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Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions

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Many conservation organizations use spatial prioritization to help identify locations in which to work. Increasingly, prioritizations seek to account for spatial heterogeneity in the costs of conservation, motivated in part by claims of large efficiency savings when these costs are included. I critically review the cost estimates on which such claims are based, focusing on acquisition and management costs associated with terrestrial protected areas. If researchers are to evaluate how including costs affects conservation planning outcomes, estimation methods need to preserve the covariation between and relative variation within costs and benefits of conservation activities. However, widely used methods for estimating costs and incorporating them into prioritizations may not meet these standards. For example, among relevant studies, there is surprisingly little attention given to the costs that conservation organizations actually face. Instead, there is a heavy reliance on untested proxies for conservation costs. Analytical shortcuts are also common. Now that debate is moving beyond whether to account for costs in conservation planning, it is time to evaluate just how we can include them to greatest effect.

Keywords: economic; reserve; land use; site selection; targeting; space

Introduction

Prioritization is central to much of conservation, reflecting the basic challenge of allocating limited resources effectively to counter losses of biodiversity and ecosystem services. Numerous methods and tools are available to help conservation organizations prioritize their activities, as exemplified by spatial planning.[1–3] Spatial planning involves prioritizing a subset of locations for conservation action (e.g., setting up protected areas) from within a larger set of candidate sites. Various factors can be included to shape this decision, including the nature and immediacy of threats to those places[4,5] and the likelihood of conservation success from investing in them.[6–9] Here, I focus on one factor that has received increasing attention in recent years, namely spatially heterogeneous costs associated with conservation activities.

The growing and changing influence of costs on conservation practice is apparent from how spatial patterns of conservation investment have changed through time.[10] Today consideration of the cost of different conservation activities is often written into conservation planning guidelines (e.g., Refs. 11–13), although there is variation between conservation organizations regarding if, when, and how costs get considered in their prioritization processes.

This changing influence of costs is paralleled in research writings on spatial planning. Early research on spatial prioritization ignored heterogeneity in costs and focused on the biological benefits of conserving different locations.[14,15] Then, in the late 1990s, studies started to appear showing how conservation prioritizations changed when also recognizing spatial cost heterogeneity.[16–18] Interest in including costs in conservation planning grew slowly at first,[19] but over the past decade expanded rapidly (Table 1).

In this paper, I first review the role that conservation costs can play in shaping outcomes of spatial planning. Then, I examine methods used to include these costs into planning tools. I review how people have estimated costs, how resulting estimates

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Table 1. Examples of recent papers testing how including heterogeneous costs affects prioritization outcomes

		Conservation costs considered				Prioritization		Conclusions		
Reference (source for cost data)	Location	Manage. or acqn.	Estimation method	Spatial grain	Summary (2012 USD $1000s/ha or /ha/year) min/max/mean/SD	Biodiversity target	Spatial grain	Correl (b_i,c_i)	b_i/c_i target > b_i target	c_i target > b_i target
Global studies										
Murdoch *et al.*[20] (Wilson *et al.*[21])	17 Mediterranean ecoregions	M&A	Various estimates from literature	Country	0.006/49/5.3/10.0	IUCN Red list plant and vert. species	17 ecoregions		Y	
Bode *et al.*[22] (Moore *et al.*[23])	34 hotspots	M&A	Hypothetical cost survey	Country	0.025/41/4.0/8.3	Species from seven taxonomic groups	Hotspots (ave. 0.7M km^2)	$r_s = -0.09$	Y	
Carwardine *et al.*[24] (Naidoo & Iwamura[25])	Globe	A	Gross revenue (outputs only) from ag.	~85 km^2	0/8.7/0.073/0.17 (0/170/1.5/3.5)	Terrestrial mammal species	10,000 km^2		Y	
Naidoo & Iwamura[25]	Globe	A	Gross revenue (outputs only) from ag.	~85 km^2	0/8.7/0.073/0.17 (0/170/1.5/3.5)	Endemic species	825 ecoregions		Y	Y
Eklund *et al.*[6]	Globe		Nominal GDP per capita	Country		Terrestrial mammal species	~124 km^2	$r_s = 0.88$		
Continental										
Luck *et al.*[26]	Australia		Population density	~20 km^2		Species from five taxonomic groups	12,000 km^2	$r_s = 0.64$	Y	
Moore *et al.*[23] (Balmford *et al.*[27])	Africa	M	Hypothetical cost survey	Country	3×10^{-4}/0.16/0.013/0.032 (0.007/3.2/0.27/0.64)	Vertebrate species	118 ecoregions (ave. 0.3M km^2)	$r_s = 0.42$ $r_s = 0.33$ (endemics)	Y	Y
Carwardine *et al.*[28] (state land valuation offices;	Australia	M	Gross margin (outputs–inputs) from ag.	1 km^2		2600 features (inc. veg. types and species)	100 km^2			
Hajkowicz & Young[29])		A	Sales of unimproved land	ave. 9000 km^2						
Jantke & Schneider[30]	Europe	A	Gross margin (outputs–inputs) from ag.	Country	0.012/0.58/0.21/0.16 (0.24/11.5/4.3/3.3)	69 wetland vertebrate species	2500 km^2			
Jantke *et al.*[31] (Lee *et al.*[32])	Europe	A	Gross margin (outputs–inputs) from ag.	Country	0.013/0.54/0.14/0.13 (0.26/11/2.7/2.5)	72 wetland species				
			Gross margin (outputs–inputs) from ag.	~85 km^2	0/0.76/0.14/0.12 (0/15/2.8/2.4)	72 wetland species				
National										
Murdoch *et al.*[20] (USDA[33])	U.S.A. 21 ecoregions	A	Ag. land sales	County	2.2/26/5.5/5.6	Plant and vert. species	Ecoregions (avg. 140,000 km^2)	$r_s = -0.05$	Y	
Strange *et al.*[34] (Statistics Denmark)	Denmark	A	Ag. land sales	County	12/31/–/–	763 species: various taxonomic groups	100 km^2	$r_s = 0.43$	Y	
Chiozza *et al.*[35] (Natl. Ag. Adv. Service)	Uganda	A	Gross margin (outputs–inputs) from ag.	Census Tracts	0/0.59/0.15/– (0/12/2.9/–)	377 vertebrate species	25 km^2		Y	
Withey *et al.*[36] (Lubowski *et al.*[37])	U.S.A. (less HI & AK)	A	Ag. land sales	County	0.056/44/–/–	Terrestrial vertebrates	Counties avg. 3000 km^2		Y	
Within country										
Adams *et al.*[38] (Naidoo & Adamowicz[39])	Mbaracayu Forest Biosphere Reserve, PRY(3000 km^2)	A	Gross margin (outputs–inputs) from ag.	0.01 km^2	0/1.1/0.073/6	13 veg. classes	0.25 km^2	$r = 0.01$		
Carwardine *et al.*[40] (state land valuation offices)	Queensland, AUS (1.8M km^2)	A	Sales of unimproved land	100 km^2	–/–/0.47/–	2600 features (inc. veg. types and species)	100 km^2			
Polasky *et al.*[41]	Willamette Basin, U.S.A. (~30,000 km^2)	M&A	Ag. and timber gross margins, sales of unimproved land	0.0009–7.5 km^2	–/–/7.4 (ag.) 12 (forest) 13 (residential)/–	267 vertebrate species	0.0009–7.5 km^2		Y	
Visconti *et al.*[5]	Hunter Valley, AUS (~600 km^2)	A	Urban and ag. land sales	0.01–0.34 km^2		Three vertebrate species	0.01–0.34 km^2	$r = 0.19$, 0.04, 0.06	Y	
Perhans *et al.*[42]	Gavleborg, SWE (~22, 500 km^2)	A	Gross margin (outputs–inputs) from forestry	0.0025 km^2	0.002/0.018/0.008/0.003	620 species; habitat characteristics	0.0025 km^2	$r_s = -0.26$	Y	Y

Note: To aid comparisons, in column 6, when costs were given as annual costs, I have provided an approximate present value equivalent when assuming a 5% discount rate (values in parentheses). Final two columns indicate whether study conclusions include that benefit–cost targeting (b_i/c_i) outperforms benefit only (b_i) targeting and whether cost-only (c_i) targeting outperforms benefit-only targeting. Min, minimum; max, maximum; SD; standard deviation; Ag, agriculture. Vert, vertebrate.

are incorporated into planning, and assumptions about costs that underlie these approaches.

