Empirical evaluation of proxies for the acquisition costs of protected areas suggests care is needed to deliver the promise of cost-effective conservation

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ABSTRACT

Given limited budgets, conservation organizations need to efficiently allocate their resources for biodiversity protection. While many organizations combine socioeconomic and biological data to identify areas with the highest biological return per dollar invested, it is less clear how uncertainty in socioeconomic data affects this planning process. In Chapter 1, we show how uncertainty due to proxy choice and spatial averaging affect conservation planning by comparing average agricultural land values, a common proxy for the acquisition costs of protected areas, to a case study recent protected area investments in the Eastern US. We find this proxy explains little variation and significantly overestimates the parcel-level acquisition costs of protected areas. Furthermore, our results demonstrate errors due to proxy choice result in conservation plans that substantially overestimate the costs of protected areas for both a local and a complementarity richness objective. In Chapter 2, we investigate spatial averaging further by systematically manipulating the spatial grain of our biological and socioeconomic data in concert, and then demonstrating how the conclusion of a classic debate in conservation planning depends on the spatial grain of the data being used. Specifically, we find the relative performance of cost and benefit targeting is sensitive to spatial grain, and that combining data over different spatial grains inflates the apparent effectiveness of a cost targeting strategy. We recommend that future studies account for uncertainty in their socioeconomic data by first matching the spatial grain of their data sources with their planning units, and then by collecting socioeconomic data that more reliably reflect the costs of acquiring protected areas.

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INTRODUCTION

Conservation organizations routinely purchase land for protection to stem the loss of biodiversity. Unfortunately, there is a clear disparity between conservation spending and need (James et al. 1999). In response, conservation science has developed a variety of tools to help organizations distribute scarce resources across a landscape (Moilanen et al. 2005; Ball et al. 2009). At the most basic level, these tools all use variation in costs and benefits to create a spatially explicit map of priorities, and are intended to elicit potentially cost-effective opportunities to invest in biodiversity protection. However, few assessments based on these quantitative tools have subsequently affected local action (Knight & Cowling 2007; Arlettaz et al. 2010; Pressey et al. 2013), and in this analysis we evaluate how uncertainty due to *spatial grain* and *proxy choice* can bias the prioritization of areas for protection. In Chapter 1, we compare these two sources of uncertainty by testing the predictive capacity of a commonly used proxy for the acquisition costs of protected areas. In Chapter 2, we further break down the effect of spatial averaging effect by demonstrating how the conclusion of a classic debate in the conservation planning literature depends on the spatial grain of the data being used.

Systematic conservation planning was developed as a response to the perception that organizations were acting opportunistically, and acquiring land for protection without regard to its ecological value (Pressey et al. 1993). This argument was further justified as the distribution of protected areas disproportionately covered high-elevation sites with poor soil quality (Scott et al. 2001; Aycrigg et al. 2013). If opportunistic conservation was protecting 'rocks and ice' rather than encapsulating the full range of biodiversity, it was argued a more biodiversity-centric approach would allow for better species persistence and representation into the future.

Systematic conservation planning depends on quantitative tools that maximize the biological features of a set of protected areas. Early reserve selection models were based on heuristic algorithms (Kirkpatrick & Harwood 1983), but linear programming methods from operations research were quickly adopted (Cocks & Baird 1989; Pressey 2002). While these early studies generally focused on maximizing known occurrences of biodiversity, today more comprehensive models account for uncertainty in a species' probability of persistence due to variable habitat quality (Schapaugh & Tyre 2012), reserve connectivity (Teeffelen et al. 2006), species turnover (Margules et al. 1994), and species interactions (Rayfield et al. 2009).

In contrast, there has been comparatively less attention devoted to how uncertainty in socioeconomic data affects conservation planning. Early studies generally assumed the acquisition costs of protected areas scaled linearly with area (Margules et al. 1988; Pressey & Nicholls 1989), whereas acquisition cost have been shown to vary widely (Davies et al. 2010). More recently, the planning literature has emphasized the importance of the socioeconomic

context of conservation in achieving cost-effective outcomes (see Naidoo et al. 2006; Duke et al. 2013 for a review). However, due to the paucity of transactional data on the acquisition costs of protected areas, planning studies have relied on a variety of proxies to prioritize scarce resources.

These proxies differ from the acquisition costs that conservation organizations face when establishing a protected area in two important ways. First, they are often averaged within a spatial unit larger than a single parcel. Averaged data may be appropriate in large-scale studies that are conducted at the same coarse spatial grain, but are problematic when used to prioritize areas for protection at a finer spatial grain (Jantke et al. 2013). Second, these proxies are most commonly based on variation in agricultural land values (Table 1); these data would a pose problem if the market for protected areas is different from agricultural land, or if organizations are not acquiring parcels for protection that would otherwise be agriculturally productive.

Review of cost data used in conservation planning studies

I collated information from 19 prominent studies to demonstrate the scope for uncertainty due to spatial grain and proxy choice to bias conservation planning (Table 1). I screened any studies that did not incorporate heterogeneous costs in their analysis, and limited my sample to studies published within the last decade. I divided this sample into global, continental, national, and regional spatial extents. Where possible I extracted the summary statistics for each study's socioeconomic data, the type of biodiversity targeted, and the correlation of costs and biodiversity. When a study used socioeconomic data from another source, I referenced the original publication to extract any summary statistics. Basic descriptions of socioeconomic data were frequently missing, and in these cases I contacted any authors to confirm the validity of my data extraction. All costs were converted into 2012 USD ha^{-1} with the consumer price index (BLS 2014), and annual costs were converted into net present values with a 5% discount rate.

Proxy choice

Our survey of conservation planning studies used either proxies for human activity or the acquisition costs of protected areas. First, a small number of studies used proxies derived from human population density (Luck et al. 2004) or nominal gross domestic product per capita (Eklund et al. 2011). Although these proxies likely captured coarse-grain variation in the costs of protected areas, many conservation organizations only operate regionally (LTA 2010), and do not make decisions this scale. Second, many studies used the net present value of agricultural land as a measure of the future acquisition costs of protected areas (Naidoo & Iwamura 2007; Perhans et al. 2008; Chiozza et al. 2010; Adams et al. 2010; Visconti et al. 2010; Jantke et al. 2013). These costs were generally derived from census data (NASS 2007) or models that converted estimates of agricultural productivity into a net present value. Census data based on stated valuations have been shown to overestimate land values in

Table 1. Summary of cost data from prominent conservation planning studies

Authors	Location	Summary of Cost Data							
		Source (if different)	Estimation Method	Spatial grain of cost data	Spatial grain of prioritization	Summary statistics (2012 USD ha^{-1})			
						min	max	mean	stdev
Global									
Murdoch et al., 2007	17 Mediterranean Ecoregions	Wilson et al,. 2007	Varied estimates from literature	Country	17 ecoregions (avg 10,463 km^2)	5.71	49,252.47	5,286.20	9,957.15
Bode et al., 2008	34 biodiversity hotspots	Moore et al., 2004	Hypothetical cost survey	Country averaged to hotspot	14 ecoregions (avg. 690,888 km^2)	24.80	41,303.95	4,016.97	8,271.65
Carwardine et al., 2008a	Globe	Naidoo & Iwamura 2008	Potential agricultural rent (gross)	85 km^2	10,000 km^2	0.00	173,328.80	1,466.60	3,466.60
Naidoo & Iwamura, 2008	Biodiversity hotspots & Global 200 Ecoregions		Potential agricultural rent (gross)	5 arcminutes ~ 85 km^2	825 global ecoregions (avg 10,279 km^2)	0.00	173,328.80	1,466.60	3,466.60
Eklund et al., 2011	Globe	World Development Report 2009 (World Bank)	Nominal GDP per capita	Country	124 km^2				
Continental									
Luck et al. 2004	Australia	Gridded Population of the World (NASA)	Population density	20 km^2	12,392 km^2				
Moore et al. 2004	Africa	Balmford et al., 2003	Survey of hypothetical costs + published /unpublished sources	Country	118 ecoregions (avg. 252,490 km^2)	6.60	3,245.80	267.80	642.40
Carwardine et al. 2008b	Australia	Hajkowicz & Young, 2002	NPV of potential agricultural rent	1 km^2	10 km^2				
		AU Bureau of Ag. and Resouce Economics	State appraisal of unimproved land purchases	Local Government Area, interpolation at 15 km^2					
Jantke et al. 2011	Europe	Eurostat	Agricultural rent (gross)	Country	UTM 50 (~2,500 km^2)	238.60	11,526.20	4,251.20	3,288.20
Jantke et al. 2013	Europe	Lee et al., 2009	Agricultural rent (gross)	Country	variable (avg. 300 km^2)	263.00	10,701.60	2,706.60	2,510.40
			Potential agricultural rent (gross), weighted by soil productivity model	5 arcminutes ~ 85 km^2	variable (avg. 300 km^2)	0.00	15,282.40	2,789.00	2,432.00
National									
Murdoch et al., 2007	US, 21 Terrestrial ecoregions	USDA Census 2007	Average agricultural land values averaged within ecoregion	US County	21 temperate ecoregions (avg. 137,986 km^2)	2,249.19	26,388.35	5,551.58	5,622.88
Strange et al. 2007	Denmark	Statistics Denmark	Average county-level agricultural land purchases	EU County	100 km^2 UTM grid	12,068.28	30,663.28		
Chiozza et al., 2010	Uganda	National Agricultural Advisory Service	Agricultural Rent	Census Tracts	25 km^2	0.00	11,789.40	2,929.00	
Withey et al., 2012	US (less HI & AK)	Plantinga et al., 2002 Lubowski et al., 2006	Average land purchase price, derived from econometric model	US County	US County (avg. ~ 3,000 km^2)	55.79	43,858.89		
Within country									
Adams et al., 2010	Mbaracayu Forest Biosphere Reserve, Paraguay (3,000 km^2)	Naidoo & Adamowicz 2006	NPV of agricultural rent	0.01 km^2 - averaged across 0.25 km^2 planning unit	0.25 km^2	0	1,126.70	72.93	
Carwardine et al., 2010	Queensland, AU (1,800,000 km^2)		State appraisal of unimproved land purchases	100 km^2	100 km^2			467.08	
Polasky et al., 2008	Willamette Basin, OR USA (~30,000 km^2)		NPV of agricultural and timber rent, average price of residential parcels	Parcels, 0.0009-7.5 km^2	Parcels, 0.0009-7.5 km^2			7402.81 (ag) 12,471.27 (for) 13,002.19 (res)	
Visconti et al., 2010	Hunter Valley, AU (~600 km^2)		NPV of agricultural rent	0.01 to 0.34 km^2	0.01 to 0.34 km^2				
Perhans et al., 2008	Boreal Sweden (~22,500 km^2)		NPV of timber rent	0.0025 km^2	0.0025 km^2	2.13	18.35	8.09	CV=0.43

