A reliance on agricultural land values in conservation planning alters the spatial distribution of priorities and overestimates the acquisition costs of protected areas.

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Highlights:

- Agricultural land values are often used to approximate the costs of protected areas.
- We examine when this proxy is inaccurate and what that implies for conservation plans.
- The accuracy of the proxy varies with the spatial grain of the comparison being made.
- Using agricultural land values overestimates the cost of meeting conservation targets.
- Using agricultural land values alters the distribution of conservation priorities.

Abstract

A common focus for conservation planning is to identify locations for siting potential protected areas, something that requires estimates for the costs of setting up these areas and benefits for biodiversity of doing so. When cost data are not available over relevant scales, conservation planners commonly rely on proxy data that they hope will estimate conservation costs. Here, we assessed how accurately agricultural land values, a commonly used proxy for cost data in conservation planning, estimates the actual acquisition costs of protected areas, focusing on a case study from the central and southern Appalachians. We compared plans based on cost estimates derived from different sources and that involved different levels of spatial aggregation to understand how a reliance on these estimates would impact conservation planning. We found the average agricultural land value in a county did not accurately predict the acquisition costs of protected areas in that county. This lack of accuracy was a result of choosing agricultural land values as a proxy for acquisition costs, and not spatial averaging. A reliance on agricultural land values risks diverting limited funds for establishing protected areas away from parcels that offer the greatest return-on-investment. It would also lead a conservation organization to overestimate the budget needed to protect a given number of species. Our findings highlight the importance of incorporating data on how much protected areas actually cost in future conservation planning studies.

1. Introduction

Many conservation organizations purchase and set aside land to stem the loss of biodiversity, but are limited in the opportunities they can pursue by budget constraints. In response, they have developed planning tools and guidance to help identify opportunities that offer the greatest return-on-investment (ROI) given spatially explicit estimates of the costs and benefits of protected areas (Amundsen, 2011). This regional planning improves an organization's ability to place a given conservation opportunity in a landscape context (Groves et al., 2002). Given the tradeoff between the spatial extent and grain, or resolution of available cost data (Tobler, 1988), conservation planning studies have generally relied on aggregated cost estimates to prioritize areas for protection (Armsworth, 2014). Our goal in this study is to understand the type, direction, magnitude, and consequences of estimation errors associated with one type of relevant data, conservation costs (Langford et al., 2009).

Conservation planning studies have generally reached a consensus that socioeconomic dimensions of land protection such as economic costs (Naidoo et al., 2006), landowner willingness to sell (Knight et al., 2011), and even access to greenspace (Miller and Hobbs, 2002) should be factored into the planning process along with other biological objectives (but for a contrasting perspective see Arponen et al., 2010). However, while parcel-level cost estimates may be available within individual municipalities, it can be difficult to collect such fine-grain information across the entire spatial extent of a regional conservation plan (but see Polasky et al., 2008; Torrubia et al., 2014 for examples). As a consequence, conservation planners often estimate costs of protected areas based on costs for other land uses or data on drivers of land use change, such as average agricultural land values (e.g. Ando, 1998; Ando and Mallory, 2012; Chiozza et al., 2010; Jantke and Schneider, 2010; Jantke et al., 2013; Di Minin et al. 2013; Murdoch et al., 2007; Strange et al., 2006; Withey et al., 2012), average agricultural yields (Carwardine et al., 2008; Naidoo and Iwamura, 2007; Wilson et al., 2011), the value of standing timber (Perhans et al. 2008; Polasky et al., 2008), gross domestic product (Eklund et al., 2011), or human population density (Luck et al., 2003; Williams et al., 2003).

Moreover, the cost estimates used in conservation planning studies are often spatially aggregated, or averaged within an areal unit such as municipalities. Spatial aggregation has been shown to affect the accuracy of biodiversity data used in conservation planning (Hess et al., 2006; Hurlbert and Jetz, 2007; Rahbek, 2004; Seo et al., 2009) as well as the locations identified as conservation priorities (Arponen et al. 2012; Hermoso and Kennard, 2012; Mills et al., 2010; Shriner et al., 2006; Warman et al., 2004). However, similar issues resulting from the reliance on spatially aggregated cost estimates have received less attention (but see Jantke et al., 2013; Richardson et al., 2006; Sutton & Armsworth, 2014).

In this study we examine how accurately the *ex post* costs of designating protected areas as a land use are predicted by spatially averaged cost estimates derived from an agricultural land use (Fig. 1 – scenario 1). If average agricultural land values do not reliably predict variation in acquisition costs of individual protected areas, this could be due to spatial averaging (Fig. 1 – scenarios 2a and 2b) or to relying on costs based on an alternative land use, in this case being agriculture (Fig. 1 – scenarios 3a and 3b). To distinguish between these possibilities, we quantify the accuracy of cost estimates in five different combinations of data sources and levels of spatial aggregation. However, more important than the accuracy of the estimates given by the proxies per se are the potential consequences for the efficacy of conservation plans. Therefore, we also compare the performance of hypothetical conservation plans based on a subset of the most salient data scenarios (Fig. 1 – scenarios 1, 2b, and 3b).

Figure 1. We compared how accurately three different cost estimates compared to the acquisition costs of protected areas in a case study of recent transactions made by The Nature Conservancy. These estimates were created in two levels of spatial aggregation (rows) and sources of land values (columns).

Among wider writings on the effects of accounting for costs in spatial conservation planning (Carwardine et al., 2008; Murdoch et al., 2007; Naidoo and Iwamura, 2007; Withey et al., 2012), the most immediately relevant precursors to our work include two studies that examined the effect of spatial aggregation of cost estimates on conservation plans (Jantke et al., 2013; Sutton and Armsworth, 2014). However, the present study appears to be the first attempt to partition whether conservation plans are affected more by choosing a poor proxy for costs of establishing protected areas or by relying on data that have been spatially aggregated to a coarser resolution than actual conservation measures.