I focus on costs that a conservation organization faces when setting up and managing terrestrial protected areas. In particular, I focus on acquisition costs involved in securing land for protection and management costs associated with ongoing stewardship, monitoring, and enforcement activities on the site once it has been protected. Transaction costs associated, for example, with negotiating agreements to protect a particular property can also be important, but are not reviewed here. Also, I restrict attention to private costs faced by conservation organizations setting up and managing terrestrial protected areas, as opposed to wider social costs or benefits of protecting land. To bound the task further, I do not review the growing literature on how incorporation of economic costs affects planning for marine protected areas (e.g., Richardson *et al.*,[43] Ban and Klein,[44] Weeks *et al.*,[45] and Klein *et al.*[46]), for which the relative importance of the various cost components is quite different. Finally, to maintain a clear focus on conservation costs, I also limit consideration of the biological benefits of different conservation activities or of the threats facing the biota on candidate sites to the intersection of these factors with costs, while recognizing that each of these topics is worthy of reviewing critically in its own right.

Use of conservation cost data in conservation planning studies

Box 1 outlines a basic framework for examining the role of heterogeneous conservation costs in spatial prioritizations. As exemplified in Box 1, prioritizations commonly call for conservation cost data in a particular form; specifically, they call for datasets that provide a unique cost estimate c_i of undertaking a conservation activity in each location (or for each action–location pair[21]). Conservation scientists have devoted less effort to collating such data than they have to collecting data on distributions of biodiversity. Similarly, we have not spent nearly as much time studying process-based models of what determines costs as we have process-based models that describe the responses of the biota to human activities. As such, spatial prioritization studies have often relied on available proxies for actual conservation cost data.

Table 1 summarizes cost estimates relied on in recent conservation planning studies (see Appendix for more details). When compiling the table, it was apparent that important details were often not well documented in studies examining the role of conservation costs in conservation planning. Despite testing effects of accounting for cost heterogeneity, it was surprisingly common for authors not to report anything about spatial patterns in cost data they were using, and instead only to comment on their impact on prioritization outcomes. Alternatively, if something was reported about patterns in the cost data, key details were lacking; for example, a lack of clarity over the units being used to report costs was common. The relevant units should be currency year per unit area or currency year per unit area per unit time (e.g., 2012 USD$/ha or 2012 USD$/ha/year). In preparing the table, I have tried to standardize cost data to 2012 USD$/ha or 2012 USD$/ha/year using the CPI to adjust for inflation (U.S. Bureau of Labor Statistics[51]; Appendix).

Various trends in studies are apparent from the table. First, there is tremendous variation in the spatial extent and grain considered in studies examining the role of conservation costs in influencing prioritization outcomes. Some are global analyses whereas others are finer-grain studies in particular places. There is also an obvious coverage bias of the subglobal studies toward well-studied, data-rich locations (the United States, Australia, and Europe).

While I sought to include prioritization studies that accounted for both management and acquisition costs (see Appendix for a discussion of how opportunity costs were treated), there were many more studies focused on acquisition costs than management costs, and very few studies accounted for both cost components. Some authors also did not state what aspect of costs they were considering.

Studies vary widely in the empirical methods they rely upon to estimate conservation costs. They also vary in just how those cost estimates are treated in prioritization analyses. I discuss some of the approaches taken and their relative merits and demerits below.

Looking across the studies, the cost estimates involved vary widely. For the lower bound, a number of studies estimate that conservation activities in some locations would cost nothing. For the upper bound, maximum values in the range 2012 USD $10,000–50,000/ha (roughly equivalent to an annual rent of 2012 USD $500–2500/ha/year) are commonly reported. This variation will reflect, in part, actual variation in the costs of different conservation activities and, in part, variation across studies in how costs have been estimated.

The specific focus of the different studies in Table 1 varies, but some claims about how accounting for economic costs influences prioritization

Box 1

A typical spatial prioritization might consider an optimization problem of the form

$$\max_x B(x) \text{ subject to } \sum c_i x_i \leq C, \quad (1)$$

where vector x comprises a choice of conservation activities x_i undertaken on site i. For example, x might govern the choice of sites to acquire as protected areas ($x_i = 1$) and those to leave unprotected ($x_i = 0$). Benefit function B here summarizes how well a particular choice of conservation activities (x) performs at achieving the objectives of the prioritization. For example, B might represent the overall set of species or habitats covered by the particular choice of protected areas when accounting for complementarity between sites.[1]

The second part of Eq. (1) describes the budget constraint. This constraint requires that the overall cost summed across conservation activities be less than or equal to the overall budget available, C. The constraint accounts for spatial variation in costs by allowing c_i, the cost of undertaking a specified conservation activity at location i, to vary across candidate locations (or activity–location pairs).

Various authors have sought to build intuition about how accounting for cost heterogeneity changes conservation planning outcomes by starting from an even simpler version of the problem in Eq (1),[17,19,47–49] In particular, they focus on a case in which the benefits of a particular set of activities are assumed to be additive. For the case, where $x_i = 0$ or 1, this gives

$$B(x) = \sum b_i x_i, \quad (2)$$

where b_i is the conservation benefit that accrues if action i is taken ($x_i = 1$). This formulation would apply, for example, if choosing between regions and scoring benefits based on numbers of endemic species found there (e.g., Naidoo and Iwamura[25]). An important variant of Eq. (2) arises when the probability (threat) of losing conservation value on a site in the absence of investment is also heterogeneous. In this case, b_i represents the difference in the expected benefit provided by site i with and without investment.[8,48]

When using a benefit function of the form shown in Eq. (2), a rule of targeting properties for protection based on maximizing the benefit to cost ratio b_i/c_i is usually an effective strategy. Indeed, something similar to this would be the best possible strategy if investments in different locations i could be continuous (area on which to act) rather than discrete (act or do not act). When accounting for heterogeneous threats as well, this rule becomes one of maximizing the ratio between the change in expected benefit and the cost.[48] Comparisons are often made between this benefit–cost targeting strategy and two other targeting strategies. In one (benefit-only targeting), sites are prioritized based only on their biological value (b_i) without considering effects of costs (see Brooks *et al.*[50] for prominent examples). In the other (cost-only targeting), only the cheapest sites are protected, regardless of the benefits that they offer (prioritizing only on c_i), which is equivalent to maximizing area coverage when focusing on a protected area strategy.

Various authors have highlighted how the distributions of benefits (b_i) and costs (c_i) across candidate sites in Eqs. (1) and (2) determine the scope for conservation gains from benefit–cost targeting[19] and also the relative effectiveness of this strategy when compared to benefit-only or cost-only targeting.[17,19,47] Simulation results in Figure 1 illustrate common take-homes from these studies (see Babcock *et al.*[17] for the original, more detailed treatment). Panel A shows results when the benefit and cost data are positively correlated and panel B when they are negatively correlated. Correlations could arise here because the distribution of biodiversity across sites and the cost of land respond to similar drivers (e.g., elevation and soil productivity), or, in the probabilistic problem, because of correlations between threats to sites and costs of conserving them. For each type of correlation structure, simulation results are presented for low- and high-cost variability and low- and high-benefit variability scenarios. Within each of the eight scenarios, I compared the average performance of the three different targeting strategies (benefit-only targeting, cost-only targeting and benefit–cost targeting).

Conservation gains available from benefit–cost targeting are greater when benefits and costs are negatively correlated (comparing the height of the third bar in each grouping in Fig. 1A with those in 1B). Moreover, the relative improvement offered by benefit–cost targeting over either benefit-only targeting or cost-only targeting depends on this correlation, as well as the relative variability in the benefit and cost data (comparing how the difference in height between the third bar and the first and second bar in each grouping varies across the eight scenarios). Finally, as the figure makes clear, of the other two strategies, whether benefit-only targeting or cost-only targeting performs better also depends on the correlation between and relative variation within benefits and costs (whether the first and second bar in each grouping is taller varies across the eight scenarios).

outcomes recur. The most commonly reported conclusion is that prioritizations that fail to account for cost heterogeneity are inefficient compared to those that recognize cost variation (second to last column in Table 1). In the formulation in Box 1, this amounts to claiming that benefit–cost targeting (ranking on b_i/c_i) outperforms benefit-only targeting (ranking on b_i only). Quantitative claims about how large the possible efficiency savings can be striking. For example, Naidoo and Iwamura[25] compare benefit–cost targeting to a hotspots approach, which ignores cost heterogeneity.[52] They conclude that the same number of species can be protected for just one-eighth of the cost of a hotspots strategy when cost heterogeneity is considered.