Table 1 (continued). Summary of cost data from prominent conservation planning studies

Authors	Location	Prioritization	Results		
		Biodiversity Target	Correlation of costs and benefits	Ignoring costs inefficient	Cost targeting outperforms benefit targeting
Global					
Murdoch et al., 2007	17 Mediterranean Ecoregions	Plants and vertebrates on IUCN red list		Y	
Bode et al., 2008	34 biodiversity hotspots	7 taxonomic groups (mammals, birds, amphibians, reptiles, freshwater fishes, tiger beetles, & vascular plants)	r_s = -0.09	Y	
Carwardine et al., 2008a	Globe	Terrestrial mammal species		Y	
Naidoo and Iwamura, 2008	Biodiversity hotspots & Global 200 Ecoregions	Endemic species within ecoregion		Y	Y
Eklund et al., 2011	Globe	Terrestrial mammal species	r_s = 0.88		
Continental					
Luck et al. 2004	Australia	Birds, mammals, reptiles, amphibians, and butterflies	r_s = 0.64	Y	
Moore et al. 2004	Africa	Selected vertebrate groups	r_s = 0.42 (richness) r_s = 0.3 (end. richness)	Y	Y
Carwardine et al. 2008b	Australia	2590 biodiversity feastures (vegetation types, environmental domains, species distributions of non-vagrant birds, floral and faunal species of significance)			
Jantke et al. 2011	Europe	69 tetrapod wetland species			
Jantke et al. 2013	Europe	72 wetland species 72 wetland species			
National					
Murdoch et al., 2007	US, 21 Terrestrial ecoregions	Vertebrate and vascular plant species	r_s = -0.05	Y	
Strange et al. 2007	Denmark	763 species of orchids, birds, amphibians, reptiles, and insects	r_s = 0.43	Y	
Chiozza et al., 2010	Uganda	377 vertebrates		Y	
Withey et al., 2012	US (less HI & AK)	Terrestrial vertebrates		Y	
Within country					
Adams et al., 2010	Mbaracayu Forest Biosphere Reserve, Paraguay (3,000 km^2)	Vegetation classes	r = 0.01		
Carwardine et al., 2010	Queensland, AU (1,800,000 km^2)	2590 biodiversity feastures (vegetation types, environmental domains, species distributions of non-vagrant birds, floral and faunal species of significance)			
Polasky et al., 2008	Willamette Basin, OR, USA (~30,000 km^2)	267 vertebrate species		Y	
Visconti et al., 2010	Hunter Valley, AU (~600 km^2)	3 vertebrate species	r = 0.19 squirrel glider r = .04 sooty owl r = .06 yellow-bellied glider	Y	
Perhans et al., 2008	Boreal Sweden (~22,500 km^2)	P/A of 620 spp. of bryophytes, lichens, and wood-living beetle, as well as habitat characteristics	r_s = -0.26 local richness	Y	Y*

comparison with market transactions (Goodman & Ittner 1992). Furthermore, proxies derived from agricultural productivity potentially misestimate acquisition costs because they assume that conservation organizations are acquiring land that could otherwise be used for agriculture.

Given the ubiquitous use of proxy data, it is surprising so few studies have attempted to map their socioeconomic predictions to the realities faced organizations working to implement their plans (but see Adams et al. 2011 for an example). In Chapter I, I accomplish this goal by comparing average agricultural land values to a sample of land transactions recently undertaken by a conservation nonprofit to protect forests in the eastern US. I then use these data to address the following questions: i) are average agricultural land values' lack of predictive capacity a result of spatial averaging or proxy choice? and, ii) how do spatial averaging and proxy choice affect the performance of return-on-investment targeting?

Spatial grain

My survey of conservation planning studies also demonstrated there was a clear tradeoff between the extent and spatial grain of available socioeconomic data. The spatial grain of the socioeconomic data varied widely from 0.0009 km^2 to the country-level. While the spatial grain of the prioritization in each study had a similar range of values, there were frequently large differences between the spatial grain of socioeconomic data and planning units used in a single study (Table 1). Moreover, these differences were often an order of magnitude in size, and fell disproportionately in studies with a global or continental spatial extent (Table 1, compare spatial grain of socioeconomic data and planning units across rows). Differences between the spatial grain of socioeconomic data and planning units occurred both in fine-grain values that had been averaged within a larger planning unit (Naidoo & Iwamura 2007; Murdoch et al. 2007; Carwardine et al. 2008; 2010), and in coarse-grained values that had been used to prioritize areas in smaller planning units (Jantke & Schneider 2011; Eklund et al. 2011; Jantke et al. 2013). More troublingly, of these studies only Jantke et al. (2013) conducted of robustness checks to verify their spatial priorities were not sensitive to the uncertainty in their spatially averaged socioeconomic data. In contrast, conservation planning studies with a smaller extent more consistently matched the spatial grain of their socioeconomic data and planning units (Strange et al. 2006; Polasky et al. 2008; Perhans et al. 2008; Adams et al. 2010; Visconti et al. 2010; Withey et al. 2012).

Given the prevalence of grain mismatches in conservation planning studies with a large spatial extent, my goal in Chapter 2 is to use a classic debate between opportunistic and systematic conservation planning to exemplify how spatial prioritizations are generally sensitive to the spatial grain of the biological and socioeconomic data used to support them. To accomplish this goal, I use the same case study of recent land transactions as Chapter 1 to

estimate the parcel-level acquisition costs and biodiversity benefits of protected areas. I then use these unusually fine-grain data to address the following questions: i) does spatial variation in acquisition costs trump spatial variation in biodiversity benefits when prioritizing areas for protection? ii) how does each strategy compare to a more integrative return-on-investment approach? and most importantly, iii) how sensitive are those results to the spatial grain of the socioeconomic and biological data being used?

CHAPTER 1:

Proxies for the acquisition costs of protected areas are conservative and underestimate the potential benefits of a conservation action

A version of this chapter will be submitted for publication by Nathan J. Sutton and Paul R. Armsworth:

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This chapter does not reflect changes that will happen before publication during the internal and external review process. Nathan Sutton developed the idea for this manuscript, conducted the analysis, and wrote the manuscript. Paul Armsworth is a co-author of this work, and was responsible for feedback at early stages of this manuscript's development, providing the necessary transactional data from the Nature Conservancy, and helping with editing.

ABSTRACT

Given limited budgets, conservation organizations frequently combine socioeconomic and biological data to identify areas with the highest biological return on their investment. Here, we show how uncertainty in socioeconomic data due to proxy choice and spatial averaging affect the prioritization of areas for protection. To accomplish this goal, we evaluate the predictive capacity of average agricultural land values, a common proxy for the acquisition costs of protected areas, with a case study of recent investments undertaken by a conservation nonprofit to protect hardwood forests. We find average agricultural land values explain little variation in the acquisition costs of protected areas. We then show how the use of proxy data overestimates acquisition costs while underestimating the potential biological benefits of conservation action. This suggests that plans based on socioeconomic proxies are generally conservative relative to the future landscape of opportunities faced by conservation organizations.

INTRODUCTION

Facing tight resource constraints, conservation organizations utilize spatial variation in socioeconomic costs and biological benefits to cost-effectively acquire land for protection (see Naidoo et al. 2006 for a review). While early systematic conservation planning studies prioritized known occurrences of biodiversity in a landscape (Kirkpatrick & Harwood 1983), more recent work explicitly accounts for uncertainty in a species' probability of persistence due to variable habitat quality (Schapaugh & Tyre 2012), reserve connectivity (Teeffelen et al. 2006), species turnover (Margules et al. 1994), or species interactions (Rayfield et al. 2009). In contrast, comparatively less attention has been devoted to understanding how uncertainty in socioeconomic data affects the prioritization of areas for protection (but see Richardson et al. 2006; Carwardine et al. 2010 for examples).