2. Methods

2.1 Choice of case study and cost data

As a case study, we focus on a set of recent transactions made by a conservation nonprofit between 2000 and 2009 to protect hardwood forests within three contiguous ecoregions in the Eastern US (Fig. A1). The Nature Conservancy (TNC) is the largest of the land trusts working in the United States with over \$5.4 billion in assets and \$950 million in annual revenue (Armsworth et al., 2012; TNC, 2013). Despite this size, their acquisition costs have previously been shown to be comparable to smaller regional land trusts (Armsworth, 2014). Here our goal to understand how common *ex ante* cost estimates available during the planning stage, such as values derived from other land uses, differ from the *ex post* costs of acquiring land for biodiversity protection. Then, we break down if this disparity between a cost estimate and cost data is a result of the choice of cost estimate or simply the level of spatial aggregation in that cost estimate.

TNC provided data on the actual acquisition cost they paid to protect each parcel of land as well as the cadastral boundaries (Fig 1 – top right). The property rights of these parcels were all acquired outright under a fee simple arrangement (as opposed to a more limited purchase through conservation easements or other means – see Rissman et al., 2007). We excluded parcels that were donated to TNC, for which agricultural land values would clearly offer a poor estimate of acquisition costs. These exclusions reduced our original sample of 183 parcels to a subset of 96 parcels in 26 counties (mean=2.76, sd=2.41, range=[2-12]). We only included the amount TNC actually paid to acquire each parcel, as we did not expect any associated fees or stewardship endowment with a transaction to be reflected by agricultural land values. All costs were calculated in 2005 U.S. dollars using the consumer price index (BLS, 2013).

2.2 Estimates used to approximate the acquisition costs of protected areas

We focused on agricultural land values, as opposed to values derived from other land uses, because these data have been frequently used as an estimate in prominent conservation planning studies (Armsworth 2014). In particular, we designed our study to distinguish how a reliance on either average or agricultural land values impacted conservation planning. To make the relevant comparisons, we assembled three sets of cost estimates. First, we spatially aggregated the actual acquisition costs of protected areas in each county (Fig. 1 – bottom right). This allowed us to assess how spatial aggregation alone affected resulting conservation plans. To ensure this spatially aggregated cost estimate would be different than our cost data, we excluded counties from our study area where TNC only acquired one protected area.

To evaluate the consequences of relying on agricultural land values as an estimate for the acquisition costs of protected areas, we assembled two additional cost estimates at the same levels of spatial aggregation (the parcel scale and the county scale). Average agricultural land values are available within each county in our study area from the US Department of Agriculture

(NASS, 2007). These data were based on landowners' estimates from the agricultural census, and were spatially aggregated within counties to ensure confidentiality (Fig. 1 – bottom left). We also obtained fine-grain agricultural land values by focusing on sales data from county courthouse records and other sources (Fig. 1 – top left). These fine-grain agricultural land values were available for a subset of 26 counties in our study area. We defined agricultural parcels in these counties by an intersection with an agricultural land use from the National Land Cover Database (Fry et al., 2011). The number of transactions in this dataset was much larger ($n=98\,000$) than the number of parcels TNC acquired to establish protected areas ($n=96$). To account for this difference in sample size, we used 1000 bootstrap replicates to compare a subset of transactions that took place in the same each county and year as a TNC parcel. Within each bootstrap replicate, agricultural parcels were sampled without replacement.

2.3 Metrics of accuracy

We chose to define the accuracy of a cost estimate based on mean square error, or MSE, following Bainbridge (1985; but see Walther and Moore, 2005 for other estimators). Nash-Sutcliffe efficiency is a normalization of MSE that has historically been used in other fields to calibrate models with observed data (Nash and Sutcliffe, 1970). We used a related normalization, Kling-Gupta efficiency (KGE), to break down MSE into three components: variability, bias, and correlation (Gupta et al., 2009). We considered a cost estimate to be accurate if it had a similar amount variability, low bias, and high correlation with our cost data.

The components of the KGE index are additive and depend on α , the ratio of estimated to observed standard deviations, β , the ratio of estimated to observed means, and r , the Pearson product-moment correlation coefficient. Following Gupta et al.'s derivation (2009):

$$\text{KGE} = 1 - \sqrt{(\alpha - 1)^2 + (\beta - 1)^2 + (r - 1)^2} \quad (1)$$

where $\alpha = \sigma_{\text{estimate}} / \sigma_{\text{actual}}$, and $\beta = \mu_{\text{estimate}} / \mu_{\text{actual}}$

Under this framework, we ascribed the relative contribution of each component (g_i) to MSE in terms of a percentage as:

$$g_i = G_i / \sum_i G_i \quad (2)$$

where $G_1 = (\alpha - 1)^2$, $G_2 = (\beta - 1)^2$, and $G_3 = (r - 1)^2$

The KGE index ranges from negative infinity (no accuracy) to 1, (perfect accuracy). In practice, the maximum KGE index of our cost estimates is equal to r .

2.4 Biodiversity data

TNC has set quantitative goals within each ecoregion to ensure the long-term survival for each species and natural community that was identified as a conservation target (Kareiva et al., 2014). We represented biodiversity benefits of protected areas with survey records of 95 species that were published as conservation targets within the ecoregional plans in our study area (TNC, 2010; for a full list see SI). We downloaded survey records for these species from the publicly available Biodiversity Information Serving Our Nation database (USGS, 2013). These biodiversity data only represent species presences, and were not systematically sampled across the landscape (Rondinini et al. 2006), an issue that we return to in the Discussion. We excluded fossil records and those without a known type. We aggregated these records within equal area 5 km buffers to mimic the separation protocol used to convert raw survey data into more meaningful element occurrences (Hammerson and Nichols, 2009).

2.5 Conservation objectives

We made a number of simplifying assumptions to link protected area establishment to species persistence. Then, we compared the performance of hypothetical conservation plans based on different sets of cost estimates. We defined the performance of these plans firstly by their selected parcels' contribution to regional persistence when accounting for species complementarity (Margules and Pressey, 2000). Then we examined whether the sets of locations that would be prioritized for acquisition were similar when using two different cost estimates. To represent the similarity of two sets of locations being prioritized, we used the Jaccard index of similarity (Real et al., 1996).