Several of the studies also conclude that accounting for variation in economic costs of conservation is more important than accounting for spatial variation in the biological-benefit function itself for prioritizing efficiently (last column in Table 1; i.e., cost-only targeting outperforms benefit-only targeting). If true in general, this would represent something of a reversal of the original motivation for many systematic conservation planning approaches.[1,53] A related claim, now appearing in conservation textbooks,[54] is that even if variation in costs is not so great as to swamp variation in benefits altogether, it is still great enough that other debates on which conservation biologists have focused (e.g., the relative suitability of using different indicator taxa to estimate biological benefits[22]) may be less important than originally thought.

To evaluate these claims, the cost estimates used in prioritization must preserve the underlying spatial signal in the actual costs of conservation (to preserve their spatial covariation with benefits) and must preserve the relative variability of costs and benefits. Failure to do so can lead to misleading results. For example, compare the third and fourth groupings of bars in Figure 1A, where we have assumed costs and benefits are positively correlated and benefit data show high variability. Suppose the actual costs of different conservation activities also show high variability (fourth group of bars), but we use an estimation method (see below for relevant examples) that suppresses the variance in costs (third group of bars). When relying on such a cost-estimation method, we would draw markedly different conclusions about the relative and absolute performance of different targeting strategies.

Methods used to estimate conservation costs

Estimating acquisition costs

When estimating acquisition costs of lands for protection, early prioritization studies just used land area.[14,15] Proxies, such as human population density or GDP per capita, have also been used.[6,26] However, currently most efforts to account for acquisition costs of areas for protection focus on the value of agricultural land (Table 1). The coarsest such estimates consider potential gross revenue (price × potential output [e.g., tons of wheat that could be produced given climatic conditions and irrigation potential] ignoring any costs of production) from major crops and livestock sources. For example, Naidoo and Iwamura[25] use this approach to estimate conservation costs globally. If more data are available, authors may use an estimate of gross margins from agriculture (price × output [e.g., tons of wheat] minus cost per input × inputs [e.g., tons of fertilizer used]).[31,35,39] For both methods, spatial variation derives from the spatial distribution of crops and livestock rather than from economic price estimates. Finally, when working with more richly developed datasets, estimates of costs of acquiring lands for conservation can be based on sales of agricultural land parcels (e.g., Strange *et al.*[34] and Carwardine *et al.*[28]). With all of these estimation methods, publically available datasets are often aggregated to the county or similar spatial units.

Importantly, none of these estimates focuses on actual areas being acquired for protection by conservation organizations. Protected parcels can often be quite different from surrounding farmland (e.g., more rugged parcels, wetland parcels, etc.). In addition, the negotiation dynamic present in many conservation land transactions is different from that in commercial land sales for agriculture. The potential buyers and sellers are different, their motivations are different, and they hold different amounts of information than one encounters in agricultural land markets. As such, when extrapolating cost estimates of a protected area strategy from costs of average agricultural land parcels nearby, there is a risk that the spatial pattern and amount of variation in costs will not be preserved.

For example, Figure 2 compares surrounding average agricultural land values, of the type researchers

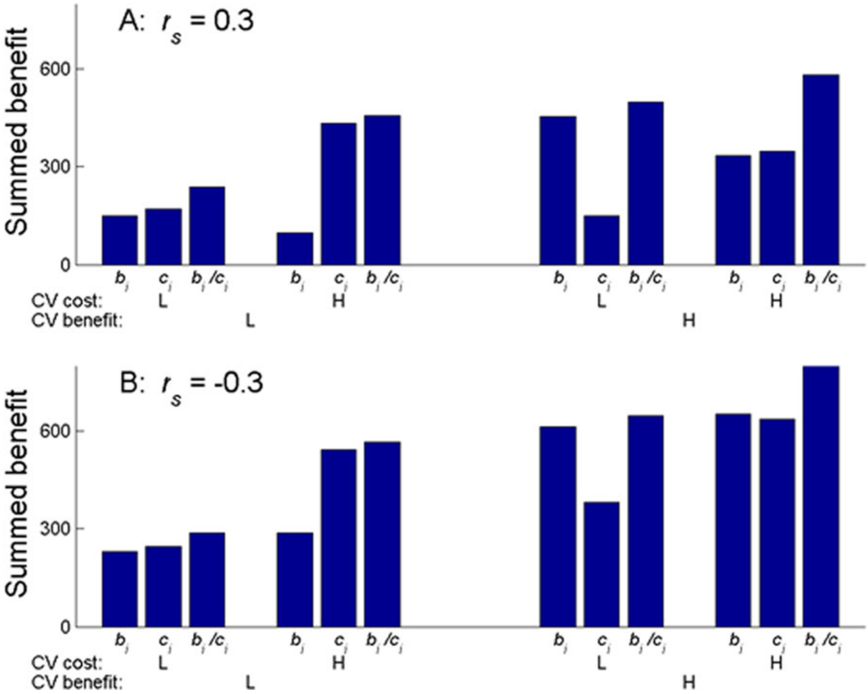

Figure 1. Relative performance of benefit targeting (b_i), cost targeting (c_i), and benefit–cost targeting (b_i/c_i) when cost and benefit data are characterized by low variability (L: coefficient of variation (CV) = 0.5) and high variability (H: CV = 2) and are (A) positively correlated (Spearman's rank correlation $r_s = 0.3$) and (B) negatively correlated ($r_s = -0.3$). Cost data were log-normally distributed with cost units (e.g., 2012 USD \$1000/ha) chosen to have a mean of 1. Biodiversity benefit data were negative binomially distributed count data, as could represent, for example, the number of occurrences of a focal taxonomic group chosen to have a mean of 10. There are 100 candidate locations for conservation and the budget is equal to 10 times the mean cost of protecting one of them. Bars show average performance of each strategy across 100 replicate simulations.

have relied on to estimate conservation costs, with the actual acquisition costs of protecting sites paid by three conservation organizations. How well agricultural land values nearby reflect spatial variation in the costs of acquiring the actual sites being protected varies from a weak positive association (Fig. 2A; Spearman's rank correlation $r_s = 0.18$; $P < 0.05$; $n = 183$) to a negative association (Fig. 2B; $r_s = -0.41$; $P < 0.05$; $n = 27$) to no association (Fig. 2C; $r_s = 0.03$; $P > 0.05$; $n = 12$).

Moreover, in all three examples, actual acquisition costs are much more variable than the estimated acquisition costs based on agricultural land values (comparing the spread of data on the horizontal and vertical axes in Fig. 2). In the largest study, to date, of actual conservation land transactions, Davies *et al.*[55] examined acquisition costs of 10,000 fee-simple and 1600 easement acquisitions undertaken by the Nature Conservancy across the conterminous United States. In that study, we found the same thing—actual acquisition costs faced when buying land to establish protected areas are much more variable than is being reported in the comparable studies summarized in Table 1 that are based on proxies for cost data.

