Oxford Review of Economic Policy, Volume 28, Number 1, 2012, pp. 139–163

Are investments to promote biodiversity conservation and ecosystem services aligned?

Stephen Polasky,* Kris Johnson,** Bonnie Keeler,* Kent Kovacs,* Erik Nelson,*** Derric Pennington,**** Andrew J. Plantinga,***** and John Withey******

Abstract The conservation community is divided over the proper objective for conservation, with one faction focused on ecosystem services that contribute to human well-being and another faction focused on the intrinsic value of biodiversity. Despite the underlying difference in philosophy, it is not clear that this divide matters in a practical sense of guiding what a conservation organization should do in terms of investing in conservation. In this paper we address the degree of alignment between ecosystem services and biodiversity conservation strategies, using data from the state of Minnesota, USA. Minnesota voters recently passed an initiative that provides approximately $171m annually in dedicated funding for conservation. We find a high degree of alignment between investing conservation funds to target the value of ecosystem services and investing them to target biodiversity conservation. Targeting one of these two objectives generates 47–70 per cent of the maximum score of the other objective. We also find that benefits of conservation far exceed the costs, with a return on investment of between 2 to 1 and 3 to 1 in our base-case analysis. In general, investing in conservation to increase the value of ecosystem services is also beneficial for biodiversity conservation, and vice-versa.

Key words: biodiversity, ecosystem services, conservation, land use, carbon sequestration, water quality

JEL classification: Q57, Q24, Q25, Q51

I. Introduction

Economists are used to thinking about maximizing an objective function subject to constraints. Individuals maximize utility subject to a budget constraint and perfectly

*University of Minnesota, e-mail: polasky@umn.edu; keel0041@umn.edu; kova0090@umn.edu
** The Nature Conservancy, e-mail: kjohnson@tnc.org
*** Bowdoin College, e-mail: enelson2@bowdoin.edu
**** World Wildlife Fund, e-mail: penn0107@umn.edu
***** Oregon State University, e-mail: plantinga@oregonstate.edu
****** Florida International University, e-mail: jwithey@fiu.edu

We thank the editors and an anonymous referee for helpful comments. We acknowledge support from the National Science Foundation Collaborative Research Grant 0814628 on 'Integrated dynamic modeling of ecosystem services, incentive-based policies, land-use decisions, and ecological outcomes'.
doi:10.1093/oxrep/grs011

competitive firms maximize profits given technology and prices. Though far less common, such thinking can also be applied to biodiversity conservation and environmental management. For example, several papers have analysed the objective of maximizing the number of species conserved through habitat protection given limited resources (e.g. Ando *et al.*, 1998; Wilson *et al.*, 2006; Murdoch *et al.*, 2007). Applying an economic approach to conservation and environmental management requires stating a clear objective. In the conservation realm, however, there is not universal agreement on the objective:

> As a society, we have not even come close to defining what is the objective. . . . We have to make up our minds here what it is we are optimizing. This is the essential problem confounding the preservation of biodiversity today. (Metrick and Weitzman, 1998, p. 21)

At present, there is a deep divide within the conservation community about the proper objective for conservation (Mace *et al.*, 2012; Reyers *et al.*, 2012).

One school of thought focuses on ecosystem services and emphasizes the value of conserving biodiversity and ecosystems to provide ecosystem services that contribute to human well-being (Daily, 1997; MA, 2005; TEEB, 2010; Kareiva *et al.*, 2011). Some prominent conservation organizations have adopted this approach. For example, the vision statement of the Convention on Biological Diversity (CBD) *Strategic Plan for Biodiversity 2011–2020* is that conserving biodiversity and ecosystems is important for 'maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people' (CBD, 2010). The ecosystem services approach to conservation is consistent with a welfare economic approach that seeks to maximize social net benefits, where benefits include the contributions of ecosystems to human well-being. Of course, there are also benefits beyond ecosystem services, so that maximizing well-being and maximizing the value of ecosystem services are not synonymous. This approach requires integrated ecological-economic modelling that demonstrates the link between ecosystem management, ecological processes, the provision of ecosystem services, and consequent impacts on human well-being (Daily *et al.*, 2009; NRC, 2005).

A second school of thought is that conservation should be based on ethical arguments about the intrinsic value of nature (Rolston, 1988; McCauley, 2006; Redford and Adams, 2009; Vira and Adams, 2009). In this school of thought, biodiversity is to be conserved for its own sake, whether or not it contributes to human well-being (Ehrenfeld, 1988). This does not mean that biodiversity does not also contribute to human well-being, but that the motivation for conservation comes from the intrinsic value of nature. The intrinsic value of nature motivation for conservation represents a fundamental departure from a welfare economics perspective, where nature has instrumental value (i.e. it contributes to human well-being). Under the intrinsic value of nature approach, biodiversity conservation is an ethical obligation and should occur even when doing so imposes burdens upon society that reduce human well-being. We revisit the relationship between ecosystem services, biodiversity, and human well-being in the discussion section.

Though the divisions between focusing on human well-being versus focusing on the intrinsic value of nature can be deep in terms of underlying philosophy, do they matter in a practical sense in terms of land use or resource allocation? Do management decisions of a conservation agency aimed at maximizing the value of ecosystem services differ dramatically from management decisions aimed at conserving biodiversity? If management prescriptions from these two approaches closely align, then we would argue that conservation planners can proceed without worrying too much about the underlying philosophical debates. If this is the case, disputes over the proper goal for conservation would be yet another example of the famous saying about debates in academia: 'The politics of the university are so intense because the stakes are so low', which is also known as Sayre's Law (Shapiro, 2006, p. 670). If, on the other hand, management prescriptions do not closely align, then conservation managers will need to address the question of the proper objective function before deciding what actions to take.

In this paper, we address the degree of alignment between ecosystem services and biodiversity conservation using data from the state of Minnesota, USA. In 2008, Minnesota voters passed the Clean Water, Land and Legacy Amendment (Legacy Amendment). The Legacy Amendment increased the state sales tax by three-eighths of 1 per cent for 25 years, likely raising more than \$250m per year. Of these funds, 33 per cent are allocated to a Clean Water Fund to conserve and enhance water quality and 33 per cent are dedicated to an Outdoor Heritage Fund to protect and restore prairies, forests, wetlands, and other wildlife habitat. Together these two funds will provide an estimated \$171m annually for conservation in Minnesota. We analyse whether using the Legacy Amendment Funds towards a strategy that aims to maximize the value of ecosystem services will choose similar land for conservation compared to a strategy that aims to maximize the conservation of biodiversity.

While it would be ideal to include the value of all ecosystem services and all biodiversity, doing so is well beyond current capabilities. Here we model the provision and value of carbon sequestration and the reduction of phosphorus in waterbodies, the latter being the most important factor for surface water quality in the state, which closely matches with the goals of the Clean Water Fund. As our measure of biodiversity we use the predicted occurrences of vertebrates (including breeding, game, and listed species) because their distributions and associations with land use and land cover are well known compared to other organisms, and match the general goals for the Outdoor Heritage Fund.

We compare the ecosystem service and biodiversity strategies on a static landscape in which the only change in land use is brought about by purchase of land for conservation ('static analysis'), and on a more realistic case in which conservation occurs amidst the backdrop of other land-use change ('dynamic analysis'). We find that in both static and dynamic analyses purchasing land for one objective has a positive effect on the other objective, but that the alignment of objectives is far from perfect. In the case of static land use, targeting ecosystem services generated a biodiversity score that was 53 per cent of the maximum score obtained when targeting biodiversity. When we targeted biodiversity we generated a value of ecosystem services that was 70 per cent of the maximum value of ecosystem services obtained when targeting services. In the dynamic land-use case, targeting ecosystem services generated 47 per cent of the biodiversity score as compared to targeting biodiversity, and targeting biodiversity generated 65 per cent of the value of ecosystem services as compared to targeting services.

Most prior work looking at the spatial pattern of the provision of bundles of ecosystem services and biodiversity describes the degree of spatial correlation given the current pattern of land use (e.g. Chan *et al.*, 2006; Egoh *et al.*, 2008, 2009; Naidoo *et al.*, 2008; Raudsepp-Hearne *et al.*, 2010). Different land uses generate different bundles of services. For example, intensive agricultural production is associated with high production of agricultural products but low water quality and carbon storage, while conserved forested areas often have high carbon storage, habitat, and recreation value but low commercial returns. In this paper, we address the more policy relevant question of how to maximize the increase in the provision of ecosystem services or biodiversity conservation through changes in land use for a given cost. The closest prior papers in this vein are Naidoo and Ricketts (2006), Nelson *et al.* (2008, 2009), and Polasky *et al.* (2008, 2011). Apart from Egoh *et al.* (2010) these papers do not directly address the question of alignment between ecosystem service objectives and biodiversity conservation objectives.

We describe the data and models used to perform this analysis in section II. Results are presented in section III. Section IV contains a brief summary of major findings as well as comparisons of our results to prior work in a similar vein. We conclude section IV with a discussion of outstanding issues that require further research.

