patterns with those likely to emerge as a result of decisions by landowners under various land-use conservation policy scenarios and conservation program budgets. Efficient outcomes occur when it is not possible to increase one desired objective without simultaneously decreasing another desired objective. In other words, all potential "win–win" possibilities have been realized. We summarize the set of efficient outcomes, with efficiency frontiers that show the maximum feasible combinations of multiple outputs that can be generated by the landscape.

In principle, an efficient outcome can be implemented by using a policy that aligns private landowner and social incentives. In practice, however, several obstacles prevent the implementation of such a policy and a realization of efficient outcomes. First, because of unobservable landowner characteristics and preferences, a government agency or conservation organization cannot predict with certainty which landowners will voluntarily accept a contract or payment scheme. Therefore, it is not possible to predict the policy-induced spatial pattern of the landscape with certainty (9). Second, because of landscape heterogeneity and spatial interactions, using incentive-based policies to generate an efficient land-use pattern may involve a complex set of various payments or contracts that go well beyond the administrative ability of an agency or organization to implement them. In addition, principles of fairness may limit differential treatment of landowners, even though landowners contribute differently to the provision of desired outcomes.

We apply this suite of land-use change and landscape-level biophysical models by using data from the Willamette Basin, Oregon [see supporting information (SI) Fig. 4]. The Basin consists of primarily forested slopes of the Coast and Cascade Mountain Ranges surrounding a relatively flat valley floor dominated by agriculture and urban centers. The valley floor and low foothills are largely privately owned, with public land dominating the higher elevations. The terrestrial species conservation model uses 37 terrestrial vertebrate species determined to be at risk or particularly sensitive to land-use change in the Basin [S.P., E.N., J. Camm, B. Csuti, P. Fackler, E.L., C. Montgomery, D.W., J. Arthur, B. Garber-Yonts, R. Haight, J. Kagan, A. Starfield, and C. Tobalske, unpublished data (available from the author upon request) and see SI Fig. 5].

We analyze the degree to which simple contracts or payment schemes to convert land to conserved land use can be expected to generate an efficient land-use outcome. We compare four targeted policies, under which only private landowners whose lands meet certain criteria are eligible, with an untargeted policy in which all private landowners are eligible to participate. The five conservation policies defined for privately owned parcels we analyze are (*i*) *All*: any parcel is eligible for a conservation contract; (*ii*) *Rare Habitat*: only parcels that could convert to particular types of rare natural habitat are eligible; (*iii*) *Carbon*: only parcels that could convert to conserved forest are eligible; (*iv*) *Riparian*: only parcels with significant stream density are eligible; and (*v*) *Species Conservation*: only parcels identified as important for vertebrate species conservation in the Basin [S.P., E.N., J. Camm, B. Csuti, P. Fackler, E.L., C. Montgomery, D.W., J. Arthur, B. Garber-Yonts, R. Haight, J. Kagan, A. Starfield, and C. Tobalske, unpublished data (available from the author upon request)] are eligible (see SI Fig. 6). The targeted policies mimic common targeting schemes used in incentive-based programs of the U.S. Department of Agriculture, such as the CRP. We compare the performance of targeted and untargeted land-use conservation payment schemes relative to the baseline land-use patterns assuming no land-use conservation policy. We also compare the performance of targeted and untargeted incentive payment schemes relative to the efficiency frontier for various levels of land-use conservation program budgets.

Results

Tradeoffs were found between carbon sequestration and species conservation on efficiency frontiers in the Willamette Basin, as indicated by the negative slope of each efficiency frontier (Fig. 1, and see SI Tables 1–4). An efficiency frontier shows the maximum amount of a given objective that can be attained on the landscape for a fixed level of the other objective and a given conservation program budget. Starting from an efficient land-use pattern, an increase in the production of one objective requires a decrease in the level of the other. Both species conservation and carbon sequestration levels on the frontiers increase as the conservation budget increases because more landowners can participate in the program. The shifting-out of the efficiency frontiers with increased conservation budget also reveals a tradeoff between species conservation/carbon sequestration and commodity production. In other words, greater levels of incentive payments corresponding to higher opportunity cost (e.g., value of foregone production) are required in order to shift land to conservation use. Results obtained with the simple carbon and biodiversity models (Fig. 1*A*) show a greater tradeoff between carbon storage and species conservation. With the complex biophysical models, we find significant portions of the efficiency frontiers where one objective can be increased without significantly lowering the other (Fig. 1*B*).

