Contents lists available at ScienceDirect

S ELSEVIE



Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Conserving ecosystem services and biodiversity: Measuring the tradeoffs involved in splitting conservation budgets



Keri B. Watson^{a,b,c,*}, Gillian L. Galford^{b,c}, Laura J. Sonter^{b,c,d,e}, Taylor H. Ricketts^{b,c}

^a Department of Earth and Environmental Systems, University of the South, Sewanee, TN, USA

^b Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA

^c Gund Institute for Environment, University of Vermont, Burlington, VT, USA

^d School of Earth and Environment Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

^e Center for Biodiversity and Conservation Science, The University of Queensland, St Lucia, QLD 4072, Australia

ARTICLE INFO

Keywords: Biodiversity Ecosystem services Conservation planning

ABSTRACT

Conservation organizations increasingly target ecosystem services alongside biodiversity, yet it remains unclear whether ecosystem service goals reinforce or detract from those for biodiversity. We assess tradeoffs between biodiversity and ecosystem services and test the hypothesis that the severity of this tradeoff is a function the breadth of taxa and ecosystem services targeted. We identify optimal conserved lands networks for four taxa, four ecosystem service, and all possible combinations of each. We then assess the amount of biodiversity and ecosystem services contained within each network, its conservation cost, and its overlap with every other network. We find that overlap varies widely across individual ecosystem services and taxa, and that networks targeting multiple services contain more biodiversity through joint optimization requires a 13% increase in conservation budgets relative to achieving targets for biodiversity alone, and results in a 22% budget savings relative to achieving targets for each though separate efforts. We conclude that including ecosystem services goals alongside those for biodiversity is likely have a net positive impact on biodiversity, especially when a broad suite of services are targeted.

1. Introduction

Supporting the wellbeing of a growing human population while avoiding biodiversity loss is a central challenge of sustainable development (ICSU, 2015; Millennium Ecosystem Assessment, 2005; Steffen et al., 2015). Ecosystem services (ES) are the benefits that people derive from nature (Daily, 1997; Millennium Ecosystem Assessment, 2005). Development-driven environmental degradation is rapidly eroding both biodiversity (Butchart et al., 2010; Ceballos et al., 2015; Newbold et al., 2015; Pimm et al., 2014) and those ecosystem services whose value is not captured in markets (Foley et al., 2005; Millennium Ecosystem Assessment, 2005; Sutton et al., 2016). By making explicit the link between the well-being of people and nature, ES have the potential to serve as common ground for human development and conservation (Millennium Ecosystem Assessment, 2005). As a result, conservation organizations and governments are increasingly prioritizing ecosystem services (Bateman et al., 2013; Donovan et al., 2015; Guerry et al.,

2015; Ruckelshaus et al., 2013).

How will an ES focus impact biodiversity? Considerable debate has arisen among the conservation community over whether an ES approach is undercutting or bolstering traditional biodiversity goals (McCauley, 2006; Revers et al., 2012). On the one hand, the resources once allocated specifically to protecting nature for its own sake are now being used to protect the parts of nature that have the highest utility to people. Although setting aside natural areas for ES conservation may not have direct negative impacts on biodiversity (Reyers et al., 2012), the financial resources for conservation are scarce- the money available to do conservation is insufficient to reach biodiversity goals (Balmford et al., 2003; Balmford and Whitten, 2003; Margules and Pressey, 2000; McCarthy et al., 2012). Because targeting conservation towards ES will capture less biodiversity than targeting biodiversity directly, tradeoffs are inevitable under a constrained budget (Goldman et al., 2011; Margules and Pressey, 2000; Naidoo et al., 2008). The human focus of ES may increase support for conservation and the resources to protect

https://doi.org/10.1016/j.ecoser.2020.101063

^{*} Corresponding author at: 735 University Ave., Sewanee, TN 37375, USA.

E-mail addresses: Keri.Watson@sewanee.edu (K.B. Watson), Gillian.Galford@uvm.edu (G.L. Galford), l.sonter@uq.edu.au (L.J. Sonter), Taylor.Ricketts@uvm.edu (T.H. Ricketts).

Received 25 January 2019; Received in revised form 21 November 2019; Accepted 9 January 2020 2212-0416/ © 2020 Published by Elsevier B.V.

natural areas (Goldman et al., 2011, 2008). The net effect of ES conservation on biodiversity thus hinges on two questions: (1) How much less biodiversity is protected when conservation efforts target ES? and (2) Does an ES focus sufficiently boost conservation budgets to compensate for this difference?