II. Data and methods

We model two important drivers of changes in ecosystem services, carbon sequestration and water quality, and the provision of habitat for biodiversity under alternative land-use scenarios and decision-making criterion. We compare the outcome of land acquisition for conservation guided by an ecosystem service objective with land acquisition guided by a biodiversity objective. We compare these objectives under an assumption of static land use and under a dynamic land-use change model. We begin this section by describing the land-use and land-cover data. Next we describe the land-use scenarios evaluated in this paper. We then discuss the models used to quantify carbon storage, water quality, and habitat for biodiversity. We discuss the opportunity cost and restoration cost of conserving land. Finally, we explain the optimization framework to guide conservation strategies that incorporates costs, biodiversity, and ecosystem service benefits.

(i) Land-use and land-cover data

We used a baseline 2001 land-use map and predicted 2026 land-use maps to examine how conservation funds should be allocated during the 25-year period over which conservation funds are available. We generated the baseline 30-metre resolution land-use map by downloading the 2001 National Land Cover Database (NLCD) for Minnesota (Homer *et al.*, 2007). We converted all NLCD land covers into one of five general land-use types (cropland, pasture, range, forest, and urban) using conversions shown in Table A-1 of the Appendix.[1] We used data from a national map of private and public lands (Conservation Biology Institute, 2010) to delineate public and private lands within the state.

[1] A detailed Appendix to this article is available online at http://oxrep.oxfordjournals.org/cgi/content-embargo/full/grs011/DC1.

Ecosystem services, habitat quality, and land values were calculated at the sub-county unit level, using boundaries defined by the Minnesota Department of Revenue for purposes of property tax reporting. For most of the state, sub-county units are townships, except in the north where townships are quite large and sub-county units are defined on a smaller area more closely resembling the size of townships in the rest of the state. This spatial delineation allows use of the greatest detail on land costs across the state, especially in the largely undeveloped northern region.

Land close to streams and rivers generally has more direct impact upon water quality (Osborne and Kovacic, 1993). To distinguish these lands we used 100-metre buffers around centrelines for 52 major rivers in the state (Minnesota Department of Natural Resources, 2012).

Combining information from these various data layers, we created maps identifying the area of each land-use type (cropland, forest, pasture, urban, and range) both within and outside of the 100-metre buffers, held in both public and private ownership, for every sub-county unit in Minnesota as of 2001.

(ii) Land-use scenarios

We analysed optimal land acquisition for conservation under static and dynamic land-use scenarios. In both scenarios, land acquired and conserved was assigned its sub-county potential natural vegetation proportional mix of forest, prairie, or wetland. The native land cover proportion was based on the LANDFIRE biophysical settings layer (NatureServe, 2009), which assigns an ecological system code to each 30-metre pixel based on potential vegetation and natural disturbance regimes. In both static and dynamic land-use scenarios, we also assumed that management of public lands remained unchanged and that all conservation funds were used to acquire and conserve lands that were private in 2001.

In the static land-use scenario, private land that was not chosen for conservation remained in its 2001 land use through 2026. In the dynamic land-use scenario, we projected land use to 2026 for private lands that were not conserved using a land-use transition matrix. The land-use transition matrix gives the probabilities of transitions from one land use to another over the 25-year period between 2001 and 2026 for each sub-county unit. Because the land use in 2026 is probabilistic, we chose a particular land use for each hectare of private land using a random number generator. By simulating the choice for each hectare, we determined the distribution of land use in 2026 by land-use type within each sub-county unit within and outside the 100-metre water buffers. This procedure was repeated 100 times for each conservation strategy, generating 100 maps of 2026 land use on private land, which we then combined with conservation and public land to generate 100 state-wide land-use maps for 2026 under the conservation strategy.

These land-use transition matrices are described in more detail in Radeloff *et al.* (2012). In that research, 5-year land-use change probabilities were used to simulate land-use change across the US. We used the land-use change probability matrices specific to Minnesota for five sequential 5-year periods to get the cumulative sum of changes over 25 years in the state. Unlike Radeloff *et al.* (2012), we have modified the transition matrices to take into account the effect of land market price feedbacks on the transition probabilities, as in Lubowski *et al.* (2006).

(iii) Carbon storage and sequestration

Although climate change mitigation was not an explicit goal of the Legacy Amendment, state policies establish aggressive greenhouse-gas emission reduction targets and identify biologic sequestration of carbon as an important strategy to achieve these goals (MCCAG, 2008). We calculated carbon storage values for soil and for biomass for each land-use type in each sub-county unit in Minnesota. We estimated carbon sequestration that would be achieved under a conservation strategy by calculating the differences in carbon storage under the strategy relative to the 2001 baseline.

To calculate the quantity of carbon stored in soils we used a national map of soil carbon (Sundquist *et al.*, 2009) combined with land cover and county boundary data to generate average soil carbon storage values for each land-use type in each county in Minnesota. We did not have data on soil carbon in wetlands. Wetlands generally have some of the higher soil carbon levels. Therefore, we used the highest observed soil carbon level for land-use types for wetlands.

We also calculated carbon storage in above-ground biomass. Because biomass from cropland, pasture, and range is generally harvested and removed each year, we assumed that each of these land-use covers stored zero above-ground carbon in biomass. To calculate biomass carbon on forest hectares we used Forest Inventory Analysis (FIA) data and Smith *et al.* (2006). The FIA dataset indicates the proportion of forest land in each county in the forest types oak-hickory, white-red-jack pine, and aspen-birch and the Faustmann rotation age of each forest type. We distinguished between management of private forest land and conservation forest land. For forests on land that was set aside under a conservation strategy we assumed that restored forest would attain biomass carbon levels of a 95-year old forest with the county's mix of forest types. Smith *et al.* (2006) provide carbon storage values for each major forest type by forest age class. We assumed private forest land was in managed rotations, where trees were harvested at specified age (the Faustmann rotation age) and steady-state harvesting maintains a constant proportion of land in each age class up to the rotation age. For Minnesota forests the Faustmann rotation age was between 30 and 60 years. Again, Smith *et al.* (2006) was used to find biomass carbon levels associated with tree ages and a county's mix of forest types to determine a private forest hectare's biomass carbon levels. Finally, we assume that an urban hectare in a county has one-tenth of the above-ground biomass carbon of a private forest hectare in the same county. See the Appendix for carbon model details.

We calculated monetary values of the changes in carbon storage using estimates of the social cost of carbon (Tol, 2009). The social cost of carbon is the cost to society incurred by the potential climate change damages from each additional tonne of carbon emitted to the atmosphere. Values for the social cost of carbon reported in the literature range from near \$0 to over \$500 per ton of carbon (Tol, 2009). In this paper, we used a base-case estimate of \$126.40 per ton carbon (\$34.47 per ton of carbon dioxide (CO_2)) in constant 2011 dollars, based on a value of \$91 in 1995 constant dollars for the median fitted distribution for social cost of assuming a 1 per cent pure rate of time preference (Tol, 2009).

(iv) Water quality: phosphorus retention

A core goal of the Legacy Amendment is to protect and restore water quality in Minnesota. Land use can impact water quality by contributing sediment, nutrients, or other pollution to surface and ground water. Conserved lands can provide an important ecosystem service by capturing polluting nutrients and sediment before they reach adjacent water bodies. In this analysis, we focus on phosphorus pollution, which is the leading cause of surface water impairment in the upper Midwest (Carpenter *et al.*, 1998). We used the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs; Tallis *et al.*, 2010, http://invest.ecoinformatics.org/) water models to estimate the water quality benefits provided by land acquisition and conservation. InVEST is a spatially explicit model that applies a two-step process to determine the influence of land cover on water quality. First, the model calculates the average annual water yield in each mapped grid cell using climate data, geomorphological information, and land-use and land-cover (LULC) characteristics. The model does not incorporate sub-surface or ground water flows but assumes that all precipitation not lost to evapotranspiration goes to surface water run-off. In the second step, water yield is combined with information about phosphorus loading and the phosphorus retention capacities of each LULC type to calculate the annual phosphorus exports from each grid cell. Phosphorus exports from cells are routed via surface water flows to other cells, where some of the phosphorus may be filtered or additional phosphorus added, until the surface water flows into a water body. Once phosphorus reaches a water body the model assumes no additional retention, or removal occurs before delivery to the mouth of the watershed.

We used the InVEST water models to calculate the phosphorus loading for the 2001 baseline map. Because the InVEST water models are spatial and rely on surface water flows to route nutrients, we ran the models using the 81 eight-digit hydrologic unit code (HUC) basins in Minnesota. Average phosphorus loadings were then assigned to each sub-county unit based upon the location of the sub-county unit within the HUC basins. We also used the 2001 baseline map to calibrate the average per-hectare phosphorus loading and phosphorus retention capacities of each LULC type, both outside and inside of the 100-metre buffers around rivers and streams. Reductions in phosphorus loading to be achieved in 2026 by conservation decisions were calculated by multiplying the LULC proportions adjusted following land acquisition by the average per-hectare loadings for each LULC type. The percentage change in the loadings of each basin was calculated by finding the difference of the loadings associated with the LULC change divided by the total baseline loading of phosphorus to the basin. Basins further downstream of where LULC change occurs also experience a change in water quality.