Due to a lack of available transactional data, conservation planning studies have relied on a variety of proxies for the acquisition costs of protected areas. These proxies differ from acquisition costs in two important ways: they are spatially averaged, and they are commonly based on variation in agricultural land values, e.g. from census data (Ando et al. 1998; Strange et al. 2006; Murdoch et al. 2007; Chiozza et al. 2010; Jantke & Schneider 2011) or models of agricultural productivity (Naidoo & Iwamura 2007; Visconti et al. 2010; Withey et al. 2012; Jantke et al. 2013). Given the ubiquitous use of proxy data, it is surprising so few studies have attempted to map these socioeconomic predictions to the realities faced by organizations working to acquire land for protection (but see Adams et al. 2011 for an example).

In this study, when we compare average agricultural land values (NASS 2007) to a case study of recent protected areas, we find this proxy explained little variation in acquisition costs (Fig. 1). This may be attributable to the fact that these data are *average* land values, or *agricultural* land values. To distinguish between these mechanisms, we ask the following questions: i) are average agricultural land values' lack of predictive capacity a result of spatial averaging or proxy choice? and, ii) how do spatial averaging and proxy choice affect the performance of a return-on-investment targeting strategy? If the lack of covariation in Figure 1 is a result of spatial averaging, we would expect there to be a decrease in predictive capacity when average agricultural land values are used to predict fine-grain acquisition costs, but high predictive capacity at matched spatial grains (Fig. 2, left panel). In contrast, if this lack of covariation is due to proxy choice, we would expect agricultural land values to have little predictive capacity across all combinations of spatial grain (Fig. 2, right panel). We then create model conservation plans based on different sets of socioeconomic data to quantify how spatial averaging and proxy choice affect the performance of a return-on-investment targeting strategy.

METHODS

Choice of case study

Land trusts have been particularly active in acquiring land for biodiversity protection in the United States, and in a recent survey of these organizations, over 1,700 land trusts helped to protect 47 million acres of land (LTA 2010). The Nature Conservancy, or TNC, is the largest of these land trusts with over $5.4 billion in net assets and $950 million in annual revenue (TNC 2013). TNC maintains records of each transaction in their Conservation Lands System database; we used this database to describe the acquisition costs of 116 recent (2000-2009) fee-simple transactions spread throughout 45 counties in the Eastern US (Fig. 5). We defined our fine-grain acquisition cost data as the per hectare costs of these recent transactions. We then spatially aggregated these data by calculating the area-weighted average cost per hectare within each county (following the same methodology used in NASS 2007). All costs were converted into 2005 USD using the consumer price index (BLS 2014).

Proxy data

We used county-level average agricultural land values from the most recent agricultural census to represent the type of coarse-grain proxy data that have been commonly used in conservation planning (NASS 2007). We also have collected fine-grain proxy data based on agricultural parcel sales within 26 counties in our study area. We defined this sample as any parcel sale that intersected with an agricultural land use from the National Land Cover Database (Fry et al. 2011), and we excluded sales that occurred outside of 2000-2009 to match the timeframe of our sample of TNC transactions. The sample size of our fine-grain proxy data was larger (n=98,000) than our acquisition cost data (n=116), and to account for this difference we repeatedly sampled with replacement within each county to assign a value to each transaction.

Biodiversity data

TNC has taken an ecoregional portfolio approach to identify priority locations based on their contribution to the persistence of conservation targets (TNC 1997). Within these ecoregional portfolios, we extracted 328 target species that were listed for their high level of conservation concern. We downloaded all element occurrences, or EOs, of these species from the Biodiversity Information Serving Our Nation database (USGS 2014). We excluded all fossil records, as well as EOs without a known type. After this screening, we had a total of 71,799 EOs within our study area. Due to this small area of most TNC land acquisitions, only 111 EOs were found within our recent transactions. Therefore, we buffered each transaction's centroid with an equal area 5 km buffer to increase our sample size to 8,874 EOs of 92 species. We represented biodiversity with known EOs, as opposed to species distribution models, because these data were utilized during the creation of TNC's ecoregional portfolios (TNC & WWF 2006). Additionally,

TNC cited the proximity to known EOs of threatened and target species as a justification for acquiring specific parcels in over three quarters of our sample of land transactions.

Metrics of predictive capacity

We described the predictive capacity of each proxy with three metrics. First, a proxy should have an equivalent amount of variation (Fig. 1, compare scaling in x and y axes). We defined the amount of variation in each proxy by its median absolute deviation, and used a Fligner Killeen test of homogeneity of variances to evaluate if there was an equivalent amount of variation in our proxy and acquisition cost data. Second, a proxy should show strong covariation with acquisition costs (Fig. 1, compare spread around 1:1 line), and for this metric we used a spearman rank correlation. Third, a proxy should not be systematically biased (Fig. 1, arrows showing residual deviation from 1:1 line). To calculate this estimation bias, we evaluated the distribution of each proxy's residual deviation from the 1:1 line with a Wilcoxon rank-sum test.

Model conservation plans

We created three model conservation plans to demonstrate how uncertainty in socioeconomic data can affect the performance of a return-on-investment targeting strategy. Given the distribution of recent TNC transactions, we created models that scored these transactions based on their contribution to local and complementarity richness objectives. We defined local richness as the total number of target species represented within a set of protected areas, whereas complementarity richness accounted for the overlap of species across protected areas (Margules & Pressey 2000). Our socioeconomic data came from three sources: the per hectare acquisition costs TNC incurred when acquiring each protected area, TNC's average per hectare acquisition costs within each county, and the average per hectare agricultural land value within each county (NASS 2007). We formulated all reserve selection models as linear integer programming problems (see SI).

RESULTS

Is it possible to downscale average agricultural land values?

We first demonstrated that average agricultural land values had little predictive capacity by all three performance metrics (Fig. 1; comparisons corresponding to diagonal arrows in Fig 2). This coarse-grain proxy had significantly less variation, as its median absolute deviation was less than TNC's acquisition costs (χ^2=55.41, df=38, p=0.034). Average agricultural land values also showed a weak association with TNC's acquisition costs; this was evidenced by a relatively poor rank correlation (r_s=0.484, n=116, p<0.001) and a significant overestimation bias (median=3739 USD ha^{-1}, V=1808, p<0.001).

Are these prediction errors due to spatial averaging or proxy choice?

For our first research question, we asked if this lack of predictive capacity was a result of spatial averaging or proxy choice. If spatial averaging was the cause, our proxy data would have good predictive capacity at matched spatial grains (Fig 2, left panel). However, we found that agricultural land values had little predictive capacity in both fine and aggregated spatial grains. Averaged across bootstrap replicates, parcel-level agricultural land values had a negative rank correlation (ρ=-0.05) as well as a large overestimation bias (median 5245 USD ha^{-1}) in comparison with TNC's parcel-level acquisition costs (Fig 3, top row). At the county-level, average agricultural land values had a marginally significant reduction in variance (χ^2=52.06, df=38 p=0.063), a stronger rank correlation (r_s=0.607, n=116, p<0.001), and median overestimation bias of 4074 USD ha^{-1} (V=5668, p<0.001) in comparison with TNC's average acquisition costs (Fig 3, bottom row). These results both supported the hypothesis that proxy choice was responsible for average agricultural land values' lack of predictive capacity. Further geographic evidence also supported the notion that TNC has not prioritized agricultural parcels for the protection of hardwood forests, as the median slope and elevation of TNC transactions fell in the 70th and 80th percentile, respectively, in comparison with other agricultural parcels in the same county.

How do spatial averaging and proxy choice affect ROI targeting?

For our second research question, we asked how spatial averaging and proxy choice affected a return-on-investment targeting strategy by comparing the total cost of conservation plans based on different sets of socioeconomic data. To isolate the effect of proxy choice, we compared plans based on TNC's average acquisition costs versus average agricultural land values (Fig. 3, bottom row). Average agricultural land values significantly overestimated TNCs average acquisition costs (median 4074 USD ha^{-1}). Consequently, conservation plans based on agricultural land values were consistently more expensive across both of our conservation goals (Fig. 4, compare grey circles and light triangles).

To isolate the effect of spatial averaging, we compared plans based on TNC's acquisition costs versus TNC's average acquisition costs (Fig. 3, left boxes in top and bottom row). In contrast with proxy choice, the effect of spatial averaging varied with our conservation objective (Fig. 4, compare black circles and grey squares across panels). Return-on-investment targeting prioritized areas with the highest ratios of benefits to costs, and plans with perfect cost information were able to protect nearly 20% of EOs based on donations alone. However, spatial averaging obscured these extreme bargains, and resulted in much more expensive conservation plans, especially at low species coverage constraints (left panel, compare grey squares and black

circles). However, this estimation bias was substantially reduced with a complementarity objective (right panel), suggesting our more resolved benefits metric minimized the impact of errors from the spatial aggregation of our socioeconomic data.

DISCUSSION

Spatially aggregated agricultural land values have been predominantly used in the conservation planning literature to cost-effectively prioritize areas for biodiversity protection (Armsworth *in prep*), and in this analysis our goal was to empirically test the predictive capacity of these data in comparison with the acquisition costs of protected areas. By focusing on actual protected area transactions, we were able to separate errors due to spatial averaging versus proxy choice by comparing the predictive capacity of agricultural land values across combinations of spatial grain.