Estimating management costs

In addition to the costs associated with acquiring land for protection, there are costs associated with ongoing stewardship of these properties. These appear to have been included in spatial prioritization studies less often than acquisition costs (Table 1), although management costs can sometimes exceed the cost of acquiring land to begin with when funded on an endowment basis.[56]

Management costs are most commonly estimated in one of two ways. First, a number of studies focus on actual spending patterns of conservation organizations involved in managing protected areas, including direct expenditure on sites (e.g., for

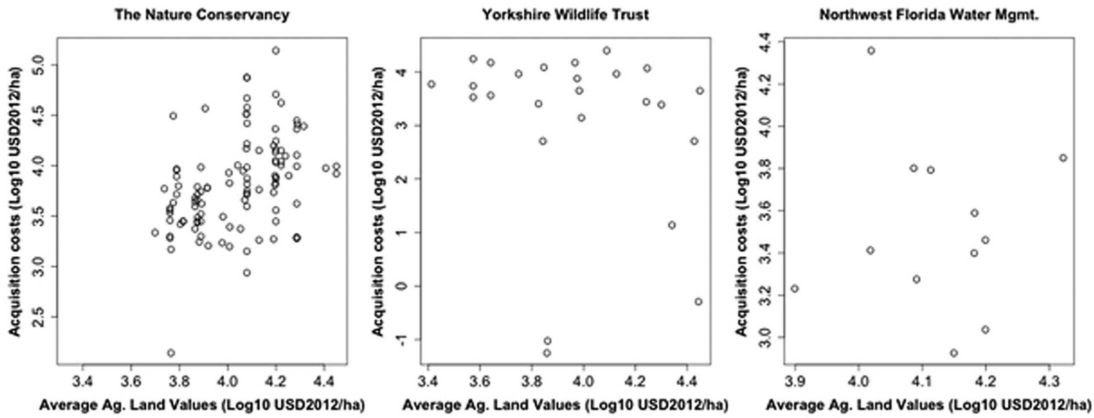

Figure 2. Comparison of average agricultural land value near protected sites and actual acquisition costs faced by conservation organizations when protecting these sites. Acquisition cost of areas protected (A) in the central and southern Appalachian mountains by the Nature Conservancy, an international land trust; (B) by the Yorkshire Wildlife Trust, a regional land trust in the United Kingdom; and (C) by the Northwest Florida Water Management District, a public agency. Average agricultural land values nearby are based on (A and C) USDA NASS data on recent land sales[33] and (B) the estimated gross margin of agriculture in the surrounding area[56] converted to a present value assuming a 5% discount rate.

equipment and supplies) and paid staff time devoted to managing them.[56,57]

A second approach has been to focus on hypothetical costs of achieving conservation goals. Common designs involve asking protected area managers how much they would ideally have available to spend on managing sites in light of their conservation goals.[27,58] While practitioners' expert judgment may be the only available source for some types of data, the questions being asked of practitioners can be sufficiently demanding (see, e.g., Laycock *et al.*[59] or Carwardine *et al.*[60] for recent designs) that there necessarily will be large uncertainties attached to any answers. There may also be systematic biases involved. For example, any cost estimates obtained are likely to reflect current ways of operating. However, if managers were actually granted a larger budget and the freedom it would provide to explore new ways of meeting conservation goals, then they might identify efficiencies that lower costs from their initial projections. There is also an obvious incentive compatibility issue involved in asking a manager heavily invested in a particular site or conservation activity how much ideally their home organization should spend on that activity; what the organization considers the ideal outlay could be very different from what the individual considers ideal.

Stated preference techniques in economics (e.g., choice experiments) provide an obvious, well-established context for navigating potential entry points of uncertainty and bias when surveying individuals on hypothetical spending. Decades of study have established that simply asking people how much they would ideally like to spend on some activity (e.g., Frazee *et al.*[58]) may not elicit particularly reliable data. Instead, today's stated preference techniques are much more tightly specified and incorporate numerous consistency checks and design features intended to elicit more reliable data. For recent applications relevant to understanding the costs of conservation programs, see Moro *et al.*[61] and Bush *et al.*[62]

How resulting cost estimates are incorporated into spatial prioritizations

Once an estimate of acquisition or management costs has been obtained, researchers still must make assumptions before prioritization can proceed.

First, researchers commonly estimate only one element of conservation costs and just assume it will reflect variation in overall costs. However, prioritizations that consider only one cost component have proven highly inefficient when tested.[38] For example, most studies include an estimate of either acquisition costs or management costs and assume that it adequately represents the other cost component (Table 1). Figure 2 shows a comparison of management and acquisition costs for two conservation organizations. For the first, management and

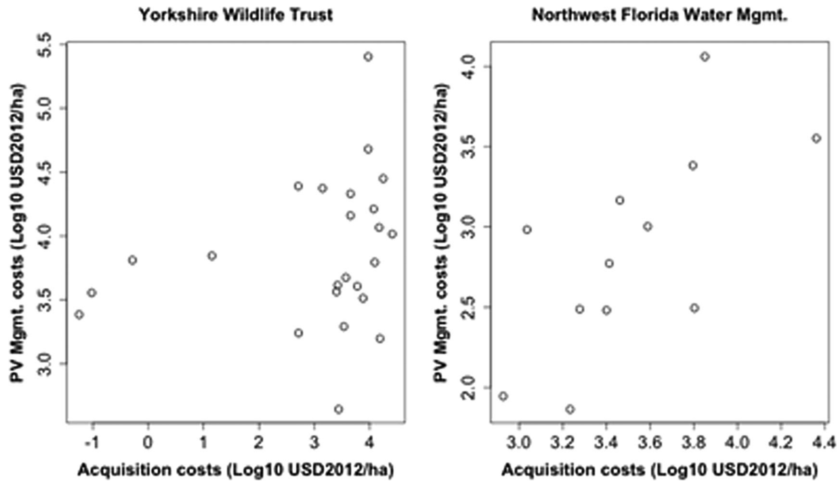

Figure 3. Comparison of acquisition costs of protected areas with the cost associated with managing these sites, which has been converted to a present value assuming a 5% discount rate. (A) Acquisition cost of areas protected by the Yorkshire Wildlife Trust, a regional land trust in the United Kingdom, and present value of management costs based on direct expenditures (e.g., supplies, equipment costs) on protected area management as well as paid staff time spent managing these sites.[56] (B) Acquisition cost of areas protected by the Northwest Florida Water Management District, a public agency, and the estimated cost of managing these sites, this time represented only by the present value of paid staff time.

acquisition costs are not correlated (Fig. 2A; Spearman's $r_s = 0.13$; $P > 0.05$; $n = 27$) whereas for the second the two are positively correlated (Fig. 2B; $r_s = 0.77$; $P < 0.01$; $n = 12$), suggesting generalities may be hard to come by.

Second, the spatial grain over which cost estimates are available is often much coarser than the spatial grain that the prioritization needs to respond to. Cost estimates that reflect averages taken over large grid cells, ecoregions, countries, or counties are all commonly used (Table 1), even though the prioritizations would ideally respond to cost variation at the scale over which conservation activities are applied (e.g., parcels or subparcels). Averaging of this type suppresses variance in cost data, something that can pose major problems for predicting the relative efficacy of different targeting strategies (Box 1; Fig. 1). Figure 4 illustrates a case where averaging could lead to suboptimal priorities being selected. Suppose a conservation organization is planning to pursue a protected-area strategy and is trying to decide in which of the two regions to work (R1 or R2). The figure shows hypothetical distributions of benefits and costs of protecting parcels in each region. Benefit–cost targeting that used average cost estimates only would prioritize R1. However, R2 contains many lower-cost parcels by dint of the greater variance in costs of parcels found there and likely would provide the more efficient choice. In essence, prioritization wants to respond to extreme values of b_i/c_i and estimates of mean b_i/c_i values unaccompanied by consideration of the variation around those means can be quite misleading.

In most applications, researchers seek to extrapolate from cost estimates made at a subset of locations to a much broader set of possible conservation projects (e.g., a gridded map). This extrapolation involves associating cost estimates, often through statistical regression, to other variables for which spatial data are more readily available (e.g., crop or livestock distributions, soil quality, or climate variables) and relying on spatial variation in those other variables to extrapolate (e.g., Moore *et al.*[23]). The accuracy of such out of sample prediction is rarely tested (but see Naidoo and Adamowicz[39] for an example). When extrapolating like this, researchers routinely use only the predicted values from the regressions and discard any uncertainty surrounding these predictions. This will tend to have a smoothing effect on cost estimates. Given the importance of preserving variability, arguably a better approach would be to use regression coefficients in conjunction with any goodness of fit statistics (e.g., R^2 values). These could be used to simulate costs that retain the degree of variability observed in the original data. The smoothing problem inherent in using

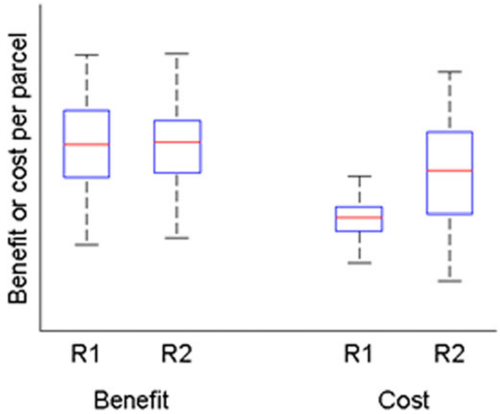

Figure 4. Hypothetical distribution of benefits and costs of protecting parcels in each of two regions (R1 and R2). In each region, the distribution of benefits offered by protecting different parcels is similar. Costs per parcel are lower on average in R1 and also have a lower variance. Costs in R2 are slightly higher on average and have a much greater variance between parcels available for protection.

only predicted values for costs may be worse than it first appears in some studies (e.g., Moore *et al.*[23] and Bode *et al.*[22]), because they rely upon fitting procedures that, because of their statistical design (see below), give inflated R^2 values.