Let i denote a set of species and j a set of parcels that could be acquired to establish a protected area. We assumed the local probability of persistence of a species near a given parcel (Ω_{ij}) scaled linearly with the area under protection (a_j). Specifically, we weighted each presence ($\Phi_{ij}=1$) of a species in a buffer by the size of the protected parcel divided by the maximum possible area (the area of the entire 5 km buffer, a_T) around each parcel's centroid:

$$\text{local persistence} = \text{species presence or absence} \cdot \text{diag}(\text{area}_{\text{parcel}} / \text{area}_{\text{buffer}}) \quad (3)$$

$$\Omega_{ij} = \Phi_{ij} \cdot \text{diag}(a_j / a_T)$$

where diag transforms a vector into a $j \times j$ diagonal matrix.

Our regional persistence objective combined these local persistence probabilities into a single metric by reducing the value of repeat occurrences of the same species across a set of protected parcels (Polasky et al., 2000), and this objective is a specific implementation of the concept of complementarity in conservation planning (Margules and Pressey, 2000) because the value of protecting a given parcel depends on which other parcels are also chosen for protection). Let x_j equal 1 if parcel j has been selected for protection and 0 otherwise. By assuming these local persistence probabilities (Ω_{ij}) were independent across species and parcels, we were able to model the regional persistence of a given species (p_i) as one minus the probability that a species did not persist in a buffer of any of the parcels selected for protection:

$$\begin{aligned} \text{regional persistence} &= 1 - \prod_{\text{parcels}} [1 - \text{local persistence} \cdot \text{diag}(\text{protected parcels})] \\ p_i &= 1 - \prod_j [1 - \Omega_{ij} \cdot \text{diag}(x_j)] \end{aligned} \quad (4)$$

where diag transforms a vector into a $j \times j$ diagonal matrix.

2.6 Hypothetical conservation plans

We focused on a hypothetical conservation planning problem in which we examined what parcels TNC should have prioritized had they faced a more restrictive budget constraint. Specifically, we assumed that the set of parcels that were actually protected defined the set of candidate sites for each hypothetical conservation plan. We compared the conservation plans that would be obtained when relying on perfect information about a parcel's actual acquisition cost, and when relying on three estimates for these costs. We evaluated the performance of each plan performance ex ante, or based on the data available at the time.

The goal of our hypothetical conservation plans was to pick a set of parcels (x_j) that had the greatest summed regional persistence (p_i):

$$\begin{aligned} \max_{\text{parcels}} \sum_{\text{species}} \text{regional persistence} & \quad \text{subject to} \quad \sum_{\text{parcels}} \text{parcel cost} \cdot \text{protected parcels} \leq \text{budget} \\ \max_x \sum_i p_i & \quad \text{subject to} \quad \sum_j c_j \cdot x_j \leq b \end{aligned} \quad (5)$$

We used an evolutionary algorithm implemented by the *rgeoud* package in R to find a near-optimal solution to this non-linear integer programming problem (Mebane and Berkeley, 2011). For each scenario and budget level we performed 100 replicate simulations and checked for

convergence based on no significant improvement in the objective function of the population after five generations. All cost estimates were calculated on a per-hectare basis and then multiplied by the size of each parcel to create a consistent cost vector for each scenario (c_j).

We maintained consistent constraints (b) across scenarios by defining a single maximum budget and then creating hypothetical plans across 2% budget intervals. To summarize these outcomes, we reported the average change between scenarios across all budget sizes [2-100%]. When graphing the results, we only show how the difference in these measures changes as we varied our budget constraint up to 30%, as we expected the scenarios to converge with less restrictive budget constraints.

2.7 Hypotheses

We first compared the average agricultural land value in a county to the acquisition costs of individual protected areas within that county (Fig. 1 – scenario 1). We hypothesized the limited accuracy of this comparison could be caused by a different amount of variability, large bias, and a weak correlation between the cost data and cost estimate. Moreover, we hypothesized this lack of accuracy would affect both the budget and spatial distribution of priorities of our hypothetical conservation plans.

If the average agricultural land value within a county did not reliably predict the acquisition costs individual protected areas within that county, they could still be useful in conservation planning operating over a coarser resolution (Fig. 1 – scenario 3b). For example, large-scale planning is often intended to identify priority counties within which to work but not yet the specific parcels to acquire (e.g. the ‘plan of the day’ per Pressey et. al 2013). To test this possibility, we compared how the average agricultural land value in a county compared to the average acquisition cost of protected areas in that county. We hypothesized average agricultural land values would have a similar amount of relative variability as the average acquisition costs of protected areas, but also have a large bias and weak correlation. We expected the substitution of average agricultural land values for the average acquisition costs of protected areas would affect both the estimated budget and spatial distribution of priorities of our hypothetical conservation plans.

Scenarios 1 and 3b compare across land use types, but we also wanted to separate out the effects of spatial aggregation in isolation. Therefore, we compared how the average acquisition costs of protected areas in a county compared to the individual acquisition costs of those protected areas (Fig. 1 – scenario 2b). We hypothesized this aggregated cost estimate would have reduced variability relative to the actual cost data. However, we also expected spatial aggregation to not affect the bias or correlation of our cost estimate. We did not expect this substitution would substantially alter the estimated budget or spatial distribution of priorities of our hypothetical conservation plans.

3. Results

3.1 How accurately do average agricultural land values represent actual acquisition costs?

Average agricultural land values in a county did not reliably predict the acquisition costs of protected areas in that county ($KGE=0.189$). This was largely due a decreased amount of variation of agricultural land values (52.4%, $\alpha=0.413$) as well as there being only a moderate correlation between average agricultural land values and the acquisition costs of protected areas (52.4%, $r=0.442$). Contrary to our initial expectations, this loss of accuracy was not attributable to bias (0.3%, $\beta=1.042$).