It has previously been suggested that spatially aggregated socioeconomic data would underestimate the cost requirements of a protected area network (Jantke et al. 2013), and we compared model conservation plans based on different sets of socioeconomic data to break down this effect into its spatial averaging and proxy choice components. In contrast to previous work, we found spatial averaging alone had a minimal impact on the total cost of our model conservation plans, as its effect was isolated to scenarios with a low coverage constraint and a local richness objective. However, conservation plans based on TNC's average acquisition costs were largely equivalent to the 'perfect information' scenario for a complementarity objective. This is likely due to increased variation in benefits (Perhans et al. 2008), and suggests that future conservation planning studies may use a more resolved benefits metric to minimize the impact of errors due to spatially aggregated socioeconomic data.

Given the tradeoffs between the resolution and extent of available socioeconomic data, we do not expect other studies to have access to cost information analogous to our case study of recent transactions. However, we found errors due to proxy choice consistently overestimated the cost of biodiversity protection. This result is relevant to conservation planning more generally because it suggests that plans based on agricultural land values, regardless of their level of spatial aggregation, are likely conservative relative to the landscape of future opportunities faced by conservation practitioners. As such, we recommend planning studies collect more relevant socioeconomic data (e.g. undeveloped land values) as opposed to simply increasing the spatial resolution of existing data sources (per Naidoo & Iwamura 2007; Bryan et al. 2011) to increase their utility to conservation practitioners.

SUPPORTING INFORMATION

Geographic Analysis

For our first research question, we asked if average agricultural land values' lack of predictive capacity was a result of spatial averaging or proxy choice. As part of this analysis we compared parcel-level agricultural land values to TNC transactions within the same county. Along with our socioeconomic data, we also extracted the average slope and elevation of each agricultural parcel and TNC transaction based on NASA's digital elevation model from the latest Global Shuttle Radar Topography Mission (Rodrigues et al. 2005). Then, we calculated the empirical cumulative distribution of slope and elevation for all parcels within each county, and used this information to calculate on average where TNC transactions fell in each county's distribution.

Model Formulation

For our second research question, we asked how spatial averaging and proxy choice affected a return-on-investment targeting strategy. To answer this, we compared the total cost of conservation plans based on three sources of socioeconomic data: the per hectare acquisition costs TNC incurred when establishing each protected area, TNC's area-weighted average cost per hectare within each county, and the average per hectare agricultural land value within each county (NASS 2007). To isolate the effect of spatial averaging, we compared conservation plans based on TNC's acquisition costs versus TNC's average acquisition costs. Similarly, to isolate the effect of proxy choice we compared conservation plans that substituted average agricultural land values for TNC's average acquisition costs. We then conducted each comparison for both a local and complementarity richness conservation objective.

We formulated all reserve selection models as linear integer programming problems. Let a_{ij} equal 1 if species $i \in I$ is present in protected area $j \in J$, and 0 otherwise. Let $x_j = 1$ if protected area j is selected for protection, and 0 otherwise. Each plan minimized the cost of protecting a set of protected areas (c_j) subject to a species coverage constraint (Eqn. 1).

$$\min \sum_{j \in J} c_j \bullet x_j \qquad (1)$$

Local Richness Objective

Our local richness objective began by treating all occurrences of target species equally, but assigned more benefits to EOs near large protected areas. All else being equal, protecting a larger area of habitat (h_j) near an EO of a target species should confer a larger benefit than protecting a smaller area, and we weighted this benefit linearly by dividing the total area of land under protection by its proportional coverage of an equal area 5 km buffer (Eqn. 2).

$$\text{Weighted Benefit} = (\text{Species P/A Matrix}) \cdot I\left(\frac{\text{hectares}_{\text{site}}}{\text{hectares}_{\text{buffer}}}\right) \qquad (2)$$

$$\Omega_{ij} = a_{ij} \cdot I\left(\frac{h_j}{h_t}\right)$$

As the identity of target species were all treated equally, our local richness objective only had a single coverage constraint for minimum total benefits, *k* (Eqn. 3).

$$s.t.\ x_j \cdot \sum_{i \in I} \Omega_{ij} \geq k \qquad (3)$$

We evaluated the impact of altering our socioeconomic data by comparing the total cost of conservation plans (Eqn. 2) along a gradient of coverage constraints (Fig. 4, x axes). For a local richness objective, we increased k from 0 to 1.51, the total weighted species richness of all protected areas, with 151 equal interval constraints

Complementarity Richness Objective

In contrast with our local richness objective, our complementarity richness objective only valued species that had not already been covered in a set of protected areas (Margules and Pressey, 2002). However, in contrast with the area-weighted benefits metric for our local richness objective, we assigned equal benefits to EOs different sized protected areas. Specifically, we assumed if protected area *j* is selected for protection, then all known occurrences of target species in a 5 km buffer were protected.

Let $y_i = 1$ if a species is randomly selected for protection. Our complementarity objective had the same objective function as a local richness objective (Eqn. 1), but had many constraints as species that were randomly selected for protection (Eqn. 4).

$$s.t.\ \sum_{i \in I} a_{ij} \cdot x_j \geq y_i \qquad (4)$$

For this objective, the total cost of prioritized areas was potentially sensitive to the identity of species selected for protection (y_i). To avoid this issue, we used 1000 bootstrap replicates to randomly select a given number of species for protection, we then reported the average cost across these replicates for our complementarity objective.

APPENDIX I

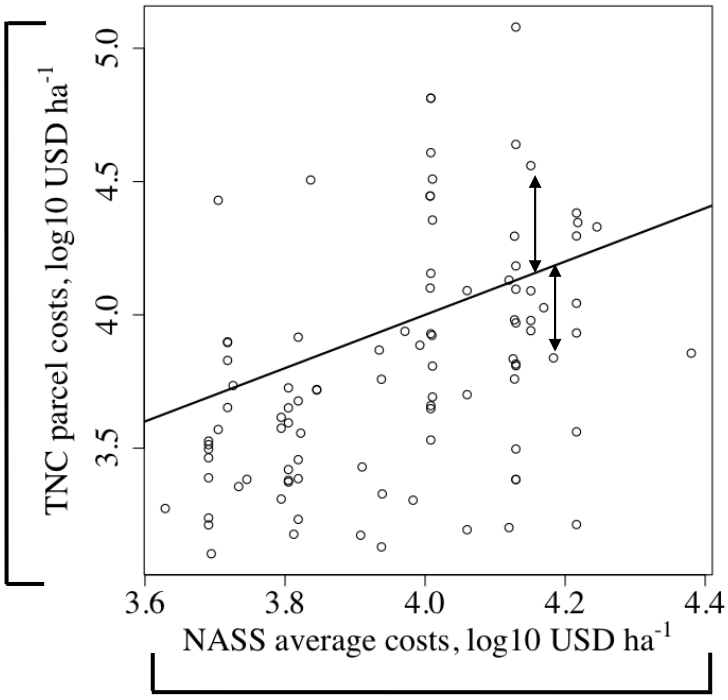


Figure 1. Bivariate plot of average agricultural land values at the county level compared to the parcel-level acquisition costs incurred by The Nature Conservancy when establishing protected areas. The 1:1 line is shown in solid. This proxy has less variance (compare scaling x and y axes) as well as minimal covariation (spread around 1:1). More pertinently for other studies, average agricultural values significantly overestimate the acquisition costs of protected areas (compare length of cumulative arrows above and below 1:1 line).

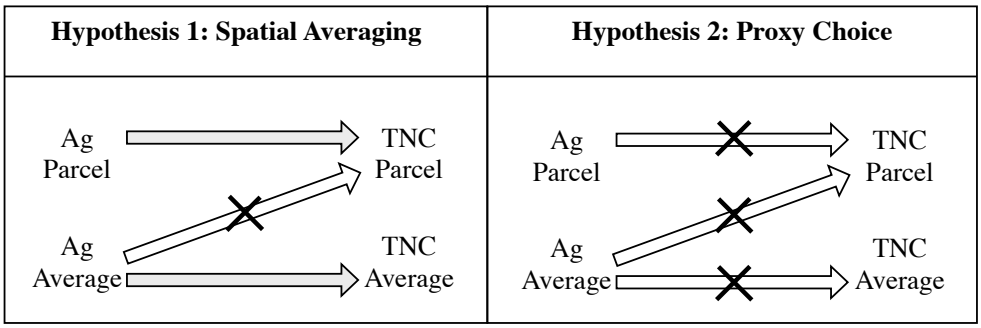


Figure 2. The expected predicted capacity of agricultural land values across three combinations of spatial grain. In Figure 1 we demonstrated that average agricultural land values could not be reliably downscaled to predict The Nature Conservancy's parcel-level acquisition costs (middle arrow). If this is due to spatial averaging, we would expect these data to have a better predictive capacity at matched spatial grains (left panel). In contrast, if this is due to proxy choice, we would expect our proxy data to have little predictive capacity across all combinations of spatial grain (right panel).