We used a national meta-analysis conducted by Johnston *et al.* (2005) to generate estimated annual per household willingness-to-pay (WTP) values for improved water quality. Following the guidelines in Johnston and Besedin (2009) we adapted parameters in the WTP function to reflect appropriate geographic area, water body type, and mean household income. The model estimates WTP as a function of changes in water quality relative to baseline conditions, with water quality described by the Resources for the Future (RFF) water quality ladder. The RFF water quality ladder links changes in water uses (drinking, boating, swimming, and fishing) to variations in biophysical characteristics (dissolved oxygen, turbidity, pH) and uses a qualitative point system to represent changes in the value of uses that correspond to changing water quality

(Carson and Mitchell, 1993). To establish baseline water quality for each HUC basin, we obtained statewide data on lake trophic state index (TSI; Carlson, 1977) from the Minnesota Pollution Control Agency (MPCA; personal communication with Steven Heiskary, 2012). We then mapped average TSI values for lakes within each HUC basin to the RFF water quality ladder. Based on consultation with local water quality experts, we assumed that a 50 per cent reduction in phosphorus loading relates to a two-point increase along the RFF water quality ladder. Combining these water quality parameters with the Johnston *et al.* (2005) WTP function, we generated estimates of annual WTP for the 50 per cent reduction of from \$24.97 to \$44.72 per household in 2011 constant dollars. The values were prorated to the percent change in phosphorus loadings modelled by InVEST; for example, for a WTP value of \$10 per household for a 50 per cent reduction, a 1 per cent reduction in phosphorus loadings was prorated to \$0.20. The prorated WTP per household is an annual value which we then converted into a present value of benefits assuming permanent water quality improvement. The future benefits of public goods should be discounted at a rate close to the market rate of return for risk-free financial assets (Howarth, 2009), which we assumed to be 2 per cent. The present value of WTP values per household for each basin are multiplied by the number of households per sub-county unit, based on the average of the number of households in 2010 and population projections for 2025 (Minnesota Department of Administration, 2007).

(v) Habitat for biodiversity

The Legacy Amendment also directs funds to protect 'fish, game and wildlife habitat' and has an explicit goal of enhancing Minnesota's capacity to conserve and enhance biological diversity. We model the baseline 2001 map and the 2026 alternative land-use scenarios to compare the potential benefits for biodiversity of alternative conservation strategies. The biodiversity model evaluates the potential for different land cover types in a sub-county unit to provide habitat for a set of vertebrate species based on current distributions and habitat associations. First, we estimate total vertebrate species richness for each LULC type at the sub-county unit level. We use information on the current predicted distribution of individual species based on actual habitat characteristics within their general ranges, as determined by the Minnesota Gap Analysis Project (MN-GAP; Drotts *et al.*, 2007). MN-GAP includes species found in Minnesota that are listed as breeding, state endangered or threatened, of special conservation concern, a fur-bearer, big game, small game, or migratory game bird. MN-GAP includes 354 vertebrate species (21 amphibians, 28 reptiles, 75 mammals, and 230 birds; the complete species list is presented in the Appendix). For sub-county units that did not contain a given LULC type, we determined county-level richness estimates and used these to substitute for the missing sub-county unit-level LULC type. We determine the habitat for biodiversity score for a sub-county unit by multiplying the species per LULC type estimate by its corresponding LULC area for the total of public, private, and conserved lands, and summed this score across all LULC types. This sum produces the number of habitat units in the sub-county unit, which indicates the conservation value of those lands to support these species. Higher scores indicate more available habitat to support more species, and therefore sub-county units with greater value for biodiversity conservation. We then sum the sub-county unit scores across all units to generate a score for the entire state under a given conservation strategy.

(vi) Conservation budget and opportunity costs

We created a conservation budget by combining the two largest allocations of the Legacy Amendment, the Clean Water Fund dedicated to improving water quality, and the Outdoor Heritage Fund targeted to preservation of wildlife habitat, which generated $171m per year. Assuming a 2 per cent real interest rate, the total present value of the conservation budget over the 25-year duration of the Amendment was $3.319 billion.

We downloaded recent land value data for private crop, timber, and pasture land uses in each sub-county unit in Minnesota (www.landeconomics.umn.edu). The statewide average land values for cropland, timberland, and pasture land are $24,989, $10,225, and $8,289 per hectare, respectively. We also used land restoration costs to estimate the transition cost of shifting from one form of private land use to a conserved native land-use type (LSOHC, 2009). The restoration cost used for conserved wetland, forest, and prairie is $2,904, $3,743, and $2,629 per hectare, respectively. We were only able to attain state-wide average numbers for restoration costs so these did not vary by sub-county unit. We combined land value data that represent the opportunity cost of conserving land and land restoration costs to estimate the total costs of switching from private to conserved land.

(vii) Optimization for targeting conservation investment

Land-use conversion causes a change in the provision of ecosystem services and habitat for biodiversity. We used the carbon, water quality, and habitat for biodiversity models described above to define the change in the value of ecosystem services and biodiversity caused by land-use change. For the static land-use scenario, the expected benefits of conservation are given by the gain in conservation score across the state of Minnesota (biodiversity score or value of ecosystem services) generated by land acquisition and restoration to the potential vegetation natural state on an otherwise static 2001 landscape. The expected benefits of conservation under the dynamic land-use scenario are given by the gain in conservation score across the state of Minnesota generated by land acquisition and restoration to the potential vegetation natural state *plus* the conservation score created by expected land-use change between 2021 and 2026 on land that remains private. The costs of conserving are the sum of the land cost plus the costs of restoring to the potential vegetation natural land cover.

We solved the static and dynamic land-use scenario problems for the ecosystem services and biodiversity objectives with the Generalized Algebraic Modeling System (GAMS) 23.5.1 using the linear programming solver CPLEX. The optimization routine finds the land conservation pattern that maximizes the expected increase in the value of ecosystem services or habitat for biodiversity given the budget constraint fixed by the amount of the Legacy Amendment Funds. The optimization model selects the land with the highest (expected) gain in conservation target value per dollar expended until the conservation budget is exhausted.

In the dynamic land-use scenario, we solved two optimization problems. In one solution, we assumed that the conservation planner was unaware of land-use change dynamics and planned as if the land use would remain constant at 2001 land use except for conservation acquisitions ('dynamic conservation solution ignoring land-use change in planning'). In the other solution, we assumed the conservation planner considers land-use change dynamics in choosing which lands to conserve ('dynamic conservation solution incorporating land-use change in planning'). In this case, it may be worthwhile conserving land not because it will increase ecosystem service or biodiversity values but simply to prevent expected land-use conversion that may result in significant declines in values. The inclusion of threat of land-use conversion can mean the dynamic and static solutions can diverge significantly. The static model will select the land for conservation that generates the largest increase in returns per dollar compared to the 2001 baseline land use while the dynamic model will select lands that generate the largest increase in returns per dollar compared to the projected distribution of land uses in 2026.

III. Results

The main issue we address in this paper is the degree of alignment between ecosystem services and biodiversity conservation strategies. We allocated the total conservation budget towards acquiring land in order to maximize the value of ecosystem services (carbon sequestration and phosphorus retention) or to maximize the value of habitat for biodiversity conservation (Table 1). On the otherwise static landscape each strategy resulted in increases in both objectives. The optimal solution when targeting ecosystem services generated 53 per cent of the biodiversity score as compared to targeting biodiversity (5.58m units versus 10.60m—note that these are not units of area or species but a combination of both to indicate conservation value of lands). The optimal solution when targeting biodiversity generated 70 per cent of the value of ecosystem services as compared to targeting services ($6.333 billion versus $9.026 billion).

Under either strategy, the benefits of conservation outweigh the costs. We take the total costs of the conservation programme to be equal to the total conservation budget available, $3.319 billion, which is equal to the sum of expenditures on land purchase and restoration costs. Land purchase costs represent the opportunity cost of forgone returns when the land is put in conservation versus some other use that generates returns for the landowner. The increase in the value of ecosystem services is $9.026 billion for

Table 1: Change in the value of ecosystem services and the biodiversity score with a static landscape under an ecosystem service objective and a biodiversity objective

Objective	Ecosystem services ($m)	Biodiversity score (m)
Ecosystem service objective	9,026	5.58
Biodiversity objective	6,333	10.6

Notes: The value of ecosystem services is reported in millions of 2011 constant dollars. Biodiversity scores are reported in millions of habitat units (representing predicted richness x habitat area).

the case where we maximize ecosystem services, which yields a return on investment of \$2.71 per dollar invested. In reality, transactions costs (expenses related to purchase, management, and administration) would inflate conservation costs. If we assume that transactions costs add an additional 20 per cent to programme costs, then full programme costs would be \$3.983 billion. In this case, the return on investment in conservation is \$2.27 per dollar invested. Benefits far exceed costs, even though we only include the value of carbon sequestration and water quality improvement but not the value of other ecosystem services or habitat conservation.