In general, species conservation is maximized when landowners who accept a conservation payment restore natural habitats that are relatively rare on the current landscape, including oak savanna, prairie, and emergent marsh. Carbon sequestration, on the other hand, is maximized when landowners who accept conservation payments restore conserved forests, including old growth, mixed, and riparian forest. Although maximizing forest cover benefits some species (e.g., the spotted owl), it provides little benefit for the majority of the 37 species analyzed. The different land-use patterns corresponding to different points on the efficiency frontier are illustrated for the policy under which all landowners are eligible for conservation payments, using the simple biophysical models (Fig. 2, and see SI Tables 5 and 6). On

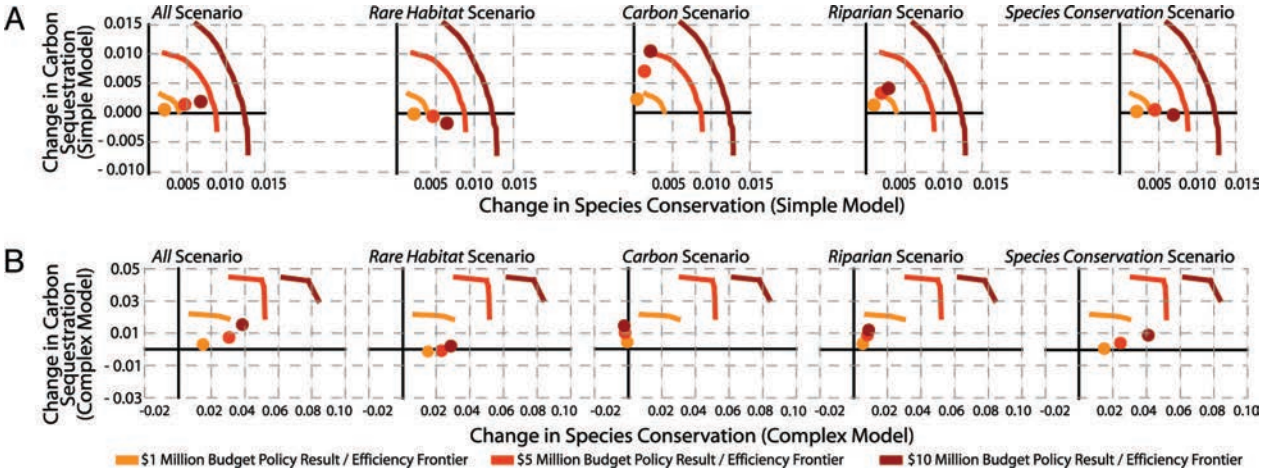

Fig. 1. Comparison of policy scenarios using the simple and complex biophysical models. (*A*) Increases in species conservation and carbon sequestration induced by each policy simulation and across each efficiency frontier, as compared with the base-case landscape with no conservation policy (the origin of each graph), using the simple species conservation and carbon sequestration models. Policy and efficiency results are shown for conservation program budget levels of $1 million, $5 million, and $10 million. Each point symbol shows the average response for the policy simulations across all 500 simulations. The leftmost graph shows the results when all private landowners are eligible for payments (the *All* policy scenario). The remaining graphs show results of targeted policies (see SI Table 1). The efficiency frontiers are shown as curved lines and assume that all private parcels eligible for a payment under the *All* policy scenario are eligible for a conservation payment when finding the frontier. The efficiency frontiers for the three budget levels are replicated on each policy graph (see SI Table 2). The baseline land-use pattern used to determine the origin of each policy graph had the mean service bundle level across all 500 simulated baseline land-use patterns. A 0.005 change on the *x* axis is equivalent to a 0.5% average change in the relative amount of a species' habitat provided by a land-use pattern. A 0.005 change on the *y* axis is equivalent to 2.1 million metric tons of carbon. (*B*) We replicate the analyses shown in *A* by using the complex species conservation and carbon sequestration models (see SI Tables 3 and 4). The efficiency frontiers in *B* represent only portions of complete frontiers because of the difficulty in finding points on the frontier with the nonlinear species conservation model. A 0.02 increment on the *x* axis is equivalent to a 2% change in aggregate species persistence. A 0.02 increment on the *y* axis is equivalent to 1.8 million metric tons of carbon sequestration.