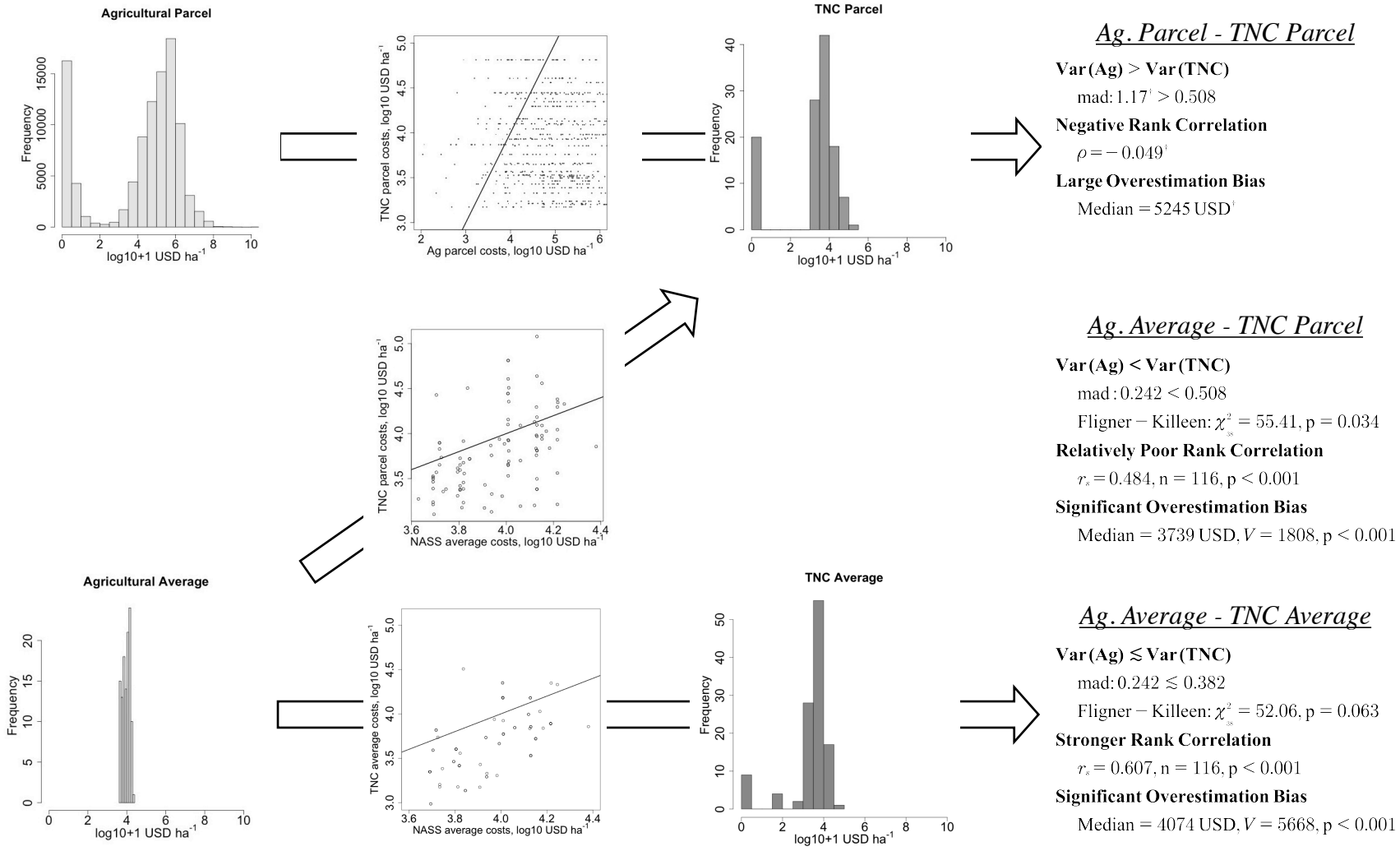


Figure 3. Histograms and bivariate plots compare agricultural land values to the acquisition costs of establishing protected areas across three combinations of spatial grain. 1:1 lines in bivariate plots are shown with solid line. Results details how each proxy compared by three performance metrics. Despite having a similar amount of variation, fine-grain agricultural land values are a poor proxy for the costs of protected areas (top panels). In contrast, average agricultural land values more reliably predict the average costs of protected areas (bottom panels).

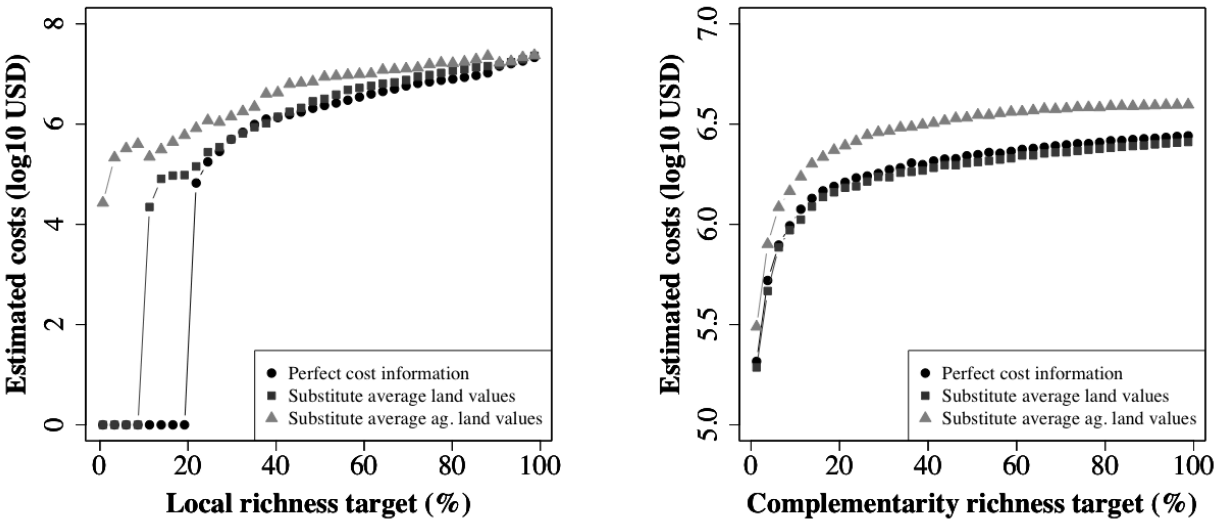


Figure 4. Errors due to proxy choice result in conservation plans that substantially overestimate the costs of protected areas for both a local (left panel) and a complementarity richness objective (right panel). All conservation plans were based on a return-on-investment targeting strategy that minimized the cost of a reserve network subject to species coverage constraint. For our complementarity objective, we used bootstrap replicates to randomly select a given number of species, and we presented the average costs of those simulations in the right panel.

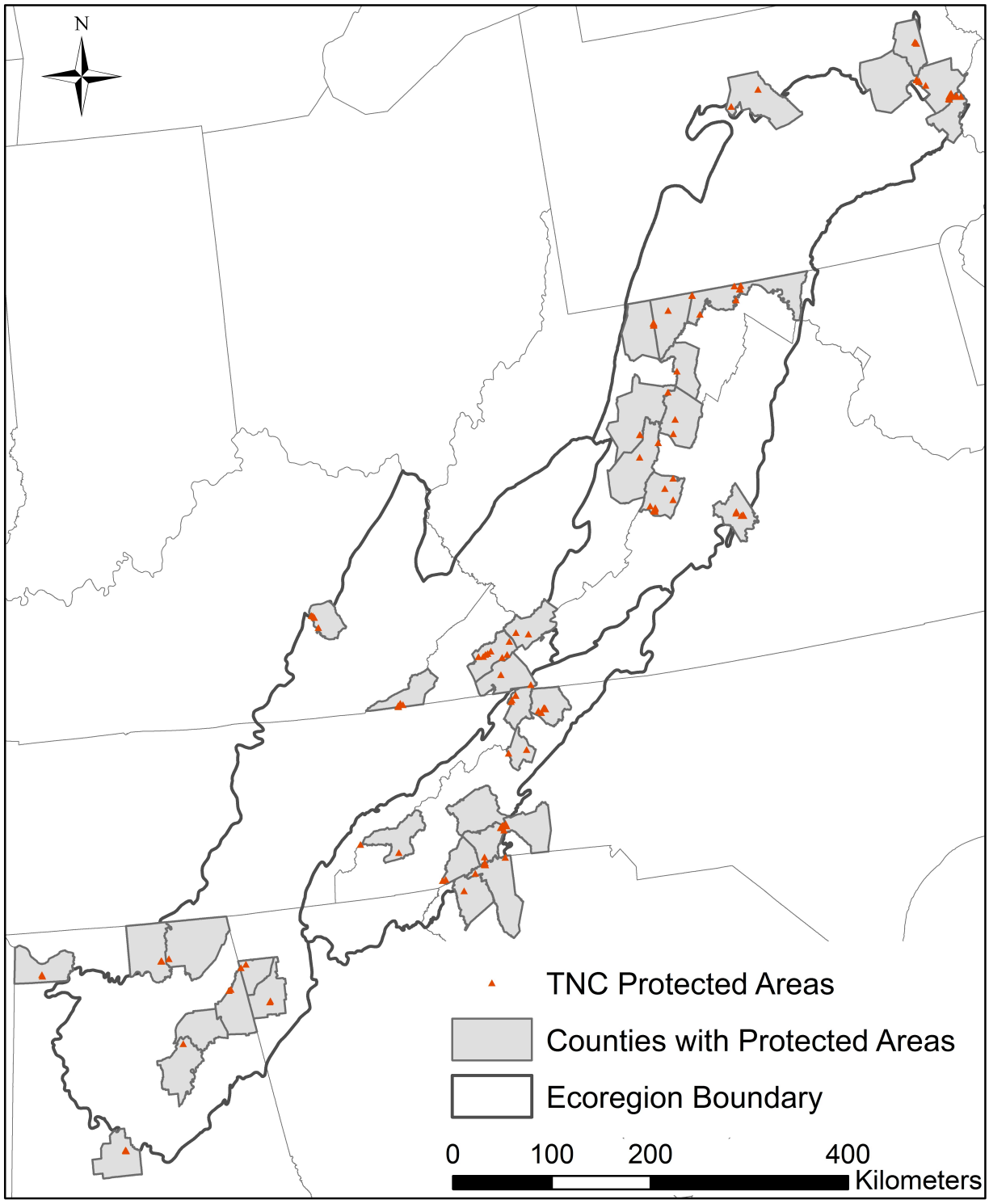


Figure 5. The spatial distribution of 116 recent fee-simple acquisitions made by the Nature Conservancy to protect hardwood forests in the Central and Southern Appalachians. We created model conservation plans that prioritized between these protected areas (shown here in orange) based on known occurrences of species-level conservation targets.