The empirical evidence assessing the biodiversity benefits of ecosystem service conservation is mixed (Cardinale et al., 2012; Harrison et al., 2014; Luck et al., 2009; Ricketts et al., 2016) despite a strong body of evidence establishing a mechanistic link between biodiversity and ecological function (Cardinale et al., 2012; Hooper et al., 2005; Tilman et al., 2012). Analyses of spatial concordance have shown promise of win–win situations in some cases (Bhagabati et al., 2014; Egoh et al., 2009; Turner et al., 2007), that planning jointly for services and diversity can facilitate achieving both targets with minimal increases in cost (Bateman et al., 2013; Egoh et al., 2011), and that the land use scenarios that perform best for ecosystem services also perform well in terms of biodiversity (Bateman et al., 2013). Other assessments warn that spatial overlap is low in many contexts (Naidoo et al., 2008), or have find correlations that are positive but weak (Chan et al., 2006).

One reason that spatial concordance may vary among studies has to do with the number of taxa and ES targeted. Priority areas for multiple ES may have greater spatial coincidence with biodiversity than priority areas for individual services. Functionally, increasing biodiversity typically has a saturating effect for any given ES, leveling off at relatively low diversity levels (Schwartz et al., 2000; Srivastava and Vellend, 2005). However, if each ES is associated with a different set of species that act as ecosystem service providers (Kremen, 2005), then greater diversity is required to support a breadth of ES (Dee et al., 2017). Secondly, places that are important in terms of multiple ES may capture more biodiversity than "hotspots" for a single service if ES are weakly correlated to each other (Egoh et al., 2009). For at least these two reasons, biodiversity and ES may be more spatially coincident when they are defined broadly in terms of many taxa and ES than when they are defined narrowly as a single ES or taxon. We know of no effort that explicitly tests this hypothesis.

Here we identify optimal networks of conserved lands for four taxonomic groups, four ES, and all possible combinations of each in Vermont, USA. We then assess the biodiversity and ES contained in each network, its cost, and its spatial coincidence with each other network. Based on this analysis, we address four questions crucial to understanding the merit of conserving ES and biodiversity simultaneously:

Q1: To what extent do conservation networks targeting biodiversity and ES overlap?

Q2: Does the degree of overlap increase as the number of taxa or ES increases?

Q3: What is the added cost of networks that meet ES goals in addition to those for biodiversity?

Q4: What is the efficiency gain of integrating ES and biodiversity goals within a single network, instead of conserving each separately?

2. Methods

2.1. Overview

We identified optimal conservation networks given a budget constraint for four taxa (birds, mammals, reptiles, and amphibians), four ES (flood mitigation, aboveground carbon storage, crop pollination, and nature-based recreation), and all possible combinations of one to four taxa and one to four ES. We then measured the overlap of the resulting networks. This allowed us to assess the potential for conservation to protect biodiversity and ES simultaneously, and the effect increasing the number of ES on overlap. To determine the additional cost of conserving ES alongside biodiversity, we set conservation targets for each ES and taxon and identified conservation networks that could meet these targets at minimal cost. We followed two different methods for including ES alongside biodiversity: "joint targeting," implemented as a formal joint optimization of ES and biodiversity, and "independent efforts" implemented as the union of the single-factor optimizations for each. We compare the cost of the optimal conservation network in the joint targeting method to the cost of the single-factor optimization for biodiversity to determine the budget increase needed to meet ES goals with no net loss of biodiversity. We compare the cost of the optimal conservation networks from the joint targeting and independent efforts methods to assess the cost efficiency of integrating ES within conservation planning for biodiversity.

2.2. Study system

We investigate these questions using Vermont, U.S.A. as a model landscape. Vermont is a primarily forested state in the Northeastern Highlands ecoregion (U.S. Environmental Protection Agency, 2013). Prior to European settlement the state was 95% forested, however 75% of the state's forests had been cleared by 1850. These trends represent those throughout USA's northeastern region and many other developed contexts where forest cover is increasing on former agricultural lands (Turner, 2002). The northern hardwood forests of Vermont have since recovered, primarily via natural afforestation of abandoned pasturelands, such that almost 80% of the state is forested today (Thompson and Sorenson, 2005). Approximately 25% of Vermont's landscape falls under some level of protected status (Sonter et al. 2016), and the most significant intuitions managing protected areas in Vermont are the U.S. Forest Service, The Nature Conservancy, and the Vermont Land Trust (Author's own calculation, TNC, 2012, Fig. A1). Following the global trend, many conservation organizations in the state have begun to incorporate ES into their missions and actions.