the mapped portion of the valley floor, the land-use pattern that maximizes species conservation contains more oak savanna, prairie, marsh, and scrub–shrub lands (shown in yellow in Fig. 2), whereas the landscape that maximizes carbon storage contains more managed forests (shown in blue in Fig. 2). Both land-use patterns have less agricultural land than the average baseline land-use pattern on which no payments are offered for private landowner conservation.

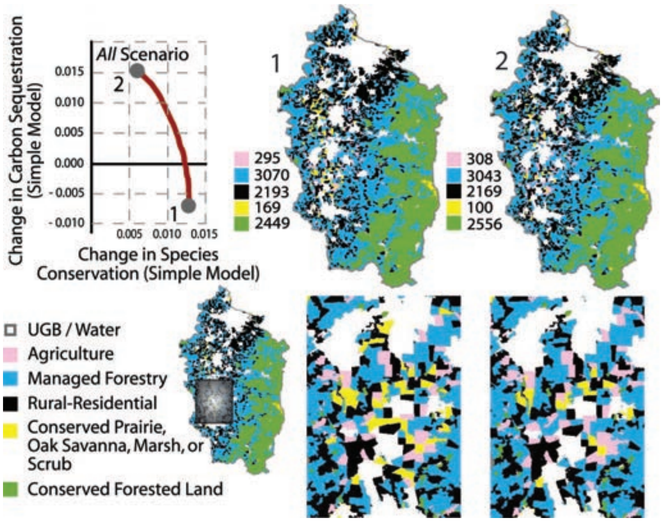

Fig. 2. Land-use patterns on the $10 million efficiency frontier (simple models). The two maps depict land-use patterns generated at two points along the $10 million budget efficiency frontier, using the simple carbon sequestration and species conservation models under the *All* policy scenario. The two maps at the top of the figure represent the entire study area at points 1 and 2 along the frontier. The blocks of numbers beside each Basin-wide map indicate the number of parcels in each land-use category on that map (see SI Tables 5 and 6). The corresponding maps directly below the Basin-wide maps show the land-use patterns in the area highlighted in gray on the small inset map.

The land-use patterns induced by the five policy scenarios considered here produce only small increases in carbon sequestration and species conservation relative to the baseline landscape with no conservation policy (indicated by the circles in Fig. 1), as compared with the feasible increases shown by the efficiency frontiers (Fig. 1, and see SI Tables 1–4). These inefficiencies are evident for both the simple and complex biophysical models and across all three conservation program budget levels.

The five policy scenarios generate very different mixes of outcomes relative to the baseline. Both the *Rare Habitat* and *Species Conservation* policies result in increases in species conservation but do not increase carbon sequestration, with actual reductions occurring under the *Rare Habitat* policy. By comparison, the *Carbon* policy, under which conservation contracts are only offered to landowners who can significantly increase the forest coverage on their land, results in increases in carbon sequestration but little increase in species conservation (simple models) or a decrease in species conservation (complex models). The *Riparian* policy provides little benefit in terms of either carbon sequestration or species conservation. Somewhat surprisingly, the untargeted policy (the *All* policy) increases species conservation as much or more than any of the targeted policies.