Once cost estimates are available, these estimates are combined with data on the biological benefits of prioritization (Box 1). The way this integration is performed can also influence conclusions one would draw about the role of costs in conservation planning. For example, Jantke *et al.*[31] and Sutton *et al.*[63] show how conclusions about the relative efficacy of benefit–cost, benefit-only and cost-only targeting change when using benefit and cost data collected over different spatial grains and involving differing amounts of spatial averaging, as is common (Table 1).

Assumptions underlying cost estimation

There are unstated assumptions that underpin all of these estimation methods that also warrant scrutiny. I highlight three.

Constant marginal costs

First, Eq. (1) and many estimation approaches assume that costs of conservation activities at a particular location do not depend on the amount of conservation activity being undertaken there (constant marginal costs). However, if we consider applications where the amount of conservation activity at a location can be varied (e.g., number of hectares purchased in a county), there are obvious circumstances that could cause the cost of each unit of conservation activity to depend on the overall amount of activity. This would require replacing the constraint in Eq. (1) with a slightly more complicated form:

$$\sum c_i(x_i)x_i \leq C, \qquad (3)$$

where the function $c_i(x_i)$ reflects the dependency of each unit of conservation cost on the amount of conservation activity undertaken at location i.

In some circumstances, we would expect c_i to be increasing in x_i (a diseconomy of scale). This could happen, for example, if a conservation organization exhausted the lowest-cost opportunities for conservation in a location first. As more conservation effort is expended in that place, the cost per unit conservation gain would rise.

Alternatively, sometimes the cost per unit conservation activity at a location may be decreasing with the amount of activity undertaken (an economy of scale). For example, management costs of protected areas may show economies of scale if staff managing larger sites are able to specialize in particular activities or to share in equipment more efficiently than managers responsible for smaller protected areas can, or if ecological processes on larger sites differ in a way that enables more cost-effective management techniques to be employed. Unfortunately, the statistics typically used to test this possibility are prone to inflated type 1 errors. The typical procedure has been to estimate the cost of managing individual protected areas, to divide by site area to obtain a management cost per hectare, and then to regress this against site area itself.[23,27,57,58,64–66] This statistical approach (regressing Y/X against X) is prone to detecting spurious correlations and giving inflated R^2 values.[67] That being said, economies of scale have still been found in management costs of protected areas when employing alternative statistical approaches that avoid these problems.[56]

Figure 5 presents a stylized illustration of how the presence of economies of scale in costs of conservation can change conservation planning outcomes. When there are economies of scale with site area, larger protected areas are optimal, as represented by the chosen grid squares being more clustered in Figure 5A (clustering coefficient $\kappa = 0.82$) than 5B

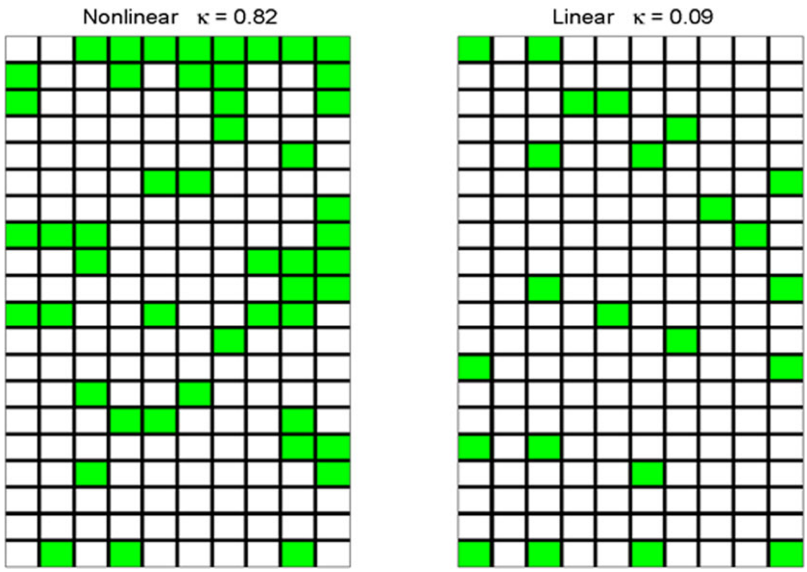

Figure 5. Illustration of how accounting for economies of scale in conservation costs can change conservation planning outcomes. The figure shows show optimal combinations of sites for protection (shaded cells) when costs of protected areas show economies of scale with protected area size (left) and where they do not (right) from 200 equal-area grid squares. Each square is associated with a randomly generated ecological community drawn from a species pool of 400 species and a randomly generated baseline cost. A branch and bound solver was used to identify the set of squares for protection that minimizes overall costs while ensuring that all 400 species occur on at least one protected square. In the left panel, protected area size is defined by protected squares that are touching (inc. diagonally).

($\kappa = 0.09$). By creating larger protected areas, the optimization is also able to reduce per-unit costs of conservation, allowing more area to be protected in the left panel at a lower total cost (83% of the cost of the areas protected in the right panel). Conversely, optimal sites will tend to be more dispersed when there are diseconomies of scale with site area.

Economies of scale and diseconomies of scale in conservation costs may also be present when looking across a whole network of protected areas. For example, if accounting for costs of traveling to sites to manage them,[68] then the cost per site will be lower if sites are clumped rather than dispersed. On the other hand, if seeking to acquire a large area of land in some region, conservation organizations may bid up the local land price by influencing overall levels of demand. This could increase costs they face on subsequent transactions.[30,69–71] More complicated interactions between conservation activities in one place and costs of conservation in another are also possible.[72] To account for economies or diseconomies of scale that arise across a network of protected areas like this, a yet more general form of the constraint in Eq. (1) is needed, one in which the cost per unit conservation activity at a particular site becomes a function of what other conservation activities are taking place on the landscape (i.e., function c_i becomes a function of the full vector of conservation activities x, $c_i(x)$, rather than just being a function of the value of x at site i as in Eq. (3)).

Uniqueness of site-specific cost estimates

A second major assumption behind efforts to estimate a cost of conservation efforts at location i is that there even exists a unique cost c_i to estimate. As noted above, for some conservation activities the cost per unit conservation effort may be a function of the amount of effort deployed. Moreover, when there are choices of conservation activities that could be pursued in each location, then the cost would be specific to a given activity–location pair.[21] For example, the cost of buying easements can be quite different from the cost of acquiring sites under a fee-simple arrangement.[55] Here, I mean something more fundamental. Namely, most estimation approaches still assume that, given an amount of conservation effort to be invested in a particular activity–location pair, there exists a unique cost per unit conservation effort.