Development and other landscape changes separate from acquiring land for conservation will likely have a much greater impact on land use in Minnesota. Therefore, we investigated the impact of expected private land-use change on ecosystem service provision and biodiversity conservation. If there were no conservation strategy on the dynamic 2001–26 landscape we predict the value of ecosystem services would rise by \$8.245 billion, while the biodiversity score would fall by 6.7m (Table 2). These results are driven by the fact that croplands are expected to decline by approximately 1.37m hectares. Forests are expected to have the largest net gain (0.63m hectares) followed by urban (0.37m hectares), range (0.26m hectares), and pasture (0.11m hectares). We show the aggregate conversion from each land use to each other land use under the no conservation strategy as well as the dynamic and static conservation strategies in Table 3. While there is considerable variation in both the value of ecosystem services and the biodiversity score within a given land-use type, on average cropland scores low in terms of both carbon sequestration and water quality relative to other land uses (Table 4). The movement out of croplands then tends to increase the value of ecosystem services generated. In terms of habitat value, however, croplands score relatively well because many species use croplands for feeding or nesting (e.g. migratory waterbirds or open-land birds and mammals), especially those adjacent to water and wetlands. The movement out of croplands and into other types of land use results in a drop in the biodiversity score.

We then analysed how well aligned the ecosystem services and biodiversity strategies were against a backdrop of on-going land-use change (Table 2). We analysed two planning strategies: (*a*) a dynamic conservation solution incorporating land-use change in planning, and (*b*) a dynamic conservation solution ignoring land-use change in planning. For both strategies, we again find that targeting ecosystem services also increases biodiversity conservation, and vice versa. For the dynamic conservation strategy incorporating land-use change in planning, the optimal solution when targeting ecosystem services generated 47 per cent of the biodiversity score as compared to targeting biodiversity. The gain in biodiversity under the ecosystem service strategy was from –6.70m to –3.17m units for an increase of 3.53m, whereas the biodiversity score increased to 0.82m under the biodiversity strategy, for an increase of 7.52m. The optimal solution when targeting biodiversity generated 65 per cent of the value of ecosystem services as compared to targeting services. The increase in the value of ecosystem services increased from \$8.245 billion without the conservation programme to \$13.650 billion with the biodiversity strategy for an increase of \$5.405 billion, and \$16.616 billion with the ecosystem services strategy, for an increase of \$8.371 billion. Taking account of land-use change over this time reduced the alignment of objectives by a small amount, but the general conclusion about the large degree of overlap remains.

Table 2: Change in the value of ecosystem services (ES) and the biodiversity score between 2001 and 2026 for the State of Minnesota with a dynamic landscape

		Private lands					Conserved land					Total (private + conserved land)	
Scenario		**Biomass carbon ($m)**	**Soil carbon ($m)**	**Water ($m)**	**ES ($m)**	**Biodiversity score (m)**	**Biomass carbon ($m)**	**Soil carbon ($m)**	**Water ($m)**	**ES ($m)**	**Biodiversity score (m)**	**ES ($m)**	**Biodiversity score (m)**
No funds for conservation	Mean	3,802	3,919	525	8,245	–6.70	0	0	0	0	0	8,245	–6.70
	SD	5.50	4.62	2.19	9.54	0.01						9.54	0.01
Dynamic conservation solution incorporating land-use change in planning													
ES objective	Mean	3,273	3,880	491	7,644	–8.36	7,737	711	525	8,973	5.2	16,616	–3.17
	SD	4.20	2.08	2.75	7.65	0.01						7.65	0.01
Biodiversity objective	Mean	3,255	4,003	515	7,774	–9.31	5,166	493	216	5,875	10.1	13,650	0.82
	SD	5.17	4.24	2.10	8.30	0.01						8.30	0.01
Dynamic conservation solution ignoring land-use change in planning													
ES objective	Mean	3,211	3,846	485	7,542	–8.65	7,661	832	533	9,026	5.6	16,568	–3.07
	SD	4.35	4.19	2.18	7.69	0.01						7.69	0.01
Biodiversity objective	Mean	3,117	4,003	510	7,630	–10.14	5,521	553	259	6,333	10.6	13,963	0.47
	SD	5.08	4.87	1.91	9.04	0.01						8.30	0.01

Notes: We report changes with no funds for conservation, and with a conservation budget of $10.559 billion. With a conservation budget we report results for the case where the planner factors in potential land-use change into the optimization routine and where the planner ignores potential land-use change. All dollar figures are reported in millions of 2011 constant dollars. Biodiversity scores are reported in millions of habitat units (representing predicted richness x habitat area).

Table 3: Average land-use change dynamics between 2001 and 2026 for Minnesota by land-use type

		Dynamic conservation solution incorporating land-use change in planning		Dynamic conservation solution ignoring land-use change in planning	
2001 to 2026	**No funds for preservation**	**ES objective**	**Biodiversity objective**	**ES objective**	**Biodiversity objective**
Cropland to cropland	62.3	61.9	62.1	61.9	62.2
Cropland to pasture	9.1	9.1	9.1	9.0	9.1
Cropland to forest	3.9	3.9	3.9	3.9	3.9
Cropland to urban	1.8	1.8	1.8	1.8	1.8
Cropland to range	3.1	3.0	3.0	3.0	3.1
Pasture to cropland	3.5	2.8	2.8	2.7	2.6
Pasture to pasture	7.1	5.7	5.4	5.6	5.0
Pasture to forest	4.7	3.7	3.5	3.5	3.2
Pasture to urban	0.8	0.7	0.6	0.6	0.6
Pasture to range	0.5	0.4	0.4	0.4	0.4
Forest to cropland	0.4	0.4	0.4	0.4	0.4
Forest to pasture	0.8	0.8	0.8	0.8	0.8
Forest to forest	26.5	26.1	25.9	26.2	26.1
Forest to urban	1.0	1.0	1.0	1.0	1.0
Forest to range	0.3	0.3	0.3	0.3	0.3
Urban to urban	9.5	9.5	9.5	9.5	9.5
Range to cropland	0.3	0.2	0.2	0.2	0.3
Range to pasture	0.7	0.5	0.6	0.6	0.6
Range to forest	0.2	0.2	0.2	0.2	0.2
Range to urban	0.1	0.1	0.1	0.1	0.1
Range to range	5.5	4.4	4.7	4.6	5.2

Notes: We report the amount of land in cropland, pasture, forest, urban, and rangeland that stayed in its initial use or converted to another land-use type between 2001 and 2026 for various conservation scenarios. All values are reported in hundred thousand hectares.

The dynamic conservation strategy incorporating land-use change in planning should be superior to the strategy that ignores potential land-use change in planning. But how much improvement does this more sophisticated strategy yield? We found that incorporating land-use change in planning did only slightly better as compared to the strategy that ignored potential land-use changes in planning for both the ecosystem services objective ($16.616 billion versus $16.568 billion or 0.5 per cent higher) and the biodiversity conservation objective (7.52m versus 7.17m, or 4.9 per cent higher). Inclusion of land-use change affects the overall outcome of biodiversity and ecosystem services but somewhat surprisingly taking this into account in planning had relatively little effect on strategy or expected outcomes.

The spatial pattern of the lands purchased for conservation under both ecosystem service and biodiversity conservation strategies for dynamic and static strategies is shown in Figure 1. The total amounts of land conserved by land-use category and the change in the value of ecosystem services and biodiversity score by land-use category with conservation are reported in Tables 5 and 6. In general, these patterns reflect the spatial distribution of the major land uses and vegetation biomes of Minnesota, with coniferous forest in the north-east, a mix of deciduous forest, croplands, and pasture

Table 4: Average impacts of land-use change on the value of ecosystem services and the biodiversity score by land-use category

2001 to 2026 land use	Water quality outside buffer ($/ha)	Water quality inside buffer ($/ha)	Soil carbon ($/ha)	Biomass carbon ($/ha)	Biodiversity (score/ha)
Cropland to cropland	0	0	0	0	0.00
Cropland to pasture	552	1,986	2,584	0	–8.16
Cropland to forest	969	2,950	2,239	5,430	–3.21
Cropland to urban	–148	–559	1,404	543	–9.06
Cropland to range	552	1,986	3,089	0	–3.27
Pasture to cropland	–552	–1,986	–2,584	0	8.16
Pasture to pasture	0	0	0	0	0.00
Pasture to forest	605	2,201	–345	5,430	4.95
Pasture to urban	–638	–2,226	–1,180	543	–0.90
Pasture to range	0	0	506	0	4.89
Forest to cropland	–969	–2,950	–2,239	–5,430	3.21
Forest to pasture	–605	–2,201	345	–5,430	–4.95
Forest to forest	0	0	0	0	0.00
Forest to urban	–1,036	–3,059	–835	–4,887	–5.85
Forest to range	–605	–2,201	850	–5,430	–0.06
Urban to urban	0	0	0	0	0.00
Range to cropland	–552	–1,986	–3,089	0	3.27
Range to pasture	0	0	–506	0	–4.89
Range to forest	605	2,201	–850	5,430	0.06
Range to urban	–651	–2,237	–1,685	543	–5.79
Range to range	0	0	0	0	0.00

in the central and south-east portions, and croplands and grassland in the west-central and south-west portions. Under the ecosystem services strategy, purchased lands were clustered in the forested north-east and the south-east, with very little land purchased in the western or central portions of the state. Lands converted from croplands, pasture, or range to conserved forest resulted in large increases in carbon sequestration, which dominated the value of ecosystem services under our baseline assumptions. The value of the increase in carbon storage made up $15.6 billion of the $16.616 billion increase in value of ecosystem services, with water quality improvements making up just over $1 billion. Under the biodiversity strategy purchased lands were spread throughout the entire state. Croplands and grasslands both had relatively high value for biodiversity, so conserving these land-cover types along with other lands added to the biodiversity score. The spatial pattern seen in the biodiversity strategy reflects the fact that we considered biodiversity in general terms, including both common and rare species, habitat generalists and specialists, and both residents and migratory (waterbird) species. Doing so gave value to protecting a broad range of habitats and locations. For example, conservation of grassland species requires conservation efforts in the west and south-western portions of the state, whereas forest species require conservation efforts in the north-east and south-east. The difference in spatial pattern of the land purchased for conservation under the different scenarios and different objectives is shown in Figure 2. In general, the dynamic land-use scenario puts a higher value on conserving land that may convert to a land use with lower conservation value, such as urban land use, and so conserves more land in regions with higher development pressure (Figures 2(A) and 2(B)). The ecosystem services objective puts great value on restoring forest lands in the