2.3. Data sources

We obtained species distributions from United States Geological Survey's GAP Dataset (U.S. Geological Survey Gap Analysis Program, 2011), which included 4 amphibian species, 194 birds, 26 mammals, and 10 reptiles within the state of Vermont. We obtained published ES maps for flood mitigation, nature-based recreation (Watson et al., 2019), and crop pollination (Koh et al., 2016), as well as data on aboveground carbon storage from remotely sensed data (Kellndorfer et al., 2012). All datasets had a 30 m resolution.

We estimated the cost of conservation using a published index of conservation costs (Watson et al., 2019) that used log-transformed land costs as a proxy for conservation cost. We untransformed those values to obtain approximate land values statewide. We expect land value to generally represent the cost of public land acquisition, and to overestimate the cost of conservation in Vermont because most recent conservation has occurred via the purchase of easements, which are cheaper than acquiring land outright. Further, this dataset has a $\sim 5 \text{ km}^2$ resolution, and included urbanized areas that were likely to be expensive, but unlikely to be conservation priorities. While we do not expect land value to strictly represent conservation costs, it does represent the opportunity cost of alternative uses of the land. We do expect land values to scale with conservation across space.

2.4. Identifying priority areas for conservation

We used the optimization program Marxan (Ball et al., 2009) to identify optimal conserved lands networks, which we will refer to from here forward as priority areas. Marxan uses simulated annealing to approximate optimal conserved lands networks that meet a conservation target at minimal cost. It does so by minimizing an objective function that includes two terms: the cost of the conserved lands network, and the shortfall of each conservation feature being targeted (in our case, species and ES) relative to a user defined target for each feature. The program also includes an optional cost-based stop rule – a budget that cannot be exceeded (Ball et al., 2009). It produces two different outputs that indicate conservation importance: the irreplaceability index, which is calculated as the number of runs in which a unit was included in the optimal network, and the best conservation network from all runs, where the best network is the one that minimizes the following objective function:

$$ObjFun_{\min} = Land \ Cost \ + \ \sum_{i} \ \lambda (Protection \ target - Protection \ achieved)_i + Cost \ constraint$$
(1)

Where:

Land Cost = the monetary cost of conserving all hexagons within the selected priority areas

i = the conservation features being targeted (in our case this included birds, mammals, reptiles and amphibians, flood mitigation, crop pollination, carbon storage, and nature-based recreation)

Protection target = the proportion of a conservation feature that the optimization seeks to achieve.

Protection achieved = the proportion of a conservation feature held within the selected priority areas.

 λ = the "species penalty factor" for missing a conservation feature's protection target.

 $Cost \ constraint = a \ penalty$ for exceeding a user defined cost threshold.

For each individual ES and taxon, and for all possible combinations of two three, and four ES and taxa, we performed 500 iterative model runs and approximate optimal conservation networks as the best network from that set.

To assess overlap (questions 1 and 2), we created networks that maximized value for each conservation feature (taxa and ES) given a cost constraint such that all networks had approximately equal area. We implemented this using the objective function above and implementing a cost constraint that allowed for approximately 15% of the landscape to be included within conserved lands networks. We set targets for each conservation feature (50% of statewide value) that were impossible to reach given that constraint, and set a cost constraint penalty high enough that the optimal network never exceeded the cost constraint.

To determine the budget increase needed to include ES alongside biodiversity and the efficiency gains of doing so (questions 3 and 4), we also identified the least cost means of meeting conservation targets. We implemented this by removing the cost constraint from the above objective function, and setting our conservation targets at twenty percent of all habitat for non-threatened species, 40% of all habitat for threatened or endangered species, and 40% of total statewide ES for each ES. We set species penalty factors high enough that the optimal network always met the conservation feature target. In other words, optimal solutions had widely varying costs, but all met the target for every conservation feature included. We calculated the total cost of each network as the sum of the cost for all included units of analysis, and compared the costs of networks that included ES to otherwise equivalent networks that did not.