However, when it comes to acquisition costs, there may not be one unique value that is relevant. Instead, there can be an interval of possible acquisition costs for any given parcel, one bounded below by the current landowners' willingness to accept (WTA) the terms of an acquisition deal and one bounded above by the conservation organization's willingness to pay (WTP) to acquire the property.[49,72] A landowner's WTA will depend on their valuation of possible alternative uses of the land and the transaction costs they would face to get an agreement in place. The conservation organization's WTP is determined by their overall budget and the availability of substitute sites for achieving their conservation goals. Any price agreed to in the interval (landowners WTA, conservation organization's WTP) would, in principle, allow an acquisition to go forward. The size of the interval is a measure of the surplus available to the two parties from the transaction. Estimates of acquisition costs based on the value of land for agriculture discussed above are based on an approximation of one part of a landowners' WTA (market value of one alternative land use). These estimation methods assume that all surplus available from the transaction goes to the conservation organization. The implicit assumption that the landowner will receive no surplus seems rather hopeful for most contexts. Instead, where we end up in the interval (landowners WTA, conservation organization's WTP) depends on the bargaining power of each party and the negotiation strategy each follows. As such, we might expect costs to be quite different for conservation acquisitions pursued piecemeal on an individual-buyer-and-seller basis, as conducted by many land trusts, from those faced in large government acquisition programs conducted on a one-buyer, many-sellers basis, where auctions and other contract allocation mechanisms are possible.[72,73]

Unlike acquisition costs, in theory at least, a unique management cost can be estimated. Once a conservation organization identifies its conservation objectives for a site, various studies have sought to identify an optimal management strategy for achieving that objective (e.g., Richards *et al.*[74] and Drechsler *et al.*[75]). This strategy can then be associated with a unique, lowest-cost estimate. If seeking to apply such ideas when estimating costs, however, one would likely come unstuck because the vagaries of conservation practice tend not to align to the tightly specified requirements of theoretical optimal management problems. Instead, site management objectives may only be specified in vague, nonquantitative terms (e.g., "preserve intact forest"). In such circumstances, the actual allocation of management effort by a conservation organization arguably provides the most reliable indicator of just what the organization's conservation objectives are for a site. For example, Armsworth *et al.*,[56] in discussing this point, considered the case of a peat bog restoration, where a conservation group chose to spend large sums to restore the site quickly (3–5 years) in the least intrusive way possible (removing felled trees by helicopter). An alternative strategy that other organizations might have favored would have been to use a much less costly approach (issuing a commercial timber license for the property), but one that would only deliver on conservation goals after 10–20 years, because of resulting disturbance to the site.

Heterogeneity in scope for cost sharing

A third assumption in most studies testing the effect of accounting for costs on prioritizations is that spatial variation in opportunities for cost sharing can be ignored. However, conservation organizations often partner with one another to share the costs associated with acquiring a particular parcel of land.[13,76] They also commonly share the ongoing management burden associated with protecting sites once acquired by partnering with each other and by drawing on volunteer labor from local communities. Indeed, conservation planning handbooks commonly recommend that practitioners scope opportunities for leveraging against actions of others and partnering with them to help meet costs of protecting sites when prioritizing activities.[12,13]

Importantly, scope for cost sharing may itself be spatially variable. For example, in Armsworth *et al.*,[77] we estimated that conservation volunteers provided labor worth, on average, 36% of the overall management cost of protecting sites to Yorkshire Wildlife Trust. Moreover, the availability of volunteer labor to support management activities varied systematically across protected areas in a way that could be reflected when prioritizing future sites for protection. Protected areas that were larger, that had been protected for longer, and that were near areas of increased population density attracted more volunteer labor.[77]

To date, there have been relatively few efforts to incorporate spatially variable scope for cost sharing into spatial prioritizations (but see Ando and Shah[78] for relevant theory). In one recent example, Kroetz *et al.*[79] examined how the recommendations from a conservation planning exercise across the conterminous United States, as might be conducted by a land trust or federal agency working nationally, changed when factoring in possible cost sharing contributions from local communities. These cost-sharing contributions were assumed to be funded through local (county level) ballot initiatives to protect open space. In that study, we found that the potential cost savings available through partnering with local initiatives in this way could be as great as 45% of the overall cost of protecting a fixed number of species nationally. Importantly, we found that the set of priorities that a national-scale planner would identify shifted when accounting for the spatially heterogeneous scope for cost-sharing contributions.

Conclusions

The importance of accounting for costs in conservation planning is increasingly accepted. As such, it is time that we approach the issue of how to estimate and include costs more critically. I suggest the following recommendations based on a review of current ways spatial planning studies try to account for the costs that a conservation organization faces when setting up and managing terrestrial protected areas.

Better estimation of conservation costs

When it comes to estimating conservation costs, conservation planning efforts would benefit from a much clearer focus on the actual costs that conservation organizations face. When estimating costs of land acquisition, we need a greater focus on the cost of lands acquired for conservation. Proxy measures for acquisition costs based on average agricultural land values nearby appear to be of limited relevance, at least when estimating the costs of many protected area programs. Similarly, when it comes to estimating management costs involved in protecting sites, researchers would be well served by focusing on actual expenditures made by conservation groups, instead of focusing on hypothetical spending. When focal questions demand hypothetical cost surveys, then researchers could draw more heavily on stated preference techniques in economics.

Better reporting of data being used in prioritization studies

Conservation planning studies would benefit from more complete reporting of their cost estimates. Minimally, authors should be clear about just what estimates they use and what they claim these estimates represent about conservation costs; what units costs are presented in; and what spatial patterns they show, especially regarding the relative variation in and covariation between costs and benefits.

Better analysis/processing of those data

Once estimates of conservation costs have been obtained, researchers need to take more care over how these data are treated to prepare them for inclusion in spatial prioritization analyses. In particular, it is important that the variation in the cost data themselves and also the patterns of covariation between benefits and cost be preserved. Common techniques that involve including some cost components only; averaging estimates to larger spatial grains without considering the variance involved; relying on poorly specified structural models in regression analyses of cost data; and extrapolating from a small number of sample points using predicted values but no goodness-of-fit statistics and no out-of-sample validation tests all put these required data characteristics in jeopardy.

Greater criticality with underlying assumptions

Finally, conservation planning researchers need to pay more attention to the assumptions that they make about costs. These should be stated and their appropriateness for the context at hand should be evaluated critically. Some common assumptions that I have highlighted that seem questionable are that management and acquisition costs of protected areas are characterized by constant marginal costs both at the scale of individual sites and across networks of protected areas; that conservation groups can buy land at a landowner's WTA and therefore gain all of the available surplus from the transaction; and that scope for cost sharing on conservation activities can safely be assumed spatially homogeneous and ignored.

Some of these recommendations can be implemented using the sort of cost data that are already available. But ultimately, obtaining better estimates of conservation costs will be important, and, as with other factors that inform a conservation plan, the cost of collating better cost data must itself be evaluated. This raises important questions about just how good a job we need to do with cost estimation to identify effective priorities and suggests a number of fruitful avenues for future conservation cost research. Specifically, we would benefit from a greater focus on:

1. **Mechanistic ecological-economic models** that jointly predict conservation costs, land use, and the biodiversity and ecosystem services benefits available from protecting particular sites.
2. **Parameterization schemes that transfer characteristics of cost data between scales of analysis**. Development of process-based understanding of conservation costs will usually require working at the smaller spatial extents and finer spatial grains evident among cost studies in Table 1. But the results of this mechanistic work need to be scaled up in some way to inform larger-scale planning efforts (top half of Table 1). Parameterization schemes that allow costs to be scaled up, but in ways that retain variation and covariation in cost data, are likely to become important; see Holzkamper and Seppelt[80] for a promising beginning.
3. **Greater sensitivity testing.** Despite the proliferation of conservation planning studies accounting for costs, we still have relatively few studies that test how sensitive prioritization outcomes are to uncertainty in cost data, the way those data are treated and what happens if particular theoretical assumptions do not hold (but see Carwardine *et al.*[40] for an example).

More generally, the conservation planning community likely has to accept that costs of conservation are context dependent. Conservation costs are bound up tightly in what organization will be implementing the resulting conservation strategy, how they work on the landscape, and what their goals are for a particular prioritization exercise. As such, studies that coopt existing cost datasets originally built to inform other kinds of conservation programs (compare Lubowski *et al.*[37] and Withey *et al.*[36]) or for analyses on very different extents and grains (e.g., see the exchange between Bode *et al.*[81] and Kremen *et al.*[82]) will always suffer from limitations. Similarly, how much detail we need to know about conservation costs to arrive at effective prioritizations is also likely context dependent. For example, in implementing a conservation plan, there is commonly a transition from regional plan to local actions.[83] Choices over local actions might concern just which parcel to acquire from among a set of four or five that are available within some target region identified by a larger-scale conservation plan. As has been found in other applications of conservation planning,[60,84,85] we might expect that these rankings of smaller numbers of choices will be more robust to uncertainty in the underlying data than will absolute benefit–cost ratios. However, in the specific context of acquiring parcels for protection, this thinning in the choice set can introduce other issues and concerns (see Lennox *et al.*[49] and Lennox and Armsworth[72]).