3.2 *How is the accuracy of the prediction affected by the spatial grain of the comparison?*

Even if average agricultural land values were a poor approximation of the actual acquisition costs of protected areas, it is still possible that their accuracy could be increased by collecting agricultural land values at matched spatial grains (Fig. 2 – scenario 3a). When comparing both types of costs at a fine spatial grain, agricultural parcel sales still did not accurately predict the acquisition costs of protected areas ($KGE = -0.303$). This was due to both an increased amount of variation (42.8%, $\alpha = 4.50$) as well as a poor correlation (52.8%, $r = 0.073$). Again, this loss of accuracy was largely not attributable to bias (4.4%, $\beta = 1.26$).

In contrast, the accuracy of agricultural land values as an approximation for the acquisition costs of protected areas was substantially improved ($KGE = 0.357$) when both sets of cost estimates were spatially aggregated to the county scale (Fig. 2 – scenario 3b). Errors in this scenario were largely attributable to a poor correlation (57%, $r = 0.582$) as well as a decreased amount of relative variability (42.1%, $\alpha = 0.582$). Again, bias did not substantially contribute to MSE (0.9%, $\beta = 1.062$). Taken together, the results of our comparisons across combinations of spatial aggregation suggest that while agricultural land values may offer a reasonable estimate for the central tendency of acquisition costs across our whole study area, a poor correlation limits their ability to act as a point-estimate for these costs at the spatial grain of parcels or counties.

Figure 2. Histograms and bivariate plots compare cost data and cost estimates across all possible combinations spatial aggregation (rows) and data sources (columns). 1:1 lines in bivariate plots are shown with a solid line. 100 bootstrap replicates sampled from agricultural parcel sales are plotted in panels 2a and 3a. The central tendency of county-level average agricultural land values was similar to the central tendency of the acquisition costs of protected areas in our case study of recent transactions made The Nature Conservancy. However, these estimates were poorly correlated with TNC's acquisition costs both the parcel level (scenario 1) and as a county-level average (scenario 3b). This poor correlation cautions against the assumption present in many conservation plans that land costs associated with other land uses can reliably estimate the costs of establishing protected areas.

We also compared how spatial aggregation in isolation affected the accuracy of our cost estimate (Fig. 2 – scenario 2b). Averaged acquisition costs were a good estimate for the acquisition costs of individual protected areas ($KGE=0.545$). Errors in this comparison were also largely due to their moderate correlation (69.5%, $r=0.621$) and diminished variability (30.4%, $\alpha=0.749$), but not substantial bias (0.1%, $\beta=0.986$). Finally, again to isolate the effect of spatial aggregation, we compared agricultural cost estimates with different levels of spatial aggregation (Fig. 2 – scenario 2a). Averaged agricultural land values did not accurately predict agricultural parcel sales in that county ($KGE= -2.613$, average across $n=1000$ bootstrap replicates). This diminished accuracy was due to substantially less variability (91.2%, $\alpha=0.224$) and poor correlation (8.3%, $r=0.005$), but not substantial bias (0.4%, $\beta=0.813$).

3.3 How would any losses in accuracy impact the efficacy of conservation plans?

To address how the diminished accuracy of cost estimates would impact conservation planning, we focused on three scenarios that seemed most relevant to current practice in conservation planning (Fig. 1 – bottom right triangle). In our first comparison (Fig 1 – scenario 1), the substitution of the average agricultural land values for the actual acquisition costs of protected areas overestimated the average budget needed to meet regional species persistence objectives by, on average, 15.3% across all budget levels from [2-100%] of the total baseline budget (Fig. 3 – compare black vs. grey diamonds). We used Jaccard similarity to quantify overlap in the sets of counties prioritized for acquisition, and the concordance of conservation plans when using average agricultural land values and actual protected area acquisition costs was, on average, 0.695 across the different budget increments considered (Fig. A2).

In our previous scenario we altered both the level of aggregation as well as source of our cost estimate. To isolate the effect of agricultural land values, we compared conservation plans based on average agricultural land values and the average acquisition costs of protected areas in the same counties (Fig. 1 – scenario 3b). As expected, this substitution increased the expected budget needed to meet regional persistence objectives by, on average, 13% across all budget levels (Fig. 3 – compare grey vs. white diamonds). In this comparison the Jaccard similarity measuring the spatial overlap of prioritized counties was, on average, 0.708 (Fig. A2).

Lastly, to isolate the effect of spatial averaging within land use types, we compared conservation plans based on average acquisition costs and the parcel-level acquisition costs of protected areas (Fig. 1 – scenario 2b). As expected, this substitution minimally increased the expected budget needed to meet a gradient of regional persistence objectives by, on average, 2.3% (Fig. 3 – compare white vs. grey diamonds). This comparison also provided the greatest Jaccard similarity in the sets of prioritized counties (avg. 0.778, Fig. A2).

4. Discussion

Given the variation in cost estimates used in conservation planning, we sought to understand the type, direction, and magnitude of the errors that would result from commonly used cost representations. To accomplish this goal, we compared cost data and cost estimates derived from two different sources and two levels of spatial aggregation. Then, we tracked how the diminished accuracy of cost estimates would affect the performance of conservation plans by diverting funds away from the highest priority locations for protection and yielding incorrect estimates of required program budgets.

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Figure 3. The poor correlation of agricultural land values with acquisition costs of protected areas altered the rank-order of parcels prioritized for protection and resulted in conservation plans that that substantially overestimated average program budgets needed to meet a gradient of regional persistence objectives (15.2% in scenario 1, 13% in scenario 3b). In contrast, average acquisition costs were moderately correlated with the acquisition costs of protected areas, and so spatial aggregation alone did not largely affect the average program budgets (2.3% in scenario 2b).