Figure 1: Maps showing the location by sub-county unit of lands purchased for conservation under both ecosystem service and biodiversity conservation strategies for dynamic and static land-use scenarios

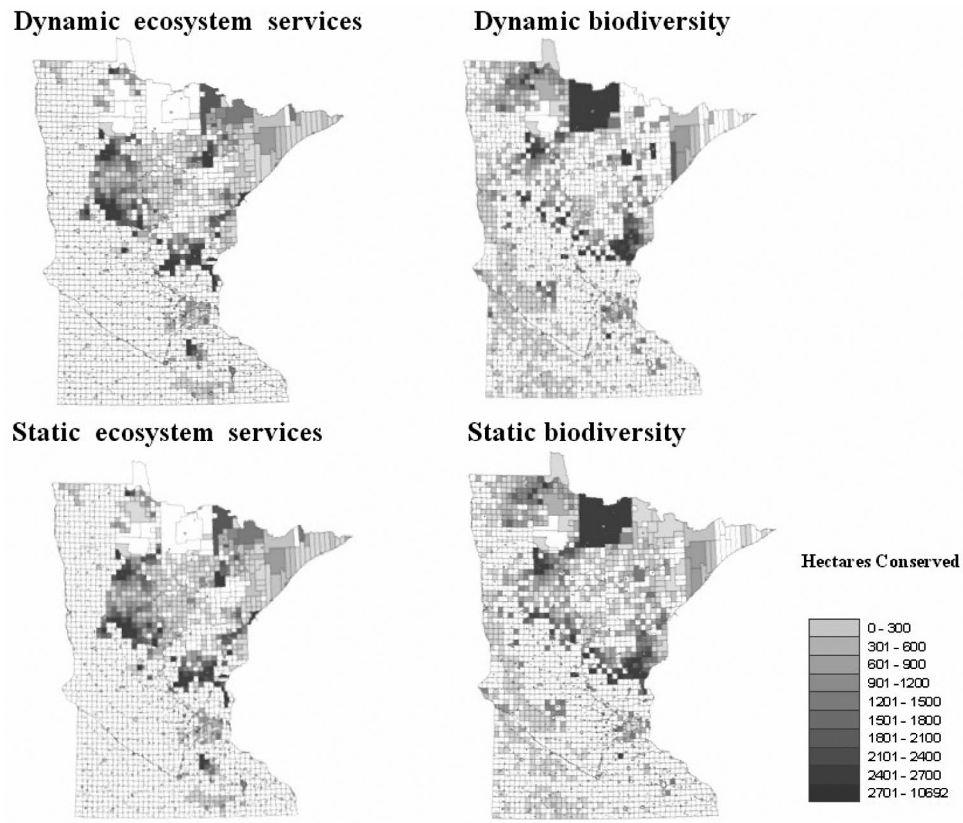


Table 5: Hectares conserved between 2001 and 2026 by land-use category

		Dynamic conservation solution incorporating land-use change in planning		Dynamic conservation solution ignoring land-use change in planning	
2001 to 2026 land use	**No funds for preservation**	**ES objective**	**Biodiversity objective**	**ES objective**	**Biodiversity objective**
Cropland to conserved	0.00	0.45	0.26	0.48	0.13
Pasture to conserved	0.00	3.27	3.85	3.68	4.81
Forest to conserved	0.00	0.46	0.66	0.33	0.40
Range to conserved	0.00	1.31	0.99	1.02	0.35

Notes: All values are reported in hundred thousand hectares.

north-east and south-east and less weight on conservation in western part of the state (Figure 2(C)).

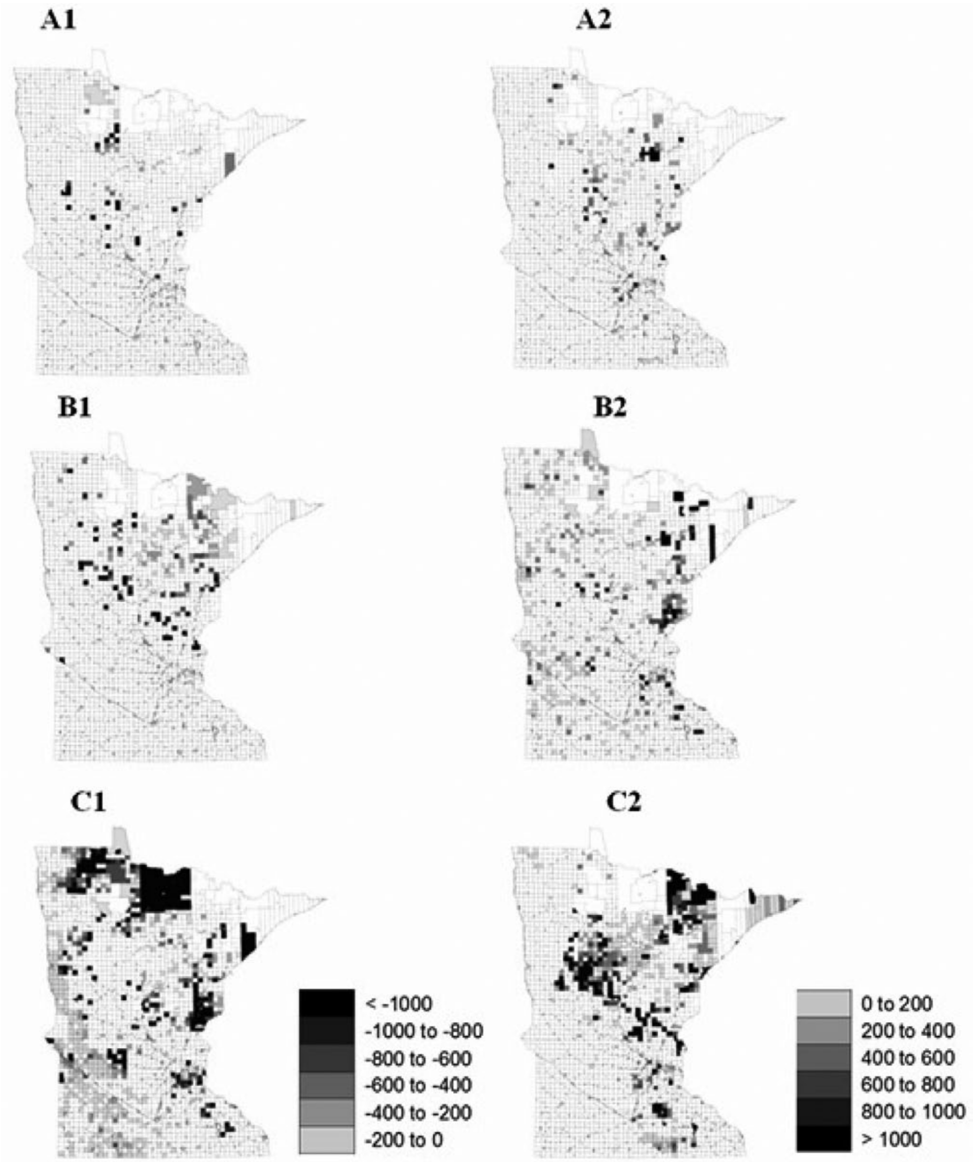
There is considerable uncertainty about many of the biophysical relationships in the biodiversity and ecosystem services models, but probably even greater uncertainty exists

Table 6: Average impacts of conserving land on the value of ecosystem services and the biodiversity score by land-use category