2.5. Quantifying overlap

We measured the overlap between any two networks as the ratio of the area included in both networks to the mean area of the two networks:

$$A_{\rm ES}U A_{\rm BD} / \left((A_{\rm ES} + A_{\rm BD})/2 \right)$$
⁽²⁾

Where:

 A_{ES} is the area of the best network for ES and A_{BD} is the area of the best network for biodiversity

We calculate the null expectation of the area included in both networks (from (Chan et al., 2006)), as:

$$A_{\rm ES} * A_{\rm BD} / A_{\rm Total}$$
 (3)

Where:

A_{Total} is the combined area of all units of analysis

Finally, we compared the observed ratio (Eq. (2)) to the equivalent ratio based on the null expectation:

$$(A_{ES} * A_{BD}/A_{Total}) / ((A_{ES} + A_{BD})/2)$$
(4)

We calculated pairwise overlap between networks for all ES, taxa, and their combinations. This resulted in 196 different overlap ratios. Sample size was unevenly distributed for question 2 (Table A1).

3. Results

3.1. Question 1 - spatial coincidence of ES and biodiversity

The average pairwise overlap between an individual ES and an individual taxon is 47%. This is high compared to a null expectation but lower than the 62% average overlap among taxa and the 49% average overlap among ES (Fig. 1). Overlap varies widely across ES-taxa pairs (Fig. 1b). Birds and reptiles overlap less with ES than do mammals and amphibians. Flooding and pollination overlap less with biodiversity than do recreation and carbon (Fig. 1b).

3.2. Question 2 – impact of the number of ES and biodiversity

The overlap between biodiversity and ES increases as the number of ES used in defining priority areas increases (Fig. 2a). Overlap also increases with the number of taxa up to three taxa, and then levels off (Fig. 2a). These trends hold true for each ES (Fig. 2b) and taxon (Fig. 2c) individually. The overlap between the best network for all four ES with the best network for all four taxa is 60%.

3.3. Question 3 – the added cost of conserving ES

The cost of meeting all biodiversity targets was 3% of the summed cost of all units of analysis (Fig. 3). This least-cost network included 39% of all units (most of the selected units were low-cost). Meeting all ES targets required 2% of the summed cost of all units, and included 36% of all units.

Reaching targets for all four ES and taxa through joint targeting required a 12% cost increase relative to meeting biodiversity targets alone (Fig. 3). On average conserving a single ES in addition to a single taxon through joint targeting had a 13% higher cost than only conserving a single taxon (Table A2). Across all pairwise combinations of a single ES and a single taxon, this cost increase ranged from 0% to 83%.

3.4. Question 4 – the efficiency gain of joint targeting

Reaching targets for all four ES and all four taxa through joint targeting was 22% less costly than reaching the same targets via separate efforts (Fig. 3). On average, conserving a single ES in addition to a



Fig. 1. A) Maps of irreplaceability indices for all ES and taxa individually, and their pairwise combinations. Priority areas for individual ES are shown in the first column, and for each taxa in the first row. The top left panel depicts irreplaceability for all taxa and ES combined. B) Pairwise overlap of best networks, where the shade of blue represents the degree of overlap C) Observed versus expected overlap between biodiversity and ecosystem services, compared with the overlap among taxa and among ES.

A	1 Taxon	2 Taxa	3 Taxa	4 Taxa	B 1	Taxon	2 Taxa	3 Taxa	4 Taxa
1 ES	0.47	0.51	0.53	0.52	Flooding	0.28	0.31	0.33	0.33
2 ES	0.51	0.55	0.58	0.57	Carbon	0.56	0.6	0.63	0.62
3 ES	0.53	0.57	0.6	0.59	Pollination	0.6	0.66	0.69	0.68
4 ES	0.54	0.58	0.61	0.6	Recreation	0.44	0.45	0.46	0.46
С	Flooding	Carbon	Pollination	Recreation					
1 ES	0.51	0.59	0.32	0.47					
2 ES	0.56	0.63	0.35	0.51					
3 ES	0.58	0.65	0.37	0.53					
4 ES	0.50			0.54					

Fig. 2. The effect of increasing the number of taxa and services used in defining biodiversity and ecosystem service priorities, respectively, on the overlap between the best conservation networks for each.