CHAPTER 2:

The spatial grain of acquisition cost and biodiversity benefit data determines the apparent effectiveness of an opportunistic conservation strategy

A version of this chapter will be published by Nathan J. Sutton and Paul R. Armsworth:

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This chapter does not reflect changes that will happen before publication during the internal and external review process. Nathan Sutton developed the idea for this manuscript, conducted the analysis, and wrote the manuscript. Paul Armsworth is a co-author of this work, and was responsible for feedback at early stages of this manuscript's development, providing the necessary transactional data from the Nature Conservancy, and helping with editing.

ABSTRACT

Facing tight resource constraints, conservation organizations must allocate funds available for habitat protection effectively. Often, they combine socioeconomic and biological data when prioritizing land for protection, and our goal is to test how sensitive resulting prioritizations are to the differences in the spatial grain of these data. To accomplish this, we demonstrate how the conclusion of a classic debate in conservation planning between cost and benefit targeting depends on the spatial grain of the data being used. As a case study, we derived parcel-level acquisition cost and biodiversity benefit data from land transactions recently undertaken by a conservation nonprofit to protect forests in the eastern US. We find that the relative performance of cost and benefit targeting is sensitive to the spatial grain of the data when prioritizing parcels based on local species richness. However, when accounting for complementarity, we find that benefit targeting consistently outperforms a cost targeting strategy regardless of the spatial grain of the data involved. More pertinently for other studies, we find that combining data collected over different spatial grains inflates the apparent effectiveness of an opportunistic targeting strategy.

INTRODUCTION

To stem ongoing habitat loss, many conservation organizations acquire land to establish protected areas, and given limited budgets, practitioners have developed resources to help prioritize areas for protection (Groves 2002; TNC 2010). The academic conservation literature also has created a rich theory of prioritization (Murdoch et al. 2007) as well as spatial planning software (Moilanen et al. 2005; Ball et al. 2009) to help conservation organizations allocate resources for protection efficiently. Increasingly, these prioritization approaches combine biological and socioeconomic data (Table 1). However, to date many conservation assessments lack robustness checks examining how sensitive resulting prioritizations are to the data used to support them (Langford et al. 2009). Of particular relevance to this study, few have examined how sensitive prioritizations are to the way in which socioeconomic and biological data are combined (but see Carwardine et al. 2008b; Hermoso et al. 2013 for examples).

One source of uncertainty in conservation planning concerns the spatial grain, or resolution, of the socioeconomic and biological data involved. Prioritization studies often rely on datasets that have been aggregated within counties, ecoregions, or large grid squares (Table 1). Coarsening to larger spatial grains is an averaging process that can obscure spatial patterns in biodiversity variation, but can be controlled by creating planning units at the same spatial grain as the biodiversity data. However, it is more difficult to match the grain of biological data, socioeconomic data, and planning units in concert. In a review of eighteen prominent conservation planning studies (Table 1), order of magnitude disparities in the spatial grain of the cost data and choice of planning units were common, especially among studies covering larger spatial extents. For example, Jantke et al. (2011) used the average agricultural land values of European countries (avg. 134,747 km^2) to prioritize wetlands within much smaller planning units (avg. 300 km^2). These grain mismatches can be a problem if, as is typically the case, uncertainty is not carried over into the resulting conservation plan, for example, through robustness checks conducted over different spatial grains (Rae et al. 2007).

Our goal is to use a classic debate between opportunistic and systematic conservation planning to exemplify how these strategies are sensitive to the spatial grain of the biological and socioeconomic data used. Specifically, we compare a simplified opportunistic conservation strategy, or cost targeting, with a more biodiversity-centered, or benefits targeting approach. We define cost targeting as a strategy that maximizes the total size of a set of protected areas. Using the classification for different types of conservation opportunity per Moon et al. (in prep), we consider cost targeting to be opportunistic in that it prioritizes a set of existing opportunities based on their socioeconomic costs. In contrast, we define benefit targeting as a strategy that maximizes biological benefits without regard to variation in the socioeconomic costs. Babcock

et al. (1997) first introduced the distinction between these two approaches, and numerous conservation planning studies have drawn contrasts between them (Ferraro 2003; Moore et al. 2004; Naidoo & Iwamura 2007; Bode et al. 2008). We also compare the relative performance of cost targeting and benefit targeting to a more integrative return-on-investment (ROI) framework that combines costs and benefits to identify locations that offer a high biodiversity return per dollar invested (Murdoch et al. 2007). Contrasting cost targeting with benefit targeting in this way is clearly a simplification of the practice of conservation planning. The concept of "opportunistic" conservation now refers to the social and economic context of biodiversity protection (Game et al. 2010; Guerrero et al. 2010), while "systematic" conservation recognizes the importance of including variation in costs in the planning process (Margules & Pressey 2000). However, we revisit this rather stylized academic debate to more generally show how conservation plans can be sensitive to the spatial grain of the socioeconomic and biological data used to support them.

Various authors have demonstrated that the relative performance of cost and benefit targeting depends on the amount of variation in costs and benefits as well as on their correlation across the landscape (Babcock et al. 1997; Ferraro 2003). In applying these ideas, some studies have argued that cost targeting outperforms benefit targeting (Moore et al. 2004; Naidoo & Iwamura 2007; Perhans et al. 2008). However, only Perhans et al. (2008) took care to match the spatial grain of their biodiversity and cost data. This grain-matching is important because the amount of variation and correlation of costs to benefits will depend on the spatial grain of the data being used (Pautasso 2006; Hurlbert & Jetz 2007).

We address the following questions: i) does spatial variation in acquisition costs trump spatial variation in biodiversity benefits when prioritizing areas for protection? ii) how does each strategy compare to a more integrative ROI approach? and most importantly, iii) how sensitive are those results to the spatial grain of the socioeconomic and biological data being used? The closest antecedent to the results that we present is the work of Jantke et al. (2013): who suggested the use of coarse-grain data in conservation planning would lead planners to underestimate the cost and area requirements of a reserve network. However, even that study had a significant disparity between the grain of its biodiversity data (50 km^2), cost layers (85 km^2), and planning units (ranged from 0.01 to 180,000 km^2, avg. 300 km^2). In contrast with previous conservation planning studies, our unusual parcel-level data allows us to compare the amount of variation in costs and benefits more cleanly, and to quantify how spatial averaging affects the relative performance of cost and benefit targeting for two common conservation objectives.

METHODS

Acquisition cost data

Our acquisition cost data were based on the same sample of recent transactions as the previous chapter, but with two important differences. First, we included conservation easements transactions in addition to fee-simple acquisitions, and this increased our sample size of transactions from 116 to 155. Second, we focused on TNC's total project cost as opposed to the acquisition cost of each protected area. Total project costs included any upfront stewardship endowment or fees associated with the transaction. These additional costs ranged from 1 to 100% of total project costs, with an average of 56%. We extracted the total project cost, parcel size, and transaction type from TNC's Conservation Lands System database. All cost data were converted to 2005 US dollars using the consumer price index (BLS 2014). To aggregate parcel-level costs, we calculated the average cost per hectare within each county, and then multiplied this average by the total hectares of each protected area.

Biodiversity data

In this chapter represented biodiversity benefits with same set of known occurrences of target species as Chapter 1. Specifically, these data represent all known EOs of target species within a 5 km buffer of our sample of protected area acquisitions. We defined the weighted species richness (Ω) of each transaction by two factors: parcel area (a) and transaction type (w). All else being equal, protecting a larger area of habitat near an EO of a target species should confer a larger benefit than protecting a smaller area, and we assume this benefit scaled linearly with the size of the protected parcel. We also assumed that conservation easements would confer less biodiversity benefits than fee-simple acquisitions because these transactions only limit a portion of a landowners' bundle of property rights (Rissman et al. 2007). Let J denote a set of protected areas. We estimated the fine-grain biodiversity benefit of purchasing each protected area as:

$$\text{Weighted Richness} = \left(\frac{\text{area}_j}{\text{area}_{buffer}}\right) \cdot \text{easement weight} \cdot \text{local richness} \qquad (1)$$

$$\Omega_j = \left(\frac{a_j}{a_T}\right) \cdot w_j \cdot b_j$$

To aggregate fine-grain weighted richness, we pooled the species present within a county, and modified the buffer area denominator to include the total buffer area within the county. We then calculated the coarse-grain weighted richness of purchasing each protected area as:

$$\text{Agg. Weighted Richness} = \left(\frac{\text{area}_j}{\text{area}_{cty\ buffer}}\right) \cdot \text{easement weight} \cdot \text{county richness} \qquad (2)$$

$$\Omega_j = \left(\frac{a_j}{a_T}\right) \cdot w_j \cdot b_j$$

Study design

We refer to parcel-level acquisition costs and biodiversity benefits of protected areas as our fine-grain data, or scenario A. We then average these data to the county-level and refer to the averages as our coarse-grain data, or scenario D. We define a mismatch grain as combining data sources created at different spatial resolutions, or scenarios B and C. We also consider two common conservation objectives, namely maximizing local richness and complementarity richness. Table 3 summarizes how we compared the relative performance of cost and benefit targeting across four combinations of spatial grain and two conservation objectives. We restricted all models to the purchase entire parcels. Our maximum budget was consistent across scenarios, and was the sum of TNC's total project costs for all 155 protected areas. We ran each model at 2% budget intervals up to a 50% total budget.