2001 to 2026 land use	Water service outside buffer ($/ha)	Water service inside buffer ($/ha)	Soil carbon ($/ha)	Biomass carbon ($/ha)	Biodiversity (score/ha)
Cropland to conserved forest	1,307	4,252	2,239	19,312	–2.32
Cropland to conserved grassland	392	1275	2,584	0	–2.80
Cropland to conserved wetland	1,307	4,252	4,248	0	1.13
Cropland to conserved (average)	784	2,551	2,837	7,013	–1.11
Pasture to conserved forest	588	2,190	–345	19,312	5.84
Pasture to conserved grassland	177	657	0	0	5.36
Pasture to conserved wetland	588	2,190	1,664	0	9.29
Pasture to conserved (average)	353	1,314	253	7,013	7.05
Forest to conserved	1	2	598	1,819	2.10
Range to conserved forest	588	2,190	–850	19,312	0.95
Range to conserved grassland	177	657	–506	0	0.47
Range to conserved wetland	588	2,190	1,159	0	4.40
Range to conserved (average)	353	1,314	–253	7,013	2.16

about the proper values for carbon sequestration and water-quality improvement. We performed a sensitivity analysis on our results by using low and high carbon value scenarios and a high water-quality value scenario (Table 7). We did not use a lower value for water than the base case as this value was already fairly low. For the low value for the social cost of carbon we used a value of $27.78 per ton of carbon ($7.58 per ton CO_2) in 2011 dollars, which corresponds to Tol's value for the 33rd percentile from the fitted distribution, assuming a 3 per cent discount rate (Tol, 2009). For the high value for the social cost of carbon we used a value of $240.32 per ton of carbon ($65.54 per ton CO_2) in 2011 dollars, which corresponds to Tol's value for the 67th percentile from the fitted distribution, assuming a 0 per cent discount rate (Tol, 2009). For the high water-quality value we used a value from Mathews *et al.* (2002), who reported an average value of $140 per household per year in 1997 dollars, or $187.46 in 2011 constant dollars, for a 40 per cent reduction in phosphorus loadings in the Minnesota River. Though the value of ecosystem services changes dramatically with the large change in values, the strategies of what lands to choose and the impact on the biodiversity objective are relatively minor. The low carbon value and high water-quality value result in virtually the same overall biodiversity score, which is somewhat lower than the score for the baseline case (–3.38 and –3.51m versus –3.17m). These scenarios turn out to be quite similar

Figure 2: The difference in lands purchased for conservation under the biodiversity conservation and ecosystem services objective across static and dynamic land-use scenarios



Notes: Sub-county units in the panels on the left indicate a decrease in the number of hectares conserved while the panels on the right indicate an increase in the number of hectares conserved. Panel A: number of hectares conserved for the ecosystem services objective under the dynamic land-use scenario minus the number of hectares conserved under the static land-use scenario. Panel B: number of hectares conserved for the biodiversity objective under the dynamic land-use scenario minus the number of hectares conserved under the static land-use scenario. Panel C: number of hectares conserved under the dynamic land-use scenario for the ecosystem service objective minus the number of hectares conserved under the dynamic land-use scenario for the biodiversity objective.

Table 7: Change in the value of ecosystem services (ES) and the biodiversity score between 2001 and 2026 for the State of Minnesota under various scenarios under low carbon, high carbon and high water quality value

		Private lands					Conserved land					Total (private + conserved land)	
Scenario		**Biomass carbon ($m)**	**Soil carbon ($m)**	**Water ($m)**	**ES ($m)**	**Biodiversity score (m)**	**Biomass carbon ($m)**	**Soil carbon ($m)**	**Water ($m)**	**ES ($m)**	**Biodiversity score (m)**	**ES ($m)**	**Biodiversity score (m)**
Dynamic conservation solution incorporating land-use change in planning													
ES objective: low carbon values	Mean	727	854	465	2,046	–8.24	1,585	147	752	2,484	4.9	4,530	–3.38
	SD	1.04	1.08	1.73	2.83	0.01						2.83	0.01
ES objective: high carbon values	Mean	6,215	7,370	501	14,085	–8.43	14,805	1,378	436	16,619	5.4	30,704	–3.06
	SD	10.24	8.13	2.19	16.24	0.01						16.24	0.01
ES objective: high water-quality value	Mean	3,345	3,892	2,822	10,059	–8.09	6,754	613	5,302	12,670	4.6	22,729	–3.51
	SD	4.71	4.70	10.35	14.92	0.01						14.92	0.01

Notes: All dollar figures are report in millions of 2011 constant dollars. Biodiversity scores are reported in millions of habitat units (representing predicted richness x habitat area).

because what matters in selecting lands to conserve is the relative weight between carbon and water. The areas important for water-quality improvement are those near population centres, where numerous households are affected by this. These areas also tend to have high land prices so that, overall, not as much land area is conserved when more attention is paid to water-quality improvements compared to carbon, which results in lower biodiversity improvement. Raising water-quality value or lowering carbon value each increase the importance of water quality relative to carbon. The high carbon value scenario does not make much change from the base-case scenario (–3.06m versus –3.17m), which already had most of the value of ecosystem services coming from carbon. Raising the carbon price skews the weight towards carbon even higher. With a low value for carbon and the base-case water-quality value, which also generated low water-quality values, we found that the increase in ecosystem service value with conservation was lower than the costs of conservation. On the other hand, for the high-value carbon case, we found a return on investment of over 4 to 1.

IV. Discussion

We find a high degree of alignment between strategies that target the value of ecosystem services and those that target habitat for biodiversity conservation. Targeting one of these two objectives generates 47–70 per cent of the maximum score of the other objective. In general, investing in conservation that increases the value of ecosystem services is also beneficial for biodiversity conservation, and vice versa. It is not surprising that there is good agreement between the outcomes of the two strategies, given the importance of biodiversity to maintaining the ecosystem function that supports the provision of ecosystem services. The choice of specific objective, however, does matter in terms of specific types of conservation investment to make. For ecosystem services under the base-case assumptions that place a relatively high weight on carbon sequestration, most conservation investments are made in the north-east and south-east portions of the state to maintain or restore forests. Little investment is made in the western portions of the state where the native habitat is grassland rather than forest. For biodiversity conservation, however, investments are made more evenly throughout the state to restore both forests and grasslands. Conservationists interested in either ecosystem services or biodiversity would do well to pay most attention to increasing the size of the conservation budget as the first-order objective. Increases in the budget will improve outcomes in terms of both objectives. The proper objective for conservation, biodiversity conservation for its own sake or increasing the value of ecosystem services, also matters and can shift the focus in terms of which particular areas are of highest priority for conservation.

We find that investing in conservation is highly beneficial. In the base-case analysis that includes the value of carbon sequestration and water quality improvements, we find a return on investment of roughly $2–3 per dollar invested. Only when we change the base case assumptions to include a low value of carbon, along with the base-case value for water quality improvement that is quite modest, do we find that the costs of conservation outweigh the benefits. Including higher values for carbon sequestration or water quality improvement, or including a wider range of services, will increase the return on investment in conservation. As the data and ecosystem service models improve, it will be possible to move towards a more complete accounting of the values of conservation.

Biodiversity is a complex concept with multiple dimensions. There is great diversity in the published definitions of biodiversity and a wide variety of ways it can be measured (Mace *et al.*, 2012). In this paper we directed conservation funds towards one particular biodiversity conservation objective, namely the goal of conserving habitat for the benefit of vertebrate species. This objective reflects the Legacy Amendment's broad goal to protect game and wildlife species. Our biodiversity target considers the habitat requirements of 354 terrestrial vertebrate species. These species require a wide variety of areas and land-cover types and resulted in the selection of areas for conservation spread across the state (as shown in Figure 1). However, a broad-brush look at vertebrates could potentially mask more nuanced patterns and trade-offs. We would probably find different conservation strategies when targeting specific species or sets of species based on functional group, habitat preference, threatened status, charismatic species, or game species. On the other hand, using vertebrate species richness is a very limited measure of biodiversity if one takes the 1993 CBD definition: 'the variability among living organisms from all sources . . . this includes diversity within species, between species and of ecosystems' (CBD, 1993). Total biodiversity, including microorganisms, primary producers, and a range of consumers including invertebrates and vertebrates, and the variability at the genetic and ecosystem levels, encompasses a wider set of biodiversity than we considered in this paper.

Our habitat for biodiversity score captures the importance of habitat to support biodiversity but ignores several other factors. This measure does not account for the impact of habitat fragmentation or spatial pattern on species, which can be important for species with limited dispersal ability or in highly fragmented landscapes (Fahrig, 2003). It also assumes constant returns to scale in habitat provision. Polasky *et al.* (2008) use a more complex biodiversity model to estimate how land-use changes will affect species, accounting for fragmentation and variable marginal value depending on contribution of additional habitat for population viability. This approach, however, requires far more data and the use of sophisticated search algorithms for optimization, which makes its use impractical in many settings. Because each species is assumed to have equal intrinsic value, our measure gives equal weight to all species so that providing habitat for common species is of equal value to providing habitat for game species or threatened and endangered species. We ignore the different values to different species, namely the many use (e.g. game, pollination) and non-use values (e.g. existence, aesthetic) people derive from biodiversity. These additional values could be addressed by introducing species weights to reflect relative value, though it can be difficult to get agreement on the proper weights to use.

While we found that our broad measure of biodiversity was generally aligned with our measure of the value of ecosystem services (carbon sequestration and water quality), it is quite possible that other measures of biodiversity, such as those discussed in the prior paragraph, or other measures of ecosystem services might generate different results in terms of the degree of alignment between biodiversity conservation and ecosystem services (Bennett *et al.*, 2009; McShane *et al.*, 2011; Reyers *et al.*, 2012). Mace *et al.* (2012) noted that there is a 'complex relationship' between biodiversity and ecosystem services. Biodiversity regulates ecological processes that support the provision of ecosystem services. In some instances, components of biodiversity contribute to the provision of services, as, for example, the contribution of genetic material to the discovery of new pharmaceuticals. In some cases, components of biodiversity are ecosystem services in their own right, as, for example, the cultural services generated by the existence or abundance of species. As regulators of ecosystem processes or as ecosystems services themselves, species and groups of species may be more closely aligned with services than is presented here.