There is considerable variation in the degree to which species conservation and carbon sequestration can be increased by a policy for a given program budget level (Fig. 3, and see SI Tables 7–10). The variation in results for a policy–budget combination, using both simple and more complex models, is largely driven by the great variation in potential land-use patterns. Such variation is indicative of the uncertainty with which land-use pattern can be predicted using empirical models of voluntary decisions. There is also greater variation in the species conservation results using the complex species conservation model where species

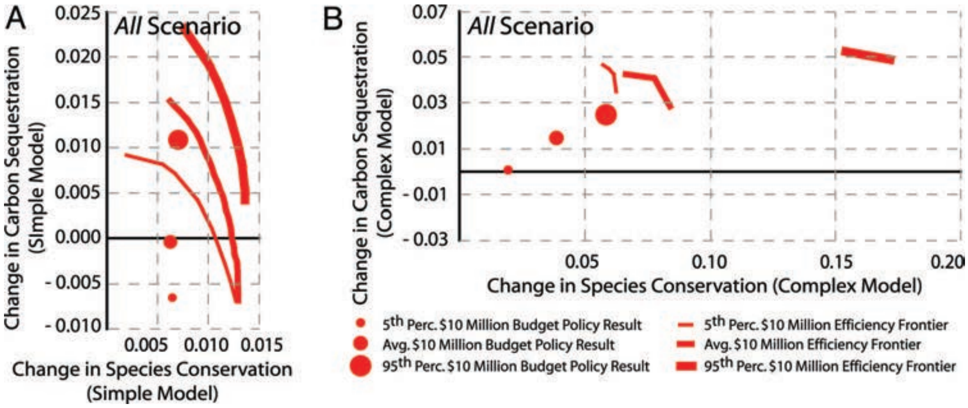

Fig. 3. Variability in results. Results are shown for three simulations that represent the 5th percentile, mean, and 95th percentile in terms of species conservation and carbon sequestration values among the 500 simulations for the *All* policy scenario with a $10 million program budget (see SI Tables 7–10), using the simple (*A*) and complex (*B*) models. The origins used in the graphs are the same as those used in the graphs in Fig. 1 *A* and *B*, respectively. Each policy result dot, and its accompanying efficiency frontier, are functions of the same baseline land-use pattern. The baseline land-use patterns that form the basis of the 5th and 95th percentile results using the simple biophysical models are not the same patterns that form the basis of the 5th and 95th percentile results using the complex biophysical models. The baseline land-use pattern that forms the basis of the mean results in both models is the same pattern that was used to create the efficiency frontiers shown in Fig. 1.

persistence probabilities increase nonlinearly with habitat and spatial configuration matters. Both the nonlinear change and the importance of spatial pattern make the species conservation score much more sensitive to which landowners accept conservation payments and results in greater variation across land-use pattern permutations than is the case with the simple model that depends only on the amount of habitat.

Discussion

We have combined a model that predicts land-use decisions by multiple private landowners with models that predict the consequences of these decisions on the provision of an ecosystem service and on biodiversity conservation. Although more sophisticated models exist for the component parts [e.g., the CENTURY model for carbon sequestration (10, 11)], these components have not been linked in a systematic fashion. We show that policies that pay private landowners to restore land to natural cover increase the provision of an ecosystem service and biodiversity conservation; however, these increases are less than what is feasible for a given budget, as shown by the efficiency frontier. It is possible that more sophisticated policies, such as auctions in which landowners submit bids of their willingness-to-accept (WTA) land use change, may be able to close the gap vis-à-vis the efficiency frontier.