The title of this review indicates that current methods for accounting for costs in conservation planning depend on limited data and hopeful assumptions. Arguably, of course, we are always working with limited datasets and hopeful assumptions in conservation. For example, the approaches most conservation planning analyses take to reflecting spatial variation in the available biodiversity benefits of conservation actions also depend on limited data and hopeful assumptions. The difference is that conservation scientists have a longer history of examining and debating the relative merits of different assumptions and data limitations relevant to biodiversity data. In contrast, to date, assumptions about conservation costs have not been given due scrutiny. It is time for that to change.

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Appendix

To evidence claims about trends in the literature concerning costs, I survey a representative sample of relevant papers in Table 1. For transparency, I detail below the processes used to arrive at the particular choice of papers. First, I searched titles, abstracts and keywords of articles (as opposed to reviews, editorials, etc.) on ISI Web of Knowledge (accessed October 7, 2013) published in the past 10 years using the following search terms:

<cost OR costs>
AND <conserv* OR protect* OR preserv*>
AND <priorit* OR plan OR plans OR planning>
AND <population* OR communit* OR species OR habitat* OR ecosystem* OR biodiversity OR ecolo*>

This provided an initial list of 1577 papers, which I sorted by relevance. I examined the abstracts for the most relevant 400 papers to determine whether they reported a specific focus in their results on how conservation planning outcomes were affected by accounting for spatially heterogeneous costs of conservation. I identified those abstracts that I felt made the most explicit claims about this point, while also applying several additional filters. Specifically, I excluded papers that focused exclusively on marine conservation as well as those that included no empirical data on costs and that instead were purely theoretical in their treatment of costs. I also favored papers that focused on protected area strategies over those that focused primarily on agrienvironment schemes, payments-for-ecosystem services programs, etc.

When a study drew on cost data from another source and did not itself provide the information for the fields shown in the table, I referred to the original references. In some instances, I also went back to the original authors to ask for additional details or clarification.

Many studies that I attributed in the table as focusing on acquisition costs claimed to examine opportunity costs of conservation. However, the cost measures these studies relied upon (e.g., estimates of the net present value of forgone rent from agricultural production) are captured in market prices for land and represent the upfront cost of acquiring the site for protection. Opportunity costs are more general than this. Were someone to estimate opportunity costs of conservation, they would also need to account for costs of managing any areas acquired as well as other social costs or benefits resulting from land protection, which might require a nonmarket valuation approach. None of these studies takes these extra steps. Because they focus only on estimating the acquisition cost piece, I coded them as such in the table.

Where studies provided costs annually, I report these values in the table. However, to aid comparison, I also provide present-value equivalent amounts in parentheses. I assumed a 5% discount rate to do so. Similarly, in preparing Figures 2 and 3, I used the present value in place of the annual equivalent. Throughout, I sought to convert all costs to consistent units (USD 2012), but in a few of the papers, it remains unclear exactly which currency year authors are using.

Conflicts of interest

The author declares no conflicts of interest.

References

1. Margules, C.R. & R.L. Pressey. 2000. Systematic conservation planning. *Nature* **405:** 243–253.
2. Moilanen, A. *et al.* 2009. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools.* New York, NY: Oxford University Press. Pp. 320.
3. Wilson, K.A. *et al.* 2009. Setting conservation priorities. *Ann. N.Y. Acad. Sci.* **1162:** 237–264.
4. Spring, D.A. *et al.* 2007. Pre-emptive conservation versus “fire-fighting”: a decision theoretic approach. *Biol. Conserv.* **136:** 531–540.
5. Visconti, P. *et al.* 2010. Conservation planning with dynamic threats: the role of spatial design and priority setting for species’ persistence. *Biol. Conserv.* **143:** 756–767.
6. Eklund, J. *et al.* 2011. Governance factors in the identification of global conservation priorities for mammals. *Phil. Trans. R. Soc. B* **366:** 2661–2669.
7. Knight, A.T. *et al.* 2011. Engage the hodgepodge: management factors are essential when prioritizing areas for restoration and conservation action. *Div. Distrib.* **17:** 1234–1238.
8. Maron, M. *et al.* 2013. Calculating the benefit of conservation actions. *Conserv. Lett.* **6:** 359–367.
9. Gren, I.-M. *et al.* 2014. Cost-effective biodiversity restoration with uncertain growth in forest habitat quality. *J. Forest Econ.* **20:** 77–92.

10. Fishburn, I.S. *et al.* 2013. Tracking a shift from opportunistic to systematic patterns of conservation investment by a major land trust. *Biol. Conserv.* **161:** 223–229.
11. Groves, C.R. 2003. *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Washington, DC: Island Press.
12. The Nature Conservancy. 2003. *The Five-S Framework for Site Conservation: A Practitioner's Handbook for Site Conservation Planning and Measuring Conservation Success.* Arlington, VA: The Nature Conservancy.
13. Amundsen, O.M., III 2011. *Strategic Conservation Planning.* Washington, DC: Land Trust Alliance.
14. Margules, C.R. *et al.*1988. Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* **43:** 63–76.
15. Pressey, R.L. 2002. The first reserve selection algorithm—a retrospective on Jamie Kirkpatrick's 1983 paper. *Prog. Phys. Geogr.* **26:** 434–441.
16. Faith, D.P. *et al.* 1996. Integrating conservation and forestry production: exploring trade-offs between biodiversity and production in regional land-use assessment. *Forest Ecol. Manage.* **85:** 251–260.
17. Babcock, B.A. *et al.* 1997. Targeting tools for the purchase of environmental amenities. *Land Econ.* **73:** 325–339.
18. Ando, A.W. *et al.* 1998. Species distributions, land values and efficient conservation. *Science* **279:** 2126–2128.
19. Naidoo, R. *et al.* 2006. Integrating economic costs into conservation planning. *Trends Ecol. Evol.* **21:** 681–687.
20. Murdoch, W. *et al.* 2007. Maximizing return on investment in conservation. *Biol. Conserv.* **139:** 375–388.
21. Wilson, K.A. *et al.* 2007. Conserving biodiversity efficiently: what to do, where, and when. *PloS Biol.* **5:** e223.
22. Bode, M. *et al.* 2008. Cost effective conservation spending is robust to taxonomic group. *Proc. Natl. Acad. Sci. USA* **105:** 6498–6501.
23. Moore, J. *et al.* 2004. Integrating costs into conservation planning across Africa. *Biol. Conserv.* **117:** 343–350.
24. Carwardine, J. *et al.* 2008. Cost-effective priorities for global mammal conservation. *Proc. Natl. Acad. Sci. USA* **105:** 11446–11450.
25. Naidoo, R. & T. Iwamura. 2007. Global-scale mapping of economic benefits from agricultural lands: implications for conservation priorities. *Biol. Conserv.* **140:** 40–49.
26. Luck, G.W. *et al.* 2004. Alleviating spatial conflict between people and biodiversity. *Proc. Natl. Acad. Sci. USA* **101:** 182–186.
27. Balmford, A. *et al.* 2003. Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proc. Natl. Acad. Sci. USA* **100:** 1046–1050.
28. Carwardine, J. *et al.* 2008. Avoiding costly conservation mistakes: the importance of defining actions and costs in spatial priority setting. *PLoS One* **3:** e2586.
29. Hajkowicz, S.A. & Young M.D. 2002. *Value of Returns and Costs of Resource Degradation.* Canberra: Consulting report to the National Land and Water Resources Audit, CSIRO Land and Water Division.
30. Jantke, K. & U. Schneider. 2011. Integrating land market feedbacks into conservation planning – a mathematical programming approach. *Env. Model. Assess.* **16:** 227–238.
31. Jantke, K. *et al.* 2013. Benefits of earth observation data for conservation planning in the case of European wetland biodiversity. *Env. Conserv.* **40:** 37–47.
32. Lee, H.-L. *et al.* 2009. An integrated global land use data base for CGE analysis of climate policy options. In *Economic Analysis of LandUse in Global Climate Change Policy*. T.W. Hertel, S.K. Rose & R.S.J. Tol, Eds: 72–88. New York, NY: Routledge.
33. US Department of Agriculture [USDA] 2007. *2007 Census of Agriculture.* Washington DC: USDA National Agricultural Statistics Service.
34. Strange, N. *et al.* 2006. Using farmland prices to evaluate cost-efficiency of national versus regional reserve selection in Denmark. *Biol. Conserv.* **128:** 455–466.
35. Chiozza, F. *et al.* 2010. The opportunity cost of conserving amphibians and mammals in Uganda. *Natureza & Conservacao* **8:** 177–183.
36. Withey, J.C. *et al.* 2012. Maximising return on conservation investment in the conterminous USA. *Ecol. Lett.* **15**, 1249–1256.
37. Lubowski, R.N. *et al.* 2006. Land-use change and carbon sinks: econometric estimation of the carbon sequestration supply function. *J. Environ. Econ. Manage.* **51**, 135–152.
38. Adams, V.M. *et al.* 2010. Opportunity costs: who really pays for conservation? *Biol. Conserv.* **143:** 439–448.
39. Naidoo, R. & W.L. Adamowicz. 2006. Modeling opportunity costs of conservation in transitional landscapes. *Conserv. Biol.* **20:** 490–500.
40. Carwardine, J. *et al.* 2010. Conservation planning when costs are uncertain. *Conserv. Biol.* **24:** 1529–1537.
41. Polasky, S. *et al.* 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv.* **141:** 1505–1524.
42. Perhans, K. *et al.* 2008. Conservation goals and the relative importance of costs and benefits in reserve selection. *Conserv. Biol.* **22:** 1331–1339.
43. Richardson, E.A. *et al.* 2006. Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. *Conserv. Biol.* **20:** 1191–1202.
44. Ban, N.C. & C.J. Klein. 2009. Spatial socioeconomic data as a cost in systematic marine conservation planning. *Conserv. Lett.* **2:** 206–215.
45. Weeks, R. *et al.* 2010. Shortcuts for marine conservation planning: the effectiveness of socioeconomic data surrogates. *Biol. Conserv.* **143:** 1236–1244.
46. Klein, C.J. *et al.* 2013. Tradeoffs in marine reserve design: habitat condition, representation, and socioeconomic costs. *Conserv. Lett.* **6:** 324–332.
47. Ferraro, P.J. 2003. Assigning priority to environmental policy interventions in a heterogeneous world. *J. Policy Anal. Manage.* **22:** 27–43.
48. Newburn, D. *et al.* 2005. Economics and land-use change in prioritizing private land conservation. *Conserv. Biol.* **19:** 1411–1420.
49. Lennox, G.D. *et al.* 2012. Landowner's ability to leverage in negotiations over habitat conservation. *Theor. Ecol.* **5:** 115–128.