Prior empirical analyses that examined different aspects of biodiversity and ecosystem services or looked at the impacts of particular decisions have found different degrees of alignment. For example, a large number of studies in ecology have examined the relationship between biodiversity (usually measured as plant species richness) and ecosystem functions and generally find increased diversity yields increased function (e.g. Loreau *et al.*, 2001; Tilman *et al.*, 2001; Balvanera *et al.*, 2006; Isbell *et al.*, 2011). Egoh *et al.* (2010), in a study in the Little Karroo in South Africa, found that meeting biodiversity conservation targets improved the provision of ecosystem services, but that for the same cost ecosystem services could be increased by far more if they were targeted instead of biodiversity. Overall, Egoh *et al.* (2010) found less congruence between biodiversity conservation and ecosystem services than we found in our analysis. Using data from the Willamette Basin in Oregon, Nelson *et al.* (2008) showed that at-risk vertebrate species were maximized when conservation funds restored rare natural habitats, including oak savanna, prairie, and emergent marsh. Carbon sequestration, on the other hand, was maximized when conservation funds restored or conserved forests, including old growth, mixed, and riparian forest. Indeed, maximizing forest cover did benefit some species (e.g. the spotted owl); however, it provided little benefit for the majority of the 37 rare species analysed. Nelson *et al.* (2009), also using data from the Willamette Basin, found that a conservation-oriented land-use scenario was better for biodiversity conservation and for non-market ecosystem services related to carbon sequestration, water quality (both reductions of phosphorus reduction and erosion), and reduction of flood risk, as compared to a business-as-usual and development-oriented land-use scenario. In Minnesota, Polasky *et al.* (2011) found trade-offs among different conservation strategies, particularly between species dependent upon different habitat types, grassland dependent birds, and forest dependent birds. However, they also found that strategies that ranked high in terms of the value of ecosystem services tend also to rank high for a general measure of biodiversity conservation. Several other studies in agricultural landscapes have found trade-offs between types of ecosystem services provided (e.g. provisioning services versus cultural and regulatory services) or between more intensive commodity production and biodiversity conservation (e.g. Santelmann *et al.*, 2004; Boody *et al.*, 2005). So, while we think that it will often be the case that what is good for promoting the supply of ecosystem services is good for biodiversity conservation and vice versa, one can always do better by targeting the objective of interest directly. Further, there is no guarantee that both objectives will always tend to be positively correlated, or that this will be true for particular components of biodiversity or particular ecosystem services.

Our analysis provides evidence on the degree of alignment between various conservation objectives, and it provides evidence on the net benefits of investing in conservation, but it is hardly the last word on either subject. In any type of integrated modelling such as this, there are always additional factors that can be considered. One important issue not considered here are land market feedbacks between conservation strategies and land prices (Armsworth *et al.*, 2006), which then might drive land-use decisions on other un-conserved land. Land market feedbacks and indirect land-use change factor into the discussion of policies to reduce deforestation such as REDD (Reducing Emissions from Deforestation and Forest Degradation; Miles and Kapos, 2008) and the impacts of biofuel expansion (Fargione *et al.*, 2008; Searchinger *et al.*, 2008). While we found positive return on investment for the level of investment in conservation under the Legacy Amendments, we did not attempt to solve for the optimal level of investment that would maximize social net benefits. Doing so would require building in price feedback effects that reflect relative scarcities that are a function of the land-use and management practices decisions made. Consideration of management practices, such as fertilizer application rates and tillage practices in agriculture, in addition to land-use change, can provide additional options that allow for improved performance on multiple dimensions. Finally, consideration of spatial interactions, where the benefit of taking action on one land parcel depends upon what actions are taken nearby, and dynamic transition paths, such as the time path of accumulation of carbon with forest maturation rather than analysis of steady-state conditions, could provide additional insights. These would be interesting avenues to pursue in future work.

References

Ando, A., Camm, J. D., Polasky, S., and Solow, A. R. (1998), 'Species Distributions, Land Values And Efficient Conservation', *Science*, **279**, 2126–2128.

Armsworth, P. R., Daily, G. C., Kareiva, P., and Sanchirico, J. N. (2006), 'Land Market Feedbacks Can Undermine Biodiversity Conservation', *Proceedings of the National Academy of Sciences*, **103**, 5403–8.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., and Schmid, B. (2006), 'Quantifying the Evidence for Biodiversity Effects on Ecosystem Functioning and Services', *Ecology Letters*, **9**, 1146–56.

Bennett, E. M., Peterson, G. D., and Gordon, L. (2009), 'Understanding Relationships among Multiple Ecosystem Services', *Ecology Letters*, **12**, 1394–404.

Boody, G., Vondracek, B., Andow, D. A., Krinke, M., Westra, J., Zimmerman, J., and Welle, P. (2005), 'Multifunctional Agriculture in the United States', *Bioscience*, **55**(1), 27–38.

Carlson, R. E. (1977), 'A Trophic State Index for Lakes', *Limnology and Oceanography*, **22**, 361–9.

Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N., and Smith, V. H. (1998), 'Nonpoint Pollution of Surface Waters with Phosphorus and Nitrogen', *Ecological Applications*, **8**(3), 559–68.

Carson, R. T., and Mitchell, R. C. (1993), 'The Value Of Clean Water: The Public's Willingness to Pay for Boatable, Fishable, and Swimmable Quality Water', *Water Resources Research*, **29**, 2445–54.

CBD (1993), *Text of the Convention on Biological Diversity*, Convention on Biological Diversity, http://www.cbd.int/convention/text/

— (2010), *Strategic Plan for Biodiversity 2011–2020*, Convention on Biological Diversity, COP 10 Decision X/2, http://www.cbd.int/decision/cop/?id=12268

Chan, K. M. A., Shaw, M. R., Cameron, D. R., Underwood, E. C., and Daily, G. C. (2006), 'Conservation Planning for Ecosystem Services', *PLoS Biology*, **4**, e379.

Conservation Biology Institute (2010), *PAD-US 1.1* (CBI Edition), May, Oregon, Corvallis.

Daily, G. C. (ed.) (1997), *Nature's Services: Societal Dependence on Natural Ecosystems*, Island Press.

— Polasky, S., Goldstein, J., Kareiva, P. M., Mooney, H. A., Pejchar, L., Ricketts, T. H., Salzman, J., and Shallenberger, R. (2009), 'Ecosystem Services in Decision-making: Time to Deliver', *Frontiers in Ecology and the Environment*, **7**(1), 21–8.

Drotts, G., Heinzen, D., *et al.*. (2007), *The Minnesota Gap Analysis Project Final Report*, Division of Fish and Wildlife and Division of Forestry, Minnesota Department of Natural Resources, St Paul, MN.

Egoh, B., Reyers, B., Rouget, M., Bode, M., and Richardson, D. M. (2009), 'Spatial Congruence Between Biodiversity and Ecosystem Services in South Africa', *Biological Conservation*, **142**(3), 553–62.

— — — Richardson, D. M., Le Maitre, D. C., and van Jaarsveld, A. S. (2008), 'Mapping Ecosystem Services for Planning and Management', *Agriculture, Ecosystems and Environment*, **127**, 135–40.

— — Carwardine, J., Bode, M., O'Farrell, P. J., Wilson, K. A., Possingham, H. P., Rouget, M., DeLange, W., Richardson, D. M., and Cowling, R. M. (2010), 'Safeguarding Biodiversity and Ecosystem Services in the Little Karoo, South Africa', *Conservation Biology*, **24**, 1021–30.

Ehrenfeld, D. (1988), 'Why Put a Value on Biodiversity?', in E. O. Wilson (ed.), *Biodiversity*, Washington, DC, National Academy Press.

Fahrig, L. (2003), 'Effects of Habitat Fragmentation on Biodiversity', *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fargione, J., Hill, J., Tilman, D., Polasky, S., and Hawthorne, P. (2008), 'Land Clearing and the Biofuel Carbon Debt', *Science*, **319**, 1235–8.

Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., Van Driel, J. N., and Wickham, J. (2007), 'Completion of the 2011 National Land Cover Database for the conterminous United States', *Photogrammetric Engineering and Remote Sensing*, **73**(4), 337–41.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., and Van Ruijven, J. (2011), 'High Plant Diversity is Needed to Maintain Ecosystem Services', *Nature*, **477**, 199–202.

Johnston, R. J., and Besedin, E. Y. (2009), 'Benefits Transfer and Meta-analysis: Estimating Willingness to Pay for Aquatic Resource Improvements', in H. W. Thurston, M. T. Heberling, and A. Schrecongost (eds), *Environmental Economics for Watershed Restoration*, Boca Raton, FL, CRC Press.

— — Iovanna, R., Miller, C. J., Wardwell, R. F., and Ranson, M. H. (2005), 'Systematic Variation in Willingness to Pay for Aquatic Resource Improvements and Implications for Benefit Transfer: A Meta-analysis', *Canadian Journal of Agricultural Economics*, **53**, 221–48.

Kareiva, P., Tallis, H., Ricketts, T. H., Daily, G. C., and Polasky, S. (eds) (2011), *Natural Capital: Theory and Practice of Mapping Ecosystem Services*, Oxford, Oxford University Press.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., Hooper, D., Huston, M., Raffaelli, D., and Schmid, B. (2001), 'Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges', *Science*, **294**, 804–8.