For a given policy scenario simulation, all landowners accepting conservation contracts receive the same payment even though their WTA varies significantly (see SI Fig. 7). The inability to price-discriminate is one of the sources of the gap between the policy-induced land-use patterns and those on the efficiency frontier. Overpayments to landowners, however, are simply transfers from the program administrator to the landowners. The true social cost of the conservation policies is equal to the sum of the WTA of landowners agreeing to conservation contracts. Evaluating the efficiency of the incentive payments by measuring social costs rather than budget costs (including transfers) leads to a more optimistic interpretation of the efficiency of our simple conservation policies. For example, under the *Species Conservation* policy, using the simple species conservation model with a $10 million budget, the conservation policy achieves 57% of the potential increase in species conservation. However, using the sum of WTA as the measure of cost, the cost of the contracts would be approximately $5 million (see SI Fig. 8). Compared with what could be achieved at this program budget level, the conservation policy achieves 81% of the potential gain in species conservation. The remaining inefficiency of incentive-based policies is because voluntary enrollment does not ensure that the specific set of landowners necessary to generate an efficient landscape pattern will enroll. Nevertheless, many agencies view the budget as a measure of cost, and overpayments to landowners can have efficiency implications if there are costs to raising and administering program funds.

Our analyses show that policies aimed at increasing the provision of an ecosystem service can, but do not necessarily, increase the provision of species conservation (and vice versa). We found some cases in which a policy directed toward one goal actually reduced the ability to attain the other goal. For example, the *Rare Habitat* scenario results in lower carbon sequestration than the case with no policy at all. If programs that pay for ecosystem services are not designed carefully, they may yield minimal gains in services of interest and may well result in harm to other services or biodiversity conservation. The consideration of a greater range of ecosystem services in a conservation policy will only magnify the degree of potential tradeoffs. Another challenge to designing an efficient targeting scheme is the fact that the optimal conservation payment will vary across landowners and may be a function of the land-use decisions of each landowner's neighbors (as it is with the complex species conservation model). Implementing a complicated incentive scheme that accounts for such interactions would not be trivial. Finally, if a targeted policy does not accurately capture desired environmental benefits, then results with targeting may be worse than without targeting. Targeting reduces the number of eligible landowners and, on average, raises the cost of a conservation contract. Only through accurate targeting of conservation contracts to landowners providing high conservation benefits will the gain of targeting be sufficient to outweigh the increase in contract cost.

Fundamental differences in model assumptions and output metrics in the simple and complex species conservation models make it difficult to directly compare their results. The simple species conservation model provides an estimate of the proportion of the landscape that provides habitat for the 37 terrestrial vertebrate species included in the analysis. This measure does not take into account species' area requirements for breeding and feeding activities or the spatial pattern of the landscape. The complex species conservation model estimates the probability that each of the 37 species would maintain a viable population in the Willamette Basin, taking into account both the species' area requirements for breeding and feeding activities and the spatial pattern of the landscape. A species that requires large contiguous blocks of habitat in a landscape that contains many small fragments of habitat may score well in the simple model, while the complex model produces a low score. In addition, it is possible for relatively small land-use changes that result in increases in key habitat to have a large impact on species conservation in the complex model that takes habitat configuration into account.

In this analysis, we investigate feasible combinations of an ecosystem service and species conservation that could be produced on the Willamette Basin ("supply side" analysis). This analysis shows tradeoffs between desired ends but does not provide information about how to choose among these ends. Combining this analysis with non-market valuation studies ("demand-side" analysis) would allow comparison of the value of different bundles of ecosystem services and species conservation to maximize the value of outcomes generated by the landscape. It is relatively straightforward to value some ecosystem services, such as those that produce marketable commodities (e.g., crops or timber). Studies of the potential losses associated with climate change and rapidly emerging carbon markets offer some hope for accurately assessing the value of carbon sequestration. At the other extreme, valuing species existence or aesthetics is fraught with difficulty (e.g., ref. 12). Even without complete valuation of all environmental goods, however, presenting decision-makers with tradeoffs among ends provides information regarding the opportunity cost of achieving particular environmental goals and, hence, a measure of the minimum value that those environmental goods must possess for a particular policy to achieve a net gain in social welfare.