Fig. 3. The monetary cost required to meet conservation targets for biodiversity, ecosystem services, and to achieve both by joint targeting and through separate efforts. Cost is shown as a percentage of the total cost for all units of analysis.

single taxon through joint targeting had a 15% lower cost than through separate efforts (Table A2). Across all pairwise combinations of a single ES and a single taxon, the efficiency gain ranged from 6% to 23%.

4. Discussion and conclusions

The spatial coincidence of biodiversity and ES is high on average, but varies widely depending on the taxa and ES considered. Priority areas for multiple ES contain high levels of biodiversity even when they are selected without explicitly seeking a biodiversity benefit. Furthermore, achieving ES goals within the framework of biodiversity conservation is only 13% more costly than meeting biodiversity goals alone, and is more cost efficient than achieving each goal separately. Collectively, these results provide general support for conserving biodiversity and ES jointly, especially when multiple ES are targeted.

In Vermont the overlap of conservation priorities for ES and biodiversity is high relative to a null expectation (Fig. 1c); however, it varies widely across service-taxa pairs (Fig. 1a, b). Similarly, the budget increase needed to meet an ES target in addition to an existing taxonomic target is 13% on average (Fig. 3), although for some service-taxa pairs, a < 1% budget increase is required (e.g. for birds and recreation, or reptiles and carbon), while others require the budget to nearly double (e.g. amphibians and flooding) (Table A2). This heterogeneity indicates that it is important for projects seeking to conserve specific taxa and ES to assess the tradeoffs involved and identify potential win–win locations on a project by project basis.

The overlap of biodiversity and ES increases with the number of ES and taxa targeted (Fig. 3). This has important conservation implications: while projects that seek to safeguard a particular ES may not protect much biodiversity in the process (Fig. 1, overlap as low as 0.16), efforts to protect a broad suite of ES will likely protect more biodiversity even when biodiversity is not explicitly sought out (Fig. 3 ES overlaps from 0.54 to 0.60). The 0.60 overlap between priority areas for all four ES and taxa is comparable to the 0.62 average overlap between taxa, indicating that in the case of Vermont conserving ES alongside biodiversity presents tradeoffs no more severe than those already faced by conservation organizations seeking to protect a diversity of taxa.

Yet some tradeoff is inevitable when increasing the number of conservation objectives within a fixed budget (Goldman et al., 2011). We estimate that meeting targets for ES and biodiversity is 13% more costly than meeting biodiversity targets alone (Fig. 3). This implies that a 13% increase in conservation budgets is needed to incorporate ES into biodiversity conservation without negatively impacting biodiversity outcomes. While we do not have evidence that this budgetary increase has occurred, an increase of this size seems feasible. The inflation-adjusted annual revenue from contributions and grants for World Wildlife Fund, The Nature Conservancy, Conservation International, and the Wildlife Conservation Society rose 18% on average between fiscal years 2011 and 2015, the interval over which many of these organization reframed their mission statements and actions to include ES. Although it is not clear that this growth was driven by an ES framing, projects that include ES have been shown to attract more than four times as much funding as projects that do not (Goldman et al., 2008).

Given the mixed results within the biodiversity-ES literature, future research investigating explicit hypotheses that explain why tradeoffs are severe in some cases and moderate in others is warranted. Here we test one of these, the number of ES and taxa targeted, for the first time. We also provide an analytical framework for how this hypothesis and others could be tested elsewhere, or even globally. The taxa and ES involved, the budget constraint, landscape diversity, land use history, and spatial scale and may all also have an effect on the degree of overlap between biodiversity and ES. For example, forests in Vermont are diverse, native-dominated stands of mixed hardwood deciduous forests (Thompson and Sorenson, 2005). Overlap between biodiversity and ES is likely to be lower where forests are non-native or highly managed; we would not expect an equivalent degree of overlap between carbon storage and biodiversity for low diversity stands managed for carbon storage or timber harvest. However, these types of forests (while they may be highly effective in rapidly sequestering carbon) are unlikely to supply high levels of a diverse suite of ecosystem services (Lamb et al., 2005). In general, we expect that our finding that priority areas targeting multiple services safeguard more biodiversity than those

targeting a single service is likely to hold across a wide array of contexts.