LSOHC (2009), 'Strategic Planning and Recommendation Development Process-Summary of Input Meetings', Lessard-Sams Outdoor Heritage Council, www.lsohc.leg.mn/materials/09_Mtg/LSOHC-planning-meetings-summary.pdf

Lubowski, R. N., Plantinga, A. J., and Stavins, R. N. (2006), 'Land-use Change and Carbon Sinks: Econometric Estimation of the Carbon Sequestration Supply Function', *Journal of Environmental Economics and Management*, **51**(2), 135–52.

MA (2005), *Ecosystems and Human Well-Being*, Millennium Ecosystem Assessment, Washington, DC, Island Press.

McCauley, D. (2006), 'Selling Out on Nature', *Nature*, **443**, 27–8.

Mace, G., Norris, K., and Fitter, A. (2012), 'Biodiversity and Ecosystem Services: A Multilayered Relationship', *Trends in Ecology and Evolution*, **27**(1), 19–26.

McShane, T. O., Hirsch, P. D., Trung, T. C., Songorwa, , A. N., Kinzig, A., Monteferri, B., Mutekanga, D., Thang, H. V., Dammert, J. L., Pulgar-Vidal, M., Welch-Devine, M., Brosius, J. P., Coppolillo, P., and O'Connor, S. (2011), 'Hard Choices: Making Trade-offs between Biodiversity Conservation and Human Well-being', *Biological Conservation*, **144**, 966–72.

Mathews, L. G., Homans, F. R., and Easter, K. W. (2002), 'Estimating the Benefits of Phosphorus Pollution Reductions: An Application in the Minnesota River', *Journal of the American Water Resources Association*, **38**, 1217–23.

MCCAG (2008), *Minnesota Climate Change Advisory Group Final Report*, Minnesota Climate Change Advisory Group, http://www.mnclimatechange.us/MCCAG.cfm

Metrick, A., and Weitzman, M. (1998), 'Conflicts and Choices in Biodiversity Preservation', *Journal of Economic Perspectives*, **12**(3), 21–34.

Miles, L., and Kapos, V. (2008), 'Reducing Greenhouse Gas Emissions from Deforestation and Forest Degradation: Global Land-use Implications', *Science*, **320**, 1454–5.

Minnesota Department of Administration (2007), '*Minnesota Minor Civil Division Extrapolated Population*', State Demographic Center, Office of Geographic and Demographic Analysis, October, http://www.demography.state.mn.us/resource.html?Id=19332

Minnesota Department of Natural Resources (2012), '*Major River Centerline Traces in Minnesota*', GIS Data Deli, Land Management Information Center, Minnesota Planning, February, available at http://deli.dnr.state.mn.us/

Murdoch, W., Polasky, S., Wilson, K., Possingham, H., Kareiva, P., and Shaw, R. (2007), 'Maximizing Return on Investment in Conservation', *Biological Conservation*, **139**, 375–88.

Naidoo, R., and Ricketts, T. H. (2006), 'Mapping the Economic Costs and Benefits of Conservation', *PLoS Biology*, **4**, e360.

— Balmford, A., Costanza, R., Fisher, B., Green, R. E., Lehner, B., Malcolm, T. R., and Ricketts, T. H. (2008), 'Global Mapping of Ecosystem Services and Conservation Priorities', *Proceedings of the National Academy of Sciences*, **105**, 9495–500.

NatureServe (2009), '*International Ecological Classification Standard: Terrestrial Ecological Classifications*', NatureServe Central Databases, Arlington, VA, data current as of 6 February 2009, available at http://www.natureserve.org/getData/vegData/ nsDescriptions.pdf

Nelson, E., Polasky, S., Lewis, D. J., Plantinga, A. J., Lonsdorf, E., White, D., Bael, D., and Lawler, J. J. (2008), 'Efficiency of Incentives to Jointly Increase Carbon Sequestration and Species Conservation on a Landscape', *Proceedings of the National Academy of Sciences,* **105**(28), 9471–6.

— Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D. R., Chan, K. M. A., Daily, G., Goldstein, J., Kareiva, P., Lonsdorf, E., Naidoo, R., Ricketts, T. H., and Shaw, M. R. (2009), 'Modeling Multiple Ecosystem Services, Biodiversity Conservation, Commodity Production, and Tradeoffs at Landscape Scales', *Frontiers in Ecology and the Environment*, **7**(1), 4–11.

NRC (2005), *Valuing Ecosystem Services: Toward Better Environmental Decision-Making*, National Research Council, National Academies Press.

Osborne, L. L., and Kovacic, D. A. (1993), 'Riparian Vegetated Buffer Strips in Water-quality Restoration and Stream Management', *Freshwater Biology*, **29**, 234–58.

Polasky, S., Nelson, E., Pennington, D., and Johnson, K. (2011), 'The Impact of Land-use Change on Ecosystem Services, Biodiversity and Returns to Landowners: A Case Study in the State of Minnesota', *Environmental and Resource Economics*, **48**(2), 219–42.

— — Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts , B., Haight, R., Kagan, J., Starfield, A., and Tobalske, C. (2008), 'Where to Put Things? Spatial Land Management to Sustain Biodiversity and Economic Returns', *Biological Conservation*, **141**(6), 1505–24.

Radeloff, V. C., Nelson, E., Plantinga, A. J., Lewis, D. J., Helmers, D., Lawler, J. J., Withey, J. C., Beaudry, F., Martinuzzi, S., Butsic, V., Lonsdorf, E., White, D., and Polasky, S. (2012), 'Economic-based Projections of Future Land Use under Alternative Economic Policy Scenarios in the Conterminous US', *Ecological Applications*, in press.

Raudsepp-Hearne, C., Peterson, G., and Bennett, E. (2010), 'Ecosystem Service Bundles for Analyzing Tradeoffs in Diverse Landscapes', *Proceedings of the National Academy of Sciences*, **107**, 5242–7.

Redford, K. H, and Adams, W. M. (2009), 'Payment for Ecosystem Services and the challenge of Saving Nature', *Conservation Biology*, **23**, 785–7.

Reyers, B., Polasky, S., Tallis, H., Mooney, H., and Larigauderie, A. (2012), 'Finding Common Ground for Biodiversity and Ecosystem Services', *BioScience*, **62**(5), 503–7.

Rolston, H., III (1988), *Environmental Ethics*, Philadelphia, PA, Temple University Press.

Santelmann, M. V., White, D., Freemark, K., Nassauer, J. I., Eilers, J. M., Vache, K. B., Danielson, B. J., Corry, R. C., Clark, M. E., Polasky, S., Cruse, R. M.,Sifneos , J., Rustigian, H., Coiner, C., Wu, J., and Debinski, D. (2004), 'Assessing Alternative Futures for agriculture in Iowa, USA', *Landscape Ecology*, **19**(4), 357–74.

Searchinger, T., Heimlich, R., Houghton, R. A., Dong, F., Elobeid, A., Fabiosa, J., Tokgoz, S., Hayes, D., and Yu, T.-H. (2008), 'Use of US Croplands for Biofuels Increases Greenhouse Gases Through Emissions from Land-use Change', *Science*, **319**, 1238–40.

Shapiro, F. (ed.) (2006), *Yale Book of Quotations*, New Haven, CT, Yale University Press.

Smith, J. E., Heath, L. S., Skog, K. E., and Birdsey, R. A. (2006), 'Methods for Calculating Ecosystem and Harvested Carbon with Standard Estimates for Forest Types of the United States', Gen Tech Rep NE-343, Newtown Square, PA, US Department of Agriculture, Forest Service, Northeastern Research Station.

Sundquist, E. T., Ackerman, K. V., Bliss, N. B., Kellndorfer, J. N., Reeves, M. C., and Rollins, M. B. (2009), '*Rapid Assessment of US Forest and Soil Organic Carbon Storage and Forest Biomass Carbon Sequestration Capacity: US Geological Survey Open-file Report, 2009-1283*', http://pubs.er.usgs.gov/usgspubs/ofr/ofr20091283

Tallis, H. T., Ricketts, T., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Lonsdorf, E., and Kennedy, C. (2010), *InVEST 1.004 beta User's Guide*, Stanford, CA, The Natural Capital Project.

TEEB (2010), *The Economics of Ecosystems and Biodiversity: Mainstreaming the Economics of Nature: A Synthesis of the Approach, Conclusions and Recommendations of TEEB*, http://www.teebweb.org.

Tilman, D., Reich, P. B., Knops, J. M. H., Wedin, D., Mielke, T., and Lehman, C. (2001), 'Diversity and Productivity in a Long-term Grassland Experiment', *Science*, **294**, 843–5.

Tol, R. S. J. (2009), 'The Economic Effects of Climate Change', *Journal of Economic Perspectives*, **23**, 29–51.

Vira, B., and Adams, W. M. (2009), 'Ecosystem Services and Conservation Strategy: Beware the Silver Bullet', *Conservation Letters*, **2**, 158–62.

Wilson, K. A., McBride, M. F., Bode, M., and Possingham, H. P. (2006), 'Prioritizing Global Conservation Efforts', *Nature*, **440**, 337–40.