Local Richness Modeling Framework

For the conservation goal of maximizing local species richness without considering complementarity, we compared the relative performance of cost and benefit targeting with the ROI solution. Let c_j represent the cost each protected area, and C total budget. Let $x_j = 1$ if protected area j is selected, and 0 otherwise. Under these conditions, the return-on-investment model picked a set of protected areas that maximized the weighted richness of the reserve network subject to satisfying an overall cost constraint – this is similar to prioritizing protected areas that offer the highest benefit to cost ratio. Benefit targeting had the same objective function, but picked protected areas without regard to their cost until the budget limit was reached. This is equivalent to ranking protected areas by their weighted richness, and picking them until a budget constraint is reached. In contrast, cost targeting maximized the overall area of the reserve network by prioritizing protected areas offering a low cost per hectare. Biodiversity benefits were not part of the objective function for cost targeting, and were calculated after reserve selections were made. We coded all the variations of local richness reserve selection as a linear integer programming problems in Eqn. 3, and used a branch and bound algorithm to find an optimal solution.

$$\begin{aligned}
&\text{Return on Investment:} && \max_{\underset{\sim}{x}} \sum_{j \in J} \Omega_j \bullet x_j && \text{subject to} && \sum_{j \in J} c_j \bullet x_j \le C \\
&\text{Benefit Targeting:} && \max_{\underset{\sim}{x}} \sum_{j \in J} \Omega_j \bullet x_j && \text{subject to} && \sum_{j \in J} c_j \bullet x_j \le C \ \text{(blind)} \\
&\text{Cost Targeting:} && \max_{\underset{\sim}{x}} \sum_{j \in J} a_j \bullet x_j && \text{subject to} && \sum_{j \in J} c_j \bullet x_j \le C
\end{aligned} \tag{3}$$

Complementarity Richness Modeling Framework

For the conservation goal of maximizing the complementarity richness of a set of protected areas, we adapted a formulation of a maximal expected coverage problem presented by Polasky et al. (2000). For these scenarios we allocated biodiversity to parcels in the same way as

a local richness objective (Eqn. 1), but interpreted this species weight (Ω) as a probability of persistence of a given element occurrence due to nearby investment. Let X_{ij} equal 1 if species i has a known occurrence in a buffer of a protected area. Let P_{ij} be equal to the probability that species $i \in I$ persists in a buffer of protected area $j \in J$ due to nearby investment, and assume this probability of persistence P_{ij} and P_{hk} is independent for $i \neq h$ and $j \neq k$. The probability that species i persists in a set of protected areas due to nearby investment is one minus the probability that species i persists in no selected protected area (Eqn. 4).

$$P_i = 1 - \prod_{j \in J} (1 - P_{ij} X_{ij}) \tag{4}$$

To aggregate these persistence probabilities to the county-level, we followed the same procedure outlined for local species richness (Eqn. 2). Our formulation of complementarity reduces the additional benefits of repeat EOs by a fraction, and not entirely as in other studies (Margules & Pressey 2000).

We assumed that if TNC purchased the entire buffer surrounding a protected area, then the probability that each species within that buffer would persist is equal to one. For simplicity, we assumed the probability of persistence decreased linearly as the proportion of area purchased to the buffer gets smaller, and by some fraction for conservation easements. Assuming independence between EOs across the landscape in this manner is obviously a simplification, as it does not account for habitat connectivity or species interactions. However, it still offers a considerable advance over the more common practice in relevant conservation planning studies of not considering persistence probability at all (Ando et al. 1998; Bode et al. 2008). For more comprehensive methods that handle persistence probabilities and habitat quality in conservation planning, see Araújo & Williams (2000), Cabeza (2003), or Visconti et al. (2010).

The goal of the ROI model was to pick a set of parcels that had the greatest summed probability of persistence of all species. Benefit targeting had the same objective function, but picked parcels without regard to the budget constraint until the budget was exhausted. The selections of cost targeting were the same in both local and complementarity richness, as the objective function did not include any measure of biodiversity. For a complementarity richness goal we coded all ROI and benefit targeting reserve models as a nonlinear integer programming problem, and then used repeat simulations of an evolutionary search algorithm to find a near-optimal solution (Mebane & Sekhon 2011).

$$\begin{array}{lll} \text{Return on Investment:} & \max_{\underset{\sim}{x}} \sum_{i \in I} P_i & \text{subject to} \quad \sum_{j \in J} c_j \cdot x_j \leq C \\ \text{Benefit Targeting:} & \max_{\underset{\sim}{x}} \sum_{i \in I} P_i & \text{subject to} \quad \sum_{j \in J} c_j \cdot x_j \leq C \text{ (blind)} \\ \text{Cost Targeting:} & \max_{\underset{\sim}{x}} \sum_{j \in J} a_j \cdot x_j & \text{subject to} \quad \sum_{j \in J} c_j \cdot x_j \leq C \end{array} \tag{5}$$

Comparison of relative performance

For each scenario we compared the relative performance of different targeting strategies by the number and identity of species present in the selected protected areas. For a local richness conservation objective, this is the sum of the weighted species richness (Ωj). For a complementarity richness conservation objective, we accounted for species overlap between protected areas (Eqn. 6).

$$\text{Local Richness Performance}: \sum_{j \in J} \Omega_j \bullet x_j \qquad (6)$$

$$\text{Complementarity Richness Performance} \sum_{i \in I} [1 - \prod_{j \in J} (1 - P_{ij} X_{ij})]$$

For our first research question our goal is to test the hypothesis that cost targeting outperforms benefit targeting. To accomplish this, we calculated each performance metric for cost, benefit, and ROI targeting in each scenario. Then, we subtracted the performance of cost targeting from benefit targeting, and standardized this difference by the performance of ROI targeting.

$$\text{Relative Performance}\,(\%) = \frac{\text{Cost targeting} - \text{Benefit Targeting}}{\text{ROI targeting}} \qquad (7)$$

For our second research question, our goal is to compare how cost and benefit targeting strategies compare to a more integrative ROI approach. To do this, we altered our performance metric as follows:

$$\text{Relative Performance}\,(\%) = \frac{\text{ROI targeting} - \text{Cost Targeting}}{\text{ROI targeting}} \qquad (8)$$

To calculate the relative performance of ROI targeting v benefit targeting, we followed the same strategy outlined above (Eqn. 8). We expect the relative performance of each targeting strategy to vary across budgets; to turn these distributions into a single comparative statistic, we calculated the average relative performance across budgets in all combinations of spatial grain.

RESULTS

Summary statistics of cost and benefit data

TNC's total project costs ranged from 0 to 143,000 USD ha^{-1}, with a median of 3,990 USD ha^{-1} and interquartile range of 10,800 USD ha^{-1}. Species richness within a 5 km buffer of TNC acquisitions ranged from 0 to 19 species, with a median of 1 and interquartile range of 2 species. The coefficient of variation for fine-grain costs (CV=1.89) and local species richness (CV=1.87) was similar. This demonstrates that fine-grain variation in acquisition costs is on par with variation in the species richness of protected areas.

Do acquisition costs trump biodiversity benefits?

For our first research question, we asked if spatial variation in acquisition costs trumped spatial variation in biodiversity benefits when prioritizing areas for protection. This question is

best answered by comparing the relative performance of cost and benefit targeting with our fine-grain data (Fig. 6, scenario A, far left panels, compare open and grey symbols). We found fine-grain variation in species richness to be on par with TNC's acquisition costs, and as a result the relative performance of cost and benefit target was roughly equivalent. When we look at relative performance across all budgets using Eqn. 7, cost targeting was only an average of 7% more efficient than benefit targeting. A similar finding held for a more resolved complementarity richness objective (Fig. 6, A2, bottom left panel, compare open and grey symbols). Although benefit targeting appeared advantageous in scenarios with small budgets, when averaged across all budget level cost targeting was only 10% less efficient than benefit targeting.

How do cost and benefit targeting compare to a more integrative ROI approach?

For our second research question, we asked how each strategy compared to a more integrative ROI approach. This is best answered by comparing the relative performance of ROI targeting versus cost and benefit targeting with our fine-grain data (Fig. 6, scenario A, far left panels, compare black with open and grey symbols). As expected, ROI targeting was more efficient than targeting costs or benefit in isolation for both conservation objectives (Eqn. 8). ROI targeting was an average of 25% and 24% more efficient than cost targeting for local richness and complementarity richness objectives, respectively. However, the relative performance of ROI targeting compared with benefit targeting varied more widely between objectives, and was an average of 32% more efficient for a local richness objective (A1, top left panel), but only 15% more efficient for a complementarity objective (A2, bottom left panel).