Further research is needed to compile datasets of ES and biodiversity and test similar hypotheses across locations. This will allow for the formation of generalizable conclusions about when tradeoffs will be severe, and when they will be manageable. For example, conservation costs partially explain why priorities for ES and biodiversity have higher overlap than the null expectation in Vermont. While low-cost areas will broadly represent opportunities to achieve a relatively high return on investment for any conservation feature, this opportunity is particularly large in Vermont because biodiversity varied less across space than did the costs of conservation, thus cost was highly influential in determining which units were included within priority areas. Within our system, we found that those services whose value varies widely across space (crop pollination and flood mitigation) have overall lower overlap relative to those services that are more evenly distributed across the landscape (recreation and carbon sequestration), in large part because a relatively even distribution of ES value allows a cost minimizing strategy to be highly effective (also see Watson et al.. 2019). This implies that the distribution of conservation cost relative to that of taxa and ES may predictably influence the severity of tradeoffs between them (Fig. A2). Vermont is a small, relatively homogenous state with many wide-ranged species. In places with high ecological heterogeneity or endemism, or highly uneven demand for ES, priority areas for biodiversity and ES may show a weaker response to conservation cost and thus less overlap with each other.

Several caveats warrant consideration in the interpretation of our results and the implementation of our approach elsewhere. First, the priority networks we present here were created for the purpose of testing a generalizable hypothesis about the spatial relationship between biodiversity and ES. Further refinement of these priority areas would be necessary before they could be instrumental in local conservation context. Secondly, the computational load of carrying out all of the optimizations required for our analysis was significant. In practice this, and the need for common units of analysis across all ES and

Appendices

Table A1

Sample size for overlap means.

taxa, limited the number and spatial scale of our planning units. In the case of pollination and carbon storage we aggregated existing datasets to fit our purpose. In the case of recreation and flood mitigation, other planning units (parcels and watersheds) would be more informative in practice, and the datasets we use are implemented in these units elsewhere for other applications (Sonter et al., 2016; Koh et al., 2016).

Although there has been significant debate about whether ES should compete with biodiversity for conservation resources (McCauley, 2006), ES are clearly critical to human well-being (Balmford et al., 2002; MEA, 2005). Their value often exceeds the cost of protecting them (Balmford et al., 2003, 2002), and we are losing them rapidly (Costanza et al., 2014; Sutton et al., 2016). Even if biodiversity and ES conservation represent distinct objectives (i.e., biodiversity per se vs. human well-being), our analysis indicates that there are significant efficiency gains associated with pursuing them jointly. While there will certainly be cases where stark tradeoffs occur between biodiversity and ES, our results indicate that ES conservation is more likely to boost biodiversity outcomes in Vermont than to undermine them.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Jesse Gourevitch, Courtney Hammond, Lindsay Barbieri, and Allison Adams for their thoughtful feedback on the figures and presentation of this research. This work was supported by the Lintilhac Foundation, the United States Department of Agriculture McIntire-Stennis award #2014-32100-06050 to the University of Vermont, and the Rubenstein School of Natural Resources. L.J.S. receives support from ARC Discovery Early Career Research Award (DE170100684).

	1 Taxa (4 combinations)	2 Taxa (6 combinations)	3 Taxa (3 combinations)	4 Taxa (1 combination)
1 ES (4 combinations)	n = 16	n = 24	n = 12	n = 4
2 ES (6 combinations)	n = 24	n = 36	n = 18	n = 6
3 ES (3 combinations)	n = 12	n = 18	n = 9	n = 3
4 ES (1 combination)	n = 4	n = 6	n = 3	n = 1

Table A2

Costs required to meet targets for all pairwise combinations of one ES and one TG through joint targeting and through separate efforts.

	Biodiversity only	With flooding	With carbon	With recreation	With pollination	Mean cost with service	Mean % increase in cost	
(A) Cost of joint optimizations								
Birds	1.713E + 10	1.868E + 10	1.745E + 10	1.735E + 10	1.903E + 10	1.813E+10	6%	
Mammals	1.334E + 10	1.447E + 10	1.332E + 10	1.338E + 10	1.572E + 10	1.422E+10	7%	
Reptiles	1.208E + 10	1.459E + 10	1.213E + 10	1.213E + 10	1.510E + 10	1.349E+10	12%	
Amphibians	6.489E+09	1.187E + 10	7.350E + 09	6.855E + 09	1.160E + 10	9.420E+09	45%	
(B) Combined cost of separate efforts								
Birds	1.713E + 10	2.178E + 10	1.876E + 10	1.848E + 10	2.361E + 10	2.066E+10	21%	
Mammals	1.334E + 10	1.783E + 10	1.458E + 10	1.447E + 10	2.039E + 10	1.682E+10	26%	
Reptiles	1.208E + 10	1.747E + 10	1.405E + 10	1.387E + 10	1.967E + 10	1.627E+10	35%	
Amphibians	6.489E+09	1.315E + 10	8.956E+09	8.916E+09	1.480E + 10	1.146E + 10	77%	