We found that relying on agricultural land values to proxy for the actual costs of acquiring protected areas, as is commonly done in conservation planning, substantially reduced the cost-efficiency of resulting conservation plans. This decline in performance was due to the poor correlation of agricultural land values with the actual acquisition costs of protected areas (Fig. 2 – scenarios 1 and 3b). Agricultural land values adequately estimated the overall average acquisition cost for our study area. However, agricultural land values were consistently poor point estimates for the acquisition costs of protected areas both at the spatial grain of an individual parcel and when averaged to the county scale. This poor correlation is likely due geographic differences between agricultural parcels and protected areas. The median slope and elevation of TNC parcels fell on average in the 70th and 80th percentile of agricultural parcels with the relevant counties, respectively. When generalizing to other locations and contexts, we believe that protected parcels will often have different geographic and biological characteristics to “average” surrounding parcels devoted to other land uses. Simply put, parcels being protected for conservation rarely have the characteristics of average agricultural land parcels nearby. This resonates with many past studies that have illustrated that protected areas are often located at higher elevations and on steeper slopes than agricultural land uses (Aycrigg et al., 2013; Dietz et al., 2015). Disparities between parcels that are protected and those impacted by other land uses have been observed in other, non-agricultural settings as well (Denning et al., 2010).

In contrast to the poor performance of relying on proxies for costs of protected areas based on other rural land uses (agriculture), our results suggested that spatial averaging of land values in constructing proxies was less of a problem. Even though variance was suppressed, something that can in principle impact the efficacy of a conservation plan (Armsworth, 2014), county level averages of protected area costs retained a sufficiently strong correlation with our fine-grain cost data so that the efficacy of resulting conservation plans was little affected (Fig. 2 – scenario 2b). A plan based on spatially averaged cost estimates would rank the return-on-investment offered by different counties for investment similarly and the spatial distribution and expected costs of subsequent plans would likely reflect the landscape of future opportunities faced by conservation organizations reasonably well.

In designing our data scenarios, we made a number of assumptions that affected the cost estimates that we examined. Among them, we feel that our decision to exclude donations warrants particular scrutiny. As a sensitivity test, we included these transactions and re-ran our analyses of hypothetical conservation plans (Supporting Information). Including donated parcels increased the expected regional persistence of target species at low budgets for plans with access to TNC’s actual costs (compare Fig. A3 with Fig. 3). However, our sensitivity test did not alter the conclusion that spatial averaging was not the primary problem; it did not substantially increase the average expected budget (2.7% vs. 2.3 % in main text) or reduce the Jaccard similarity of counties prioritized for protection (0.813 vs. 0.778 in main text). However, once again in this sensitivity test, a reliance on agricultural land values led to poor performance of conservation plans; it increased the average increase in expected budget (39.4% vs. 15.3% in main text) and decreased the overlap of counties that were prioritized for protection (Jaccard similarity = 0.671 vs. 0.708 in main text).

We also made a number of assumptions in order to create a model for the biodiversity benefits of protected areas based on survey records of target species. First, representing biodiversity with survey records, as opposed to more statistically rigorous species distribution models (see Guisan and Zimmermann, 2000 for a review) limited the accuracy of our persistence

estimates. However, species distribution models have not been widely incorporated as a criterion for individual projects (LTA, 2004), and TNC used survey records of threatened or rare species as a justification for investment in over three-quarters of our sample of recent transactions. Second, assuming persistence scaled linearly with area ignored how species may require a minimum habitat size (e.g. area-based thresholds in Kiester et al., 1996). Third, assuming independence of persistence across species ignored how biotic interactions may influence species persistence (Rayfield et al., 2009). Lastly, assuming independence of persistence across space ignored potential threats to multiple species in a single site facing pressure from development (Visconti et al., 2010). Despite these limitations we argue these assumptions all sufficed for our basic question, could be easily reproduced by the practitioner community, and more pertinently, represented an advance over the more common practice in conservation planning of ignoring species persistence entirely (Ando, 1998; Naidoo and Iwamura, 2007).

We based our hypothetical conservation plans on a return-on-investment framework to simulate how limited funds could be spent on biodiversity protection. In particular, we evaluated how variation in cost estimates derived from different sources and level of spatial aggregation impacted these plans. In building any conservation plan based on spatial optimization it is important to recognize the priorities will be driven by whichever source of data has the most variation (Arponen et al. 2010; Perhans et al. 2008). We did not explicitly compare our plans to a financially unconstrained solution, or benefit targeting, that would completely ignored these costs (Babcock et al., 1997). However, our biodiversity data had a coefficient of variation of 2.99 vs. 1.91 for fine-grain cost data or 1.97 for average agricultural land values. This suggests that the spatial distribution of target species was still very important in driving our prioritizations throughout the range comparisons we drew.

Our message for conservation practitioners is simple – whenever possible use your own cost data, or estimates of these data, in the conservation planning process. In our case study we were able to substantially improve the cost-efficiency of our hypothetical plans relative to those based on agricultural land values with only access to the average cost per hectare of TNC's transactions within a county (Scenario 3b). Furthermore, these improvements were based on relatively limited data; our fine-grain cost data represented a sample of 96 TNC transactions in 42 counties. However, if a conservation organization is opening a new protected area program in some area and or has only a limited history of past acquisition on which to draw, we suggest they integrate the experience of other organizations working in similar settings and operating similar business models when estimating likely protected area costs. Finally, our results suggest it is less desirable to fall back on estimates of conservation costs based on other land uses, like agriculture nearby, and if doing so, we recommend conservation organizations be alert to the types of error and uncertainty that can be introduced. For example, our results suggest that simply plugging in cost layers derived from other land uses into conservation planning software packages could result in plans that substantially overestimate required program budgets to meet a given conservation objective and that are based on quite different spatial priorities than would be cost effective.