50. Brooks, T.M. *et al.* 2006. Global biodiversity conservation priorities. *Science* **313:** 58–61.
51. US Bureau of Labor Statistics. 2013. Consumer Price Index. December 2013. www.bls.gov/cpi.
52. Myers, N. *et al.* 2000. Biodiversity hotspots for conservation priorities. *Nature* **403:** 853–858.
53. Arponen, A. *et al.* 2012. Costs of integrating economics and conservation planning. *Conserv. Biol.* **24:** 1198–1204.
54. Kareiva, P. & M. Marvier. 2011. *Conservation Science: Balancing the Needs of People and Nature*. Greenwood Village, CO: Roberts and Company.
55. Davies, Z.G. *et al.* 2010. Temporal patterns in the size of conservation land transactions. *Conserv. Lett.* **3:** 29–37.
56. Armsworth, P.R. *et al.* 2011. Management costs for small protected areas and economies of scale in habitat conservation. *Biol. Conserv.* **141:** 423–429.
57. Ausden, M. & G.J.M. Hirons. 2002. Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. *Biol. Conserv.* **106:** 279–291.
58. Frazee, S.R. *et al.* 2003. Estimating the costs of conserving a biodiversity hotspot: a case study of the Cape Floristic Region, South Africa. *Biol. Conserv.* **112:** 275–290.
59. Laycock, H. *et al.* 2009. Evaluating the cost-effectiveness of conservation: the UK Biodiversity Action Plan. *Biol. Conserv.* **142:** 3120–3127.
60. Carwardine, J. *et al.* 2012. Prioritizing threat management for biodiversity conservation. *Cons. Lett.* **5:** 196–204.
61. Moro, M. *et al.* 2013. An investigation using the choice experiment method into options for reducing illegal bushmeat hunting in western Serengeti. *Conserv. Lett.* **6:** 37–45.
62. Bush, G. *et al.* 2013. Measuring the local costs of conservation: a provision point mechanism for eliciting willingness to accept conservation. *Land Econ.* **89:** 490–513.
63. Sutton, N. & P.R. Armsworth. Spatial grain of acquisition cost and biodiversity benefit data determines the apparent effectiveness of an opportunistic conservation strategy. *Conserv. Biol.* Submitted.
64. James, A.N. *et al.* 1999. *A Global Review of Protected Area Budgets and Staff*. Cambridge, UK: WCMC—World Conservation Press.
65. Ausden, M. 2007. *Habitat Management for Conservation: A Handbook of Techniques*. Oxford, UK: Oxford University Press.
66. Strange, N. *et al.* 2007. Value for money: protecting endangered species on Danish heathland. *Env. Manage.* **40:** 761–774.
67. Brett, M.T. 2004. When is a correlation between non-independent variables "spurious"? *Oikos* **105:** 647–656
68. Dumoulin, C. *et al.* Locating human resources to reduce the cost of managing networks of protected areas. *Conserv. Lett.* Submitted.
69. Armsworth, P.R. *et al.* 2006. Land market feedbacks can undermine biodiversity conservation. *Proc. Natl. Acad. Sci. USA* **103:** 5403–5408.
70. Dissanayake, S.T.M. & H. Onal. 2011. Amenity driven price effects and conservation reserve site selection: a dynamic linear programming approach. *Ecol. Econ.* **70:** 2225–2235.
71. Toth, S.F. *et al.* 2011. Dynamic reserve selection: optimal land retention with land-price feedbacks. *Oper. Res.* **59:** 1059–1078.
72. Lennox, G.D. & P.R. Armsworth. 2013. The ability of landowners and their cooperatives to gain surplus from conservation contracts: worst-case scenarios, auctions and conservation objectives. *Conserv. Biol.* **27:** 625–634.
73. Latacz-Lohmann, U. & S. Schilizzi. 2005. *Auctions for conservation contracts: a review of the theoretical and empirical literature*. Edinburgh: Scottish Executive Environment and Rural Affairs Department.
74. Richards, S.A. *et al.* 1999. Optimal fire management for maintaining community diversity. *Ecol. Appl.* **9:** 880–892.
75. Drechsler, M. *et al.* 2009. Conservation planning for successional landscapes. *Ecol. Model* **220:** 438–450.
76. Sutter, R. *et al.* 2009. Evaluating the conservation outcomes of the International Paper Forest Acquisition Project: year 2 monitoring report. The Nature Conservancy, Southern Resource Office.
77. Armsworth, P.R. *et al.* 2013. Opportunities for cost-sharing in conservation: variation in volunteering effort across protected areas. *PLoS One*, **8:** e55395.
78. Ando, A.W. & P. Shah. 2010. Demand-side factors in optimal land conservation choice. *Resource Energy Econ.* **32:** 203–221.
79. Kroetz, K. *et al.* 2014. Benefits of the ballot box for species conservation. *Ecology Lett.*, in press.
80. Holzkamper, A. & R. Seppelt. 2007. Evaluating cost-effectiveness of conservation management actions in an agricultural landscape on a regional scale. *Biol. Conserv.* **136:** 117–127.
81. Bode, M., J. Watson, T. Iwamura & H.P. Possingham. 2008. The cost of conservation. *Science* **321:** 340.
82. Kremen, C. *et al.* 2008. The cost of conservation: response. *Science* **321:** 341–342.
83. Pressey, R.L. *et al.* 2013. The plan of the day: managing the dynamic transition from regional conservation designs to local conservation actions. *Biol. Conserv.* **166:** 155–169.
84. Fuller, M.M. *et al.* 2008. Testing the robustness of management decisions to uncertainty: Everglades restoration scenarios. *Ecol. Appl.* **18:** 711–723.
85. Armsworth, P.R. *et al.* 2012. The cost of policy simplification in conservation incentive programs. *Ecol. Lett.* **15:** 406–414.