Fig. A1. Landcover composition of conserved lands by sector. The top axis represents the 2006 NLCD landcover type. The bottom axis represents the sector of the relevant conservation institution. Landcover map of Vermont included for reference. Approximately 89% of federal lands in Vermont are managed by the U.S. Forest Service.



Fig. A2. Conservation cost explains 68% of the variation in the correlation between individual ecosystem services and biodiversity, and between individual taxonomic groups and ecosystem services (p = 0.007, n = 8, f = 16.02, 6df).

References

- Ball, I.R., Possingham, H.P., Watts, M., 2009. Ch 14: Marxan and relatives: Software for spatial conservation prioritisation. In: Moilanen, A., Wilson, K.A., Possingham, H.P. (Eds.), Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools. Oxford University Press, Oxford, UK, pp. 185–195.
- Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., 2002. Economic reasons for conserving wild nature. Science 297, 950–953.
- Balmford, A., Gaston, K.J., Blyth, S., James, A., Kapos, V., 2003. Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. Proc. Natl. Acad. Sci. USA 100, 1046–1050.
- Balmford, A., Whitten, T., 2003. Who should pay for tropical conservation, and how could the costs be met? Oryx 37, 238–250.
- Bateman, I.J., Harwood, A.R., Mace, G.M., Watson, R.T., Abson, D.J., Andrews, B., Binner, A., Crowe, A., Day, B.H., Dugdale, S., Fezzi, C., Foden, J., Hadley, D., Haines-Young, R., Hulme, M., Kontoleon, A., Lovett, A.A., Munday, P., Pascual, U., Paterson, J., Perino, G., Sen, A., Siriwardena, G., van Soest, D., Termansen, M., 2013. Bringing ecosystem services into economic decision-making: land use in the United Kingdom. Science 341, 45–50.
- Bhagabati, N.K., Ricketts, T., Sulistyawan, T.B.S., Conte, M., Ennaanay, D., Hadian, O., McKenzie, E., Olwero, N., Rosenthal, A., Tallis, H., Wolny, S., 2014. Ecosystem services reinforce Sumatran tiger conservation in land use plans. Biol. Conserv. 169, 147–156.
- Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Hernández Morcillo, M., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D.,

Vié, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168.

- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253.
- Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. PLoS Biol. 4, 2138–2152.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014. Changes in the global value of ecosystem services. Glob. Environ. Change 26, 152–158.
- Daily, G., 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press.
- L.E. Dee M. De Lara C. Costello S.D. Gaines 2017. To what extent can ecosystem services motivate protecting biodiversity? Ecol. Lett. https://doi.org/10.1111/ele.12790.
- Donovan, S., Goldfuss, C., Holdren, J., 2015. Incorporating Ecosystem Services into Federal Decision Making (No. M-16-01). Executive Office of the President of the United States, Washington, DC.
- Egoh, B.N., Reyers, B., Rouget, M., Richardson, D.M., 2011. Identifying priority areas for ecosystem service management in South African grasslands. J. Environ. Manage. 92, 1642–1650.
- Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol. Conserv. 142, 553–562.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., 2005. Global consequences of land use. Science 309, 570–574.
- Goldman, R.L., Daily, G.C., Kareiva, P., 2011. Trade-offs in making ecosystem services and human well-being conservation priorities. In: Leader-Williams, Nigel, Adams,

K.B. Watson, et al.

William M., Smith, Robert J. (Eds.), Trade-Offs in Conservation: Deciding What to Save. John Wiley & Sons, pp. 56–72.