Finally, predictions and policy advice generated by analyses are only as good as the models and data on which they are based. In many ways, we are still at an early stage in the analysis of the provision of ecosystem services and biodiversity conservation from landscapes, and much remains to be learned. Questions remain regarding how much detail and complexity are required in order to inform policy. In our application, it appears that greater model complexity and data did not greatly change modeling results or policy advice. Expanding the analysis to include more services risks going beyond what teams of analysts know and understand. Linking many components into a comprehensive analysis also risks magnifying any errors present in the component analyses. The joint nature of the provision of ecosystem services on landscapes, however, makes the push toward comprehensive analysis of vital importance. Further analysis, combined with monitoring and evaluation of the consequences of past decisions, should offer more confidence in predictions and policy advice generated by landscape-level analyses such as the ones undertaken here.

Materials and Methods

The Parcel Map. The Willamette Basin of Oregon was divided into 10,372 distinct parcels on the basis of a 1990 land-cover map (13). We deleted water-covered parcels and parcels inside urban growth boundaries, leaving 8,176 parcels. We obtained information on each of these parcels, including the 1990 land-cover type, current ownership and conservation status (14), pre-Euroamerican vegetation cover (15), and other physical characteristics, such as soil type (16) and location of perennial streams (ref. 17, and see *SI Text: The Parcel Map*).

Econometric Model of Land-Use Change. An econometric land-use model (1) is used to quantify the relationship between private land-use decisions, the economic net returns to alternative uses, and parcel-level characteristics (see *SI Text: Econometric Model of Land-Use Change*). Landowners are assumed to choose land uses to maximize the present discounted value of the stream of expected returns to the land net of conversion costs. Because, in practice, land-use decisions can also be influenced by unobserved factors (e.g., landowner skills), we model the probability that a land parcel will change from one use to another conditional on observed net returns and model parameters. These parameters are estimated by using a repeated sample of plot-level land-use decisions from the National Resources Inventory. The econometric analysis focuses on private land in the conterminous United States and on six major land uses (crops, pasture, forest, urban, range, and land enrolled in the CRP). The estimation yields land-use transition probabilities for all possible starting and ending uses, conditioned on net returns and plot-level soil characteristics. For this analysis, we extract the values of these conditioning variables for the Willamette Basin to produce a set of transition probabilities for each parcel.

Policy Simulation. Starting from an initial land-use pattern (circa 1990), we use the econometrically estimated transition probabilities to predict changes in the landscape over a 50-year time period (ref. 8, and see *SI Text: Policy Simulation*). Because changes on each land parcel are probabilistic, we simulate 500 baseline land-use patterns to generate a representative distribution of the range of potential landscape outcomes assuming no conservation payments to private landowners.

We then use the estimated transition probabilities to generate a probability distribution of WTA for each parcel of private land, where WTA is the minimum amount of annual payment necessary for the landowner to agree to take their land out of its current production land use and switch to conservation. For each of the 500 baseline simulations, we generate a WTA value for each privately owned parcel by randomly drawing from the parcel's WTA probability distribution. Under any policy scenario simulation, an eligible private landowner will accept a conservation contract if the contract's annual payment is equal to or exceeds the landowner's WTA. We assumed that land placed into conservation is restored to the land's pre-Euroamerican vegetation cover for that parcel. A parcel that does not contract for conservation is assumed to remain in its baseline land use (see *SI Text: Policy Simulation* and SI Table 11). Because we have 500 baseline land-use patterns and 500 accompanying vectors of private landowner WTA values, we can generate 500 policy-induced land-use patterns for each policy scenario and conservation program budget level.

We evaluate each of the five policy scenarios at three different annual budget levels: $1 million, $5 million, and $10 million. For each scenario and budget combination, we solve for the annual per-acre contract price that would enroll just enough landowners to exhaust the budget (see SI Table 12).

Carbon Sequestration Models. The simple version of the carbon model uses as its biophysical basis Intergovernmental Panel on Climate Change default terrestrial carbon storage values as a function of land use (18). Storage values as a function of land use are specific to the Basin's eco-region and climate region. Carbon stored on the land is the sum of carbon stored in five pools: soil, below-ground biomass, above-ground biomass, deadwood and litter, and harvested wood products. The difference between the carbon stored on the initial and final land-use patterns represents the carbon sequestration that occurs on the landscape over a 50-year time horizon. Because storage values are uncertain, we construct mean sequestration values to score land-use patterns (see *SI Text: Simple Carbon Sequestration Model* and SI Tables 13–18).