Our results highlight the importance of incorporating actual costs of protected areas in conservation planning efforts and not relying on proxies. In our experience, the most relevant cost data for conservation planning are typically held by those conservation organizations which are best positioned to act on any resulting conservation plan. As such, we are optimistic that open data-sharing policies would improve the cost data utilized in conservation planning studies and

further help close the knowledge-implementation gap present in the discipline (Knight et al., 2008). One exception to this might be conservation planning exercises conducted over very large scale (e.g. global - Bode et al., 2008; Brooks et al., 2006; Carwardine et al., 2008; Eklund et al., 2011; Murdoch et al., 2007; Myers et al., 2000; Naidoo and Iwamura, 2007), for which collecting cost estimates across a large enough spatial extent requires compromises that, as we have illustrated, can bias conservation planning outcomes. However, this problem may not be as great as it first appears, especially because the number of decision-makers who need planning support at a such a large scale is much smaller than the number of studies dedicated to this topic in the conservation science literature. When such large-scale prioritizations are necessary, we suggest researchers are careful to match the level of spatial aggregation of the decision-making to the resolution of the available cost and biodiversity data (Sutton and Armsworth, 2014). We also suggest there is promise in utilizing cross-scale modeling techniques (Holzkämper and Seppelt, 2007) to empirically derive the fine-grain relationships between the costs and benefits of biodiversity protection and then scale these parameters up across a larger spatial grain and extent. However, until conservation scientists have developed a richer, mechanistic understanding of what association, if any, there is between land costs associated with other land uses and the actual costs of protected areas, we suggest that less attention be given to the type of proxies for conservation costs and that more be given to collecting data on actual conservation costs.

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References

- Amundsen, O. 2011. Strategic Conservation Planning. Land Trust Alliance. Arlington, VA.
- Ando, A., 1998. Species Distributions, Land Values, and Efficient Conservation. *Science* 80, 2126–2128. doi:10.1126/science.279.5359.2126
- Ando, A.W., Mallory, M.L., 2012. Optimal portfolio design to reduce climate-related conservation uncertainty in the Prairie Pothole Region. *Proc. Natl. Acad. Sci. U.S.A.* 109, 6484–6489. doi:10.1073/pnas.1114653109
- Armsworth, P. R. 2014. Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions. *Annals of the New York Academy of Sciences* 1322:61–76. doi: 10.1111/nyas.12455
- Armsworth, P.R., Daily, G.C., Kareiva, P., Sanchirico, J.N., 2006. Land market feedbacks can undermine biodiversity conservation. *Proc. Natl. Acad. Sci. U.S.A.* 103, 5403–8. doi:10.1073/pnas.0505278103

- Armsworth, P.R., Fishburn, I.S., Davies, Z.G., Gilbert, J., Leaver, N., Gaston, K.J., 2012. The Size, Concentration, and Growth of Biodiversity-Conservation Nonprofits. *Bioscience* 62, 271–281. doi:10.1525/bio.2012.62.3.8
- Arponen, A., Cabeza, M., Eklund, J., Kujala, H., Lehtomäki, J., 2010. Costs of integrating economics and conservation planning. *Conserv. Biol.* 24, 1198–204. doi:10.1111/j.1523-1739.2010.01539.x
- Arponen, A., Lehtomäki, J., Leppänen, J., Tomppo, E., Moilanen, A., 2012. Effects of Connectivity and Spatial Resolution of Analyses on Conservation Prioritization across Large Extents. *Conserv. Biol.* 26, 294–304. doi:10.1111/j.1523-1739.2011.01814.x
- Aycrigg, J.L., Davidson, A., Svancara, L.K., Gergely, K.J., McKerrow, A., Scott, J.M., 2013. Representation of ecological systems within the protected areas network of the Continental United States. *PLoS One* 8, e54689. doi:10.1371/journal.pone.0054689
- Babcock, B.A., Lakshminarayan, P.G., Wu, J., Zilberman, D., 1997. Targeting tools for the purchase of environmental amenities. *Land Econ.* 73, 325–339. doi:10.2307/3147171
- Bainbridge, T.R., 1985. The committee on standards: precision and bias. *ASTM Stand. News* 13, 44–46.
- Bode, M., Wilson, K.A., Brooks, T.M., Turner, W.R., Mittermeier, R.A., McBride, M.F., Underwood, E.C., Possingham, H.P., 2008. Cost-effective global conservation spending is robust to taxonomic group. *Proc. Natl. Acad. Sci. U.S.A.* 105, 6498–6501. doi:10.1073/pnas.0710705105
- Brooks, T.M., Mittermeier, R. A., da Fonseca, G. A B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, a S.L., 2006. Global biodiversity conservation priorities. *Science* 313, 58–61. doi:10.1126/science.1127609
- Bureau of Labor Statistics (BLS), 2013. Consumer Price Index History Table. BLS. Washington, D.C. Available from <http://bls.gov/cpi/tables> (accessed December 2013).
- Carwardine, J., Wilson, K. A., Ceballos, G., Ehrlich, P.R., Naidoo, R., Iwamura, T., Hajkowicz, S. A., Possingham, H.P., 2008. Cost-effective priorities for global mammal conservation. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11446–50. doi:10.1073/pnas.0707157105
- Chiozza, F., Boitani, L., Rondinini, C., 2010. The Opportunity Cost of Conserving Amphibians and Mammals in Uganda. *Brazilian J. Nat. Conserv.* 08, 177–183. doi:10.4322/natcon.00802012
- Dietz, M.S., Belote, R.T., Aplet, G.H., Aycrigg, J.L., 2015. The world’s largest wilderness protection network after 50years: An assessment of ecological system representation in the U.S. National Wilderness Preservation System. *Biol. Conserv.* 184, 431–438. doi:10.1016/j.biocon.2015.02.024
- Di Minin, E, Macmillan, D.C., Goodman, P.S., Escott, B., Slotow, R., Moilanen, A., 2013. Conservation Businesses and Conservation Planning in a Biological Diversity Hotspot. *Conserv. Biol.* 27, 808–820. doi:10.1111/cobi.12048
- Denning, C.A., McDonald, R.I., Christensen, J., 2010. Did land protection in Silicon Valley reduce the housing stock? *Biol. Conserv.* 143, 1087–1093. doi:10.1016/j.biocon.2010.01.025
- Eklund, J., Arponen, A., Visconti, P., Cabeza, M., 2011. Governance factors in the identification of global conservation priorities for mammals. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366, 2661–9. doi:10.1098/rstb.2011.0114
- Fry, J.A., Xian, G., Jin, S., Dewitz, J.A., Homer, C.G., Limin, Y., Barnes, C.A., Herold, N.D., Wickham, J.D., 2011. Completion of the 2006 national land cover database for the conterminous United States. *Photogramm. Eng. Remote Sensing* 77, 858–864.

- Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., Baumgartner, J. V., Higgins, J. V., Beck, M.W., Anderson, M.G., 2002. Planning for Biodiversity Conservation: Putting Conservation Science into Practice. *Bioscience* 52, 499–512. doi:10.1641/0006-3568(2002)052[0499:PFBCPC]2.0.CO;2
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186. doi:10.1016/S0304-3800(00)00354-9
- Gupta, H. V., Kling, H., Yilmaz, K.K., Martinez, G.F., 2009. Decomposition of the mean squared error and NSE performance criteria: Implications for improving hydrological modelling. *J. Hydrol.* 377, 80–91. doi:10.1016/j.jhydrol.2009.08.003
- Hammerson, G., Nichols, J. (Eds.), 2009. Section 4 EO Specifications. NatureServe. Arlington, VA.
- Hermoso, V., Kennard, M. J., 2012. Uncertainty in coarse conservation assessments hinders the efficient achievement of conservation goals. *Biol. Conserv.* 147, 52–59. doi:10.1016/j.biocon.2012.01.020
- Hess, G.R., Bartel, R.A., Leidner, A.K., Rosenfeld, K.M., Rubino, M.J., Snider, S.B., Ricketts, T.H., 2006. Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biol. Conserv.* 132, 448–457. doi:10.1016/j.biocon.2006.04.037
- Holzkämper, A., Seppelt, R., 2007. Evaluating cost-effectiveness of conservation management actions in an agricultural landscape on a regional scale. *Biol. Conserv.* 136, 117–127. doi:10.1016/j.biocon.2006.11.011
- Hurlbert, A.H., Jetz, W., 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl. Acad. Sci. U.S.A.* 104, 13384–9. doi:10.1073/pnas.0704469104
- Jantke, K., Schleupner, C., Schneider, U. A., 2013. Benefits of earth observation data for conservation planning in the case of European wetland biodiversity. *Environ. Conserv.* 40, 37–47. doi:10.1017/S0376892912000331
- Jantke, K., Schneider, U. A., 2010. Integrating Land Market Feedbacks into Conservation Planning—A Mathematical Programming Approach. *Environ. Model. Assess.* 16, 227–238. doi:10.1007/s10666-010-9242-2
- Kareiva, P., Groves, C., Marvier, M., 2014. The evolving linkage between conservation science and practice at The Nature Conservancy. *J. Appl. Ecol.* 51, 1137–1147. doi:10.1111/1365-2664.12259
- Kiester, A.R., Scott, J.M., Csuti, B., Noss, R.F., Butterfield, B., Noss, I.R.F., 1996. Conservation prioritization using GAP data. *Conserv. Biol.* 10, 1332–1342. doi: 0.1046/j.1523-1739.1996.10051332.x
- Knight, A.T., Cowling, R.M., Rouget, M., Balmford, A., Lombard, A.T., Campbell, B.M., 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. *Conserv. Biol.* 22, 610–7. doi:10.1111/j.1523-1739.2008.00914.x
- Knight, A.T., Grantham, H.S., Smith, R.J., McGregor, G.K., Possingham, H.P., Cowling, R.M., 2011. Land managers' willingness-to-sell defines conservation opportunity for protected area expansion. *Biol. Conserv.* 144, 2623–2630. doi:10.1016/j.biocon.2011.07.013
- Land Trust Alliance (LTA) 2004. Standard 8: Evaluating and selecting conservation projects. LTA, Washington, D.C.
- Langford, W.T., Gordon, A., Bastin, L., 2009. When do conservation planning methods deliver? Quantifying the consequences of uncertainty. *Ecol. Inform.* 4, 123–135. doi:10.1016/j.ecoinf.2009.04.002

- Luck, G.W., Ricketts, T.H., Daily, G.C., Imhoff, M., 2003. Alleviating spatial conflict between people and biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* 101, 182–186. doi:10.1073/pnas.2237148100
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–53. doi:10.1038/35012251
- Mebane, W.R., Berkeley, U.C., 2011. Genetic Optimization Using Derivatives: The rgenoud Package for R. *J. Stat. Softw.* 42, 1–26. doi:10.18637/jss.v042.i11
- Miller, J.R., Hobbs, R.J., 2002. Conservation where people live and work. *Conserv. Biol.* 16, 330–337. doi:10.1046/j.1523-1739.2002.00420.x
- Mills, M., Pressey, R.L., Weeks, R., Foale, S., Ban, N.C., 2010. A mismatch of scales: challenges in planning for implementation of marine protected areas in the Coral Triangle. *Conserv. Lett.* 3, 291–303. doi:10.1111/j.1755-263X.2010.00134.x
- Moilanen, A., 2008. Generalized complementarity and mapping of the concepts of systematic conservation planning. *Conserv. Biol.* 22, 1655–8. doi:10.1111/j.1523-1739.2008.01043.x
- Murdoch, W., Polasky, S., Wilson, K. a., Possingham, H.P., Kareiva, P., Shaw, R., 2007. Maximizing return on investment in conservation. *Biol. Conserv.* 139, 375–388. doi:10.1016/j.biocon.2007.07.011
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. doi:10.1038/35002501
- Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. *Trends Ecol. Evol.* 21, 681–7. doi:10.1016/j.tree.2006.10.003
- Naidoo, R., Iwamura, T., 2007. Global-scale mapping of economic benefits from agricultural lands: Implications for conservation priorities. *Biol. Conserv.* 140, 40–49. doi:10.1016/j.biocon.2007.07.025
- Nash, J., Sutcliffe, J., 1970. River flow forecasting through conceptual models part I—A discussion of principles. *J. Hydrol.* 10, 282–290. doi:10.1016/0022-1694(70)90255-6
- National Agricultural Statistics Service (NASS), 2007. Census of Agriculture: United States Summary and State Data. Washington, D.C. Available online from <http://www.agcensus.usda.gov> (accessed December 2013).
- Perhans, K., Kindstrand, C., Boman, M., Djupström, L.B., Gustafsson, L., Mattsson, L., Schroeder, L.M., Weslien, J., Wikberg, S., 2008. Conservation goals and the relative importance of costs and benefits in reserve selection. *Conserv. Biol.* 22, 1331–9. doi:10.1111/j.1523-1739.2008.00976.x
- Polasky, S., Camm, D., Solow, A.R., Csuti, B., White, D., 2000. Choosing reserve networks with incomplete species information. *Biol. Conserv.* 94, 1–10. doi:10.1016/S0006-3207(99)00171-8
- Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv.* 141, 1505–1524. doi:10.1016/j.biocon.2008.03.022
- Pressey, R.L., Mills, M., Weeks, R., Day, J.C., 2013. The plan of the day: Managing the dynamic transition from regional conservation designs to local conservation actions. *Biol. Conserv.* 166, 155–169. doi:10.1016/j.biocon.2013.06.025