- Goldman, R.L., Tallis, H., Kareiva, P., Daily, G.C., 2008. Field evidence that ecosystem service projects support biodiversity and diversify options. Proc. Natl. Acad. Sci. 105, 9445–9448.
- Guerry, A.D., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G.C., Griffin, R., Ruckelshaus, M., Bateman, I.J., Duraiappah, A., Elmqvist, T., 2015. Natural capital and ecosystem services informing decisions: from promise to practice. Proc. Natl. Acad. Sci. 112, 7348–7355.
- Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamănă, N., 2014. Linkages between biodiversity attributes and ecosystem services: a systematic review. Ecosyst. Serv. 9, 191–203.
- Hooper, D.U., Chapin, F.S., Iii, Ewel J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

ICSU, 2015. Review of the Sustainable Development Goals: The Science Perspective. International Council for Science (ICSU), Paris.

- Kellndorfer, J., Walker, W., LaPoint, E., Bishop, J., Cormier, T., Fiske, G., Hoppus, M., Kirsch, K., Westfall, J., 2012. NACP Aboveground Biomass and Carbon Baseline Data.
- Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. USA 113, 140–145.
- Kremen, C., 2005. Managing ecosystem services: what do we need to know about their ecology? Ecol. Lett. 8, 468–479.
- Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632.
- Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R., Dawson, T.P., De Bello, F., Díaz, S., Feld, C.K., 2009. Quantifying the contribution of organisms to the provision of ecosystem services. Bioscience 59, 223–235.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338, 946–949.

McCauley, D.J., 2006. Selling out on nature. Nature 44317, 27-28.

- Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being. Island Press Washington, DC.
- Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., Ricketts, T.H., 2008. Global mapping of ecosystem services and conservation priorities. Proc. Natl. Acad. Sci. 105, 9495–9500.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace,

G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752.
- Reyers, B., Polasky, S., Tallis, H., Mooney, H.A., Larigauderie, A., 2012. Finding common ground for biodiversity and ecosystem services. Bioscience 62, 503–507.
- Ricketts, T.H., Watson, K.D., Koh, I., Ellis, A.M., Nicholson, C.C., Posner, S., Richardson, L.L., Sonter, L.J., 2016. Disaggregating the evidence linking biodiversity and ecosystem services. Nat. Commun. 7, 13106.
- Ruckelshaus, M., McKenzie, E., Tallis, H., Guerry, A., Daily, G., Kareiva, P., Polasky, S., Ricketts, T., Bhagabati, N., Wood, S.A., 2013. Notes from the field: Lessons learned from using ecosystem service approaches to inform real-world decisions. Ecol. Econ.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., van Mantgem, P.J., 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122, 297–305.
- Sonter, L.J., Watson, K.B., Wood, S.A., Ricketts, T.H., 2016. Spatial and temporal dynamics and value of nature-based recreation, estimated via social media. PLoS One 11, e0162372.
- Srivastava, D.S., Vellend, M., 2005. Biodiversity-ecosystem function research: is it relevant to conservation? Annu. Rev. Ecol. Evol. Syst. 36, 267–294.
- Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Reyers, B., Sörlin, S., 2015. Sustainability. Planetary boundaries: guiding human development on a changing planet. Science 347, 1259855.
- Sutton, P.C., Anderson, S.J., Costanza, R., Kubiszewski, I., 2016. The ecological economics of land degradation: Impacts on ecosystem service values. Ecol. Econ. 129, 182–192.

The Nature Conservancy (TNC), 2012. Secured areas dataset. TNC, Arlington, Virginia.

- Thompson, E.H., Sorenson, E.R., 2005. Wetland, woodland, wildland: a guide to the natural communities of Vermont. Vermont Dept. of Fish and Wildlife and the Nature Conservancy.
- Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc. Natl. Acad. Sci. USA 109, 10394–10397.
- Turner, B.L., 2002. Toward integrated land-change science: advances in 1.5 decades of sustained international research on land-use and land-cover change. Challenges Changing Earth. https://doi.org/10.1007/978-3-642-19016-2_3.
- Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., Da Fonseca, G.A.B., Portela, R., 2007. Global conservation of biodiversity and ecosystem services. Bioscience 57, 868–873.
- U.S. Environmental Protection Agency, 2013. Level III ecoregions of the continental United States.
- U.S. Geological Survey Gap Analysis Program, 2011. National GAP vertebrate species distribution model.
- Watson, K., Galford, G., Sonter, L., Koh, I., Ricketts, T.H., 2019. Effects of human demand on conservation planning for biodiversity and ecosystem services. Conserv. Biol.