In the more sophisticated version of the carbon model, we use detailed information specific to the Willamette Basin, including information about the distribution of tree species, tree ages, and canopy densities across the landscape, along with characteristics of each parcel and tree stand allometric tables (19), to predict annual carbon sequestration on each parcel over the 50-year modeling time horizon. Annual carbon sequestration rates are a function of the mix of softwood and hardwood trees, tree stand age, canopy density, soil type, elevation, initial and final land use on the parcel, and the timing of land-use transition (20). Annual changes in carbon sequestration are discounted at a 5% rate. Because the exact softwood and hardwood tree mix, canopy density, carbon stock in the soil and other minor carbon pools, and timing of land-use transition on each parcel are unknown, we construct mean sequestration values to score land-use patterns. The model's final output is the amount of carbon sequestered across the whole landscape over the 50-year modeling time horizon (see *SI Text: Complex Carbon Sequestration Model* and SI Tables 19–24).

Final landscape-level output from both carbon models is normalized by dividing predicted 50-year carbon sequestration levels by the maximum potential sequestration that could occur on the landscape over the same time period.

Species Conservation Models. The species conservation model translates land-use patterns into habitat maps for the 37 terrestrial vertebrate species modeled in the analysis. The simple species conservation model is solely a function of aggregate species habitat for breeding and feeding activities (see *SI Text*: *Simple Species Conservation Model*, SI Table 25, and SI Fig. 5). For each generated land-use pattern, the simple model calculates the following ratio for each species: the amount of breeding and feeding habitat area provided for the species vs. the maximum amount of breeding and feeding habitat area that could be provided if the landscape was completely managed for the benefit of the species. The overall species conservation score for a land-use pattern is the average of all 37 species ratios. Time is not a factor in the simple species conservation model.

In contrast, the complex model is spatially explicit and predicts species persistence as a function of the amount and spatial pattern of breeding and feeding habitat, as well as species' breeding and feeding area requirements and dispersal abilities. The complex species conservation model determines the expected number of species that would persist on the landscape for an indefinite time period, given a land-use pattern (ref. 21, and see *SI Text*: *Complex Species Conservation Model* and SI Tables 25–27). The complex species conservation model results are normalized by dividing a land-use pattern's predicted species conservation amount by 37.

Efficiency Frontiers. An efficiency frontier plots combinations of outcomes such that one outcome cannot be improved without reducing another outcome. We solve for a point on an efficiency frontier by finding the land-use pattern that maximizes species conservation subject to the land-use pattern meeting a specified carbon sequestration value and a given policy budget. Parcels eligible for a change when finding the efficiency frontier are the same parcels that are eligible for a conservation contract under the *All* policy scenario. The only change possible is from the baseline land use to the conservation land use. For the efficiency frontier analysis, we assume that the annual conservation payment paid to a landowner is equal the landowner's WTA.

By varying the carbon sequestration goal, we can define the efficiency frontier for a given program budget level [S.P., E.N., J. Camm, B. Csuti, P. Fackler, E.L., C. Montgomery, D.W., J. Arthur, B. Garber-Yonts, R. Haight, J. Kagan, A. Starfield, and C. Tobalske, unpublished data (available from the author upon request)]. We then solve for the efficiency frontier for three different budget levels. By increasing the budget, which represents greater opportunity cost in terms of foregone marketed commodity production, greater levels of species conservation and carbon sequestration can be obtained (see *SI Text*: *Efficiency Frontiers*).

The efficiency frontiers in Fig. 1 indicate maximum joint production on the landscape assuming a particular baseline land-use pattern; we did not find the set of efficiency frontiers associated with each baseline land-use pattern and then take the average across all frontiers.

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