- Rahbek, C., 2004. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8, 224–239. doi:10.1111/j.1461-0248.2004.00701.x
- Rayfield, B., Moilanen, A., Fortin, M.-J., 2009. Incorporating consumer–resource spatial interactions in reserve design. *Ecol. Modell.* 220, 725–733. doi:10.1016/j.ecolmodel.2008.11.016
- Real, R., Vargas, J.M., 1996. The Probabilistic Basis of Jaccard’s Index of Similarity. *Syst. Biol.* 45, 380–385. doi:10.1007/s10021-001-0077-1
- Richardson, E. a., Kaiser, M.J., Edwards-Jones, G., Possingham, H.P., 2006. Sensitivity of Marine-Reserve Design to the Spatial Resolution of Socioeconomic Data. *Conserv. Biol.* 20, 1191–1202. doi:10.1111/j.1523-1739.2006.00426.x
- Rissman, A.R., Lozier, L., Comendant, T., Kareiva, P., Kiesecker, J.M., Shaw, M.R., Merenlender, A.M., 2007. Conservation easements: biodiversity protection and private use. *Conserv. Biol.* 21, 709–18. doi:10.1111/j.1523-1739.2007.00660.x
- Rondinini, C., Wilson, K. a, Boitani, L., Grantham, H., Possingham, H.P., 2006. Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecol. Lett.* 9, 1136–45. doi:10.1111/j.1461-0248.2006.00970.x
- Seo, C., Thorne, J.H., Hannah, L., Thuiller, W., 2009. Scale effects in species distribution models: implications for conservation planning under climate change. *Biol. Lett.* 5, 39–43. doi:10.1098/rsbl.2008.0476
- Shriner, S.A., Wilson, K.R., Flather, C.H., 2006. Reserve networks based on richness hotspots and representation vary with scale. *Ecol. Appl.* 16, 1660–1673. doi:10.1890/1051-0761(2006)016[1660:RNBORH]2.0.CO;2
- Strange, N., Rahbek, C., Jepsen, J.K., Lund, M.P., 2006. Using farmland prices to evaluate cost-efficiency of national versus regional reserve selection in Denmark. *Biol. Conserv.* 128, 455–466. doi:10.1016/j.biocon.2005.10.009
- Sutton, N.J., Armsworth, P.R., 2014. The Grain of Spatially Referenced Economic Cost and Biodiversity Benefit Data and the Effectiveness of a Cost Targeting Strategy. *Conserv. Biol.* 28, 1451–1461 doi:10.1111/cobi.12405
- The Nature Conservancy (TNC), 2010. EAST: Ecoregional Status Assessment Tool. Arlington, VA. Available online from <http://www.conservationgateway.org>, (accessed December 2013).
- The Nature Conservancy (TNC). 2013. Consolidated Financial Statements for the year ended June 30, 2013. Arlington, VA. Available from <http://www.nature.org> (accessed March 2014).
- Tobler, W. 1988. Resolution, resampling, and all that. Pages 129–137 in H. Mounsey and R. Tomlinson, editors. *Building Data Bases for Global Science*. Taylor and Francis, London, England.
- Torrubia, S., Mcrae, B.H., Lawler, J.J., Hall, S.A., Halabisky, M., Langdon, J., Case, M., 2014. Getting the most connectivity per conservation dollar. doi:10.1890/130136
- United States Geological Survey (USGS), 2013. Biodiversity Information Serving Our Nation. Washington, DC. Available online from <http://www.bison.usgs.gov> (accessed December 2013).
- Visconti, P., Pressey, R.L., Segan, D.B., Wintle, B. a., 2010. Conservation planning with dynamic threats: The role of spatial design and priority setting for species’ persistence. *Biol. Conserv.* 143, 756–767. doi:10.1016/j.biocon.2009.12.018

- Walther, B.A., Moore, J.L., 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 6, 815-829. doi: 10.1111/j.2005.0906-7590.04112.x
- Warman, L.D., Sinclair, a. R.E., Scudder, G.G.E., Klinkenberg, B., Pressey, R.L., 2004. Sensitivity of Systematic Reserve Selection to Decisions about Scale, Biological Data, and Targets: Case Study from Southern British Columbia. *Conserv. Biol.* 18, 655–666. doi:10.1111/j.1523-1739.2004.00538.x
- Williams, P.H., Moore, J.L., Toham, A.K., 2003. Integrating biodiversity priorities with conflicting socio-economic values in the Guinean – Congolian forest region. *Biodivers. Conserv.* 12, 1297–1320. doi: 10.1023/A:1023092100942
- Wilson, K.A, Evans, M.C., Di Marco, M., Green, D.C., Boitani, L., Possingham, H.P., Chiozza, F., Rondinini, C., 2011. Prioritizing conservation investments for mammal species globally. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 366, 2670–80. doi:10.1098/rstb.2011.0108
- Withey, J.C., Lawler, J.J., Polasky, S., Plantinga, A.J., Nelson, E.J., Kareiva, P., Wilsey, C.B., Schloss, C. A, Nogeire, T.M., Ruesch, A., Ramos, J., Reid, W., 2012. Maximising return on conservation investment in the conterminous USA. *Ecol. Lett.* 15, 1249–56. doi:10.1111/j.1461-0248.2012.0