Relative performance of cost and benefit targeting with spatial grain

Next, we tested how our previous conclusions would change if coarser grain data were used. Differences in the relative performance of cost and benefit targeting between spatial grains can be attributed to changes in: i) the amount of underlying variation in costs and benefits, or ii) the correlation between costs and benefits. We found no change in the correlation of fine-grain acquisition costs and species richness (rho=0.10, p=0.209 n=155), and aggregating these data to the county-level did not alter this trend (rho=0.015, p=0.852, n=155). However, aggregation did reduce the amount of variation in both data sources. When we averaged costs within each county, it reduced the coefficient of variation of TNC's total project cost per hectare from 1.89 to 0.86. Aggregating benefits to a county-level pool decreased the coefficient of variation of species richness from 1.87 to 1.04.

To evaluate the potential for large-scale conservation planning studies to be sensitive to spatial grain, we compared the performance of cost and benefit targeting with models based on fine and coarse-grain cost data and benefit data (Fig. 6, scenarios A & D, far left and right panels, compare open and grey symbols). We found that reductions in variance from spatial averaging

did not alter the relative performance of cost and benefit targeting for a local richness objective (scenarios A1 and D1). Cost targeting was an average of only 1% more efficient than benefit targeting with coarse-grain data in contrast with 7% more efficient with fine-grain data. However, benefit targeting was substantially improved by using coarse-grain data with a complementarity objective (scenario A2 and D2). Benefit targeting was an average of 25% more efficient than cost targeting with coarse-grain data, as opposed to 10% with fine-grain data.

Impact of spatial grain varies with conservation objective

The widest swings in the relative performance of cost and benefit targeting occurred when data were combined over different spatial grains with a local richness objective (Fig. 6, scenarios B1 & C1, middle panels, compare open and grey symbols). For example, with only coarse-grain cost data (scenario B1), cost targeting was an average of 16% more efficient than benefit targeting across all budgets. In contrast, with only coarse-grain benefit data (Fig. 6, scenario C1), cost targeting was an average of 40% less efficient than benefit targeting. These results suggest matching the spatial grain of socioeconomic and biological data is important, and that combining data over different resolutions can inflate the apparent effectiveness of an opportunistic conservation strategy (Table 3).

In contrast, benefit targeting consistently outperformed cost targeting across all combinations of spatial grain for a complementarity richness objective (Fig. 6). In models with fine-grain cost data, cost targeting was an average of 10% (scenario A2) or 12% (scenario C2) less efficient than benefit targeting. However, this gap increased to an average 30% (scenario B2) and 45% (scenario D2) less efficient with models based on coarse-grain cost data. This result suggests that when combining data over different spatial grains, a more resolved complementarity objective may errors due to spatial aggregation.

DISCUSSION

We revisited a stylized version of the academic debate between cost and benefit targeting to demonstrate how the prioritization of protected areas is sensitive to the spatial grain of the socioeconomic and biological data being used. To accomplish this, we collected parcel-level data on both the acquisition costs and biodiversity benefits of protected areas. We used these data to answer if variation in costs trumped variation in benefits when selecting areas for protection, as well as how cost and benefit targeting compared to a more integrative ROI approach. Then, we aggregated this parcel-level data within a county to evaluate how combining data over different spatial resolutions affected the relative performance of cost and benefit targeting.

Our results demonstrate that prediction errors due to spatial aggregation has an impact on the relative efficiency of a return-on-investment targeting strategy. Errors from spatial aggregation may misestimate the costs of a parcel, or cause the different selection of parcels for protection (Jantke et al. 2013). This has broader significance because large-scale conservation planning studies frequently average cost data within larger planning units (Naidoo & Iwamura 2007; Murdoch et al. 2007). For example, Naidoo & Iwamura (2007) estimated the net present value of agriculture throughout the globe at a spatial resolution of ~85 km^2, and used these data to compare the relative performance of cost and benefit targeting within 825 ecoregions (avg. 10,279 km^2). They suggested that ROI targeting of endemic species could protect the same amount of biodiversity at 12% of the cost. In contrast, in our case study of recent investments we found that ROI targeting only covered the same set of species at 85% the cost of benefit targeting when working over a smaller spatial extent and finer grain.

More pertinently for other studies, our results suggest that combining data over different spatial grains can inflate the apparent effectiveness of an opportunistic conservation strategy. Previous estimates of the relative advantage of cost targeting are as high as 40% for a single budget (Moore et al. 2004), but these estimates were derived by combining coarse-grain cost data in smaller planning units (Table 1). In contrast, in our example we found the relative performance of cost targeting was only an average of 7% more efficient than benefit targeting when working over a smaller spatial extent and grain. The notion that socioeconomic data trumps biological data when prioritizing areas for protection has transitioned from the planning literature (Moore et al. 2004; Naidoo & Iwamura 2007; Bode et al. 2008) into conservation science textbooks (Kareiva & Marvier 2011). However, few of these studies carefully account for the impact of spatial grain when combining socioeconomic and biological data over large extents. We find that fine-grain variation in species richness is roughly on par with TNC's per hectare acquisition costs, and as result the performance of cost and benefit targeting is broadly equivalent.

We made a number of assumptions to build a model conservation plan, and we conducted sensitivity tests on two major assumptions to verify the relative performance of cost and benefit targeting was sensitive to spatial grain (see SI). First, it is possible our attribution of biodiversity benefits to conservation easements could introduce bias our prioritization, and to test this we conducted a sensitivity test in which we reduced the fractional weighting of biodiversity for easements transactions from 50% to 5%. Second, we made a choice to represent biodiversity with known EOs of target species within a 5 km buffer of protected areas; as a sensitivity test, we doubled this radius to 10 km. In both sensitivity tests we found that variation in biodiversity benefits was substantially reduced. While the absolute performance cost and benefit targeting

varied across these sensitivity tests, our conclusion that the apparent effective of these targeting strategies was sensitive to spatial grain held was consistent (Fig. 7 and 8).

We are not advocating an either-or approach to conservation planning, as a return-on-investment framework clearly outperforms both cost and benefit targeting. Instead, our goal is to show that the grain of socioeconomic and biological data affects the outcome of a spatial prioritization. Given the tradeoffs between the resolution and extent of available data, large-scale conservation planning studies have relied on coarse proxies for the socioeconomic costs of protected areas. This averaging is a problem because it suppresses the variation in costs that return-on-investment targeting relies on to prioritize land for protection. When uncertainty information is not available, as in the case of average agricultural land values derived from census data (Ando et al. 1998; Strange et al. 2006; Murdoch et al. 2007; Chiozza et al. 2010), we recommend that the goals of a conservation plan be fit to purpose by matching the spatial grain of the planning units with its cost data. However, uncertainties in costs are often discarded in models of agricultural productivity (Naidoo & Iwamura 2007; Adams et al. 2010; Carwardine et al. 2010b; Visconti et al. 2010; Withey et al. 2012). In these cases, we suggest there is scope to retain uncertainty in conservation planning with cross-scale modeling approaches such as sensitivity analyses (Crosetto & Tarantola 2001), hierarchical model specifications (Gotway & Young 2002), and other related techniques (Holzkämper & Seppelt 2007).

SUPPORTING INFORMATION

Sensitivity tests

We conducted sensitivity tests to evaluate if our main conclusion, namely that the relative performance of cost and benefit targeting is sensitive to spatial grain of the underlying data being used, was sensitive to our choice of buffer distance or assignment of species richness to conservation easement transactions.

Easement Weighting Sensitivity Test.

We fractionally weighted the biodiversity benefits of easement transactions in contrast with fee-simple acquisitions for two reasons. First, easements are a flexible contractual agreements that only limit part of a landowner's "bundle of rights", and may limit further subdivision while allowing for continued timber harvesting or agricultural practices (Rissman & Merenlender 2008) Second, the acquisition biodiversity protection of conservation easements depends on enforcement and monitoring by the easement holder, and in a recent survey of TNC activities only 20% of easements were found to be quantitatively monitored for biodiversity (Rissman et al. 2007).

We evaluated if our general conclusion was sensitive to our assignment of benefits to easement transactions by manipulating our weighting parameter (w). Our main text analysis we weighted species richness in easements transactions at half the value of fee-simple acquisitions (w=0.5). As a sensitivity test, we only weighted easement biodiversity by five percent (w=0.95), and then repeated this scenario across 5% budget intervals in all combinations of spatial grain.

Reducing our fractional weighting of easement transactions also reduced variation in weighted species richness in our sensitivity test (CV=2.93) in contrast with our main text results (CV=3.08). This trend also held when we aggregated biodiversity benefits to the county-level in our sensitivity test (CV=3.67) and main text results (CV=4.05). This reduction in variation reduced the performance of benefit targeting across all combinations of spatial grain (Fig. 7, all scenarios, compare open and grey symbols). However, the relative performance of cost and benefit targeting still varied with the spatial grain of the data being used (Table 4). For example, while cost and benefit targeting were equivalent with fine-grain data and a complementarity objective (scenario A2), when aggregating cost data in isolation cost targeting an average of 12% less efficient than benefit targeting.

Buffer Criterion Sensitivity Test

Due to the small size of most TNC's acquisitions, we buffered each parcel's centroid by 5 km to capture more spatial variation in known element occurrences of target species. We doubled the radius of this criterion to 10 km to verify our general conclusion was not sensitive to our choice of buffer distance. We repeated these scenarios runs 5% budget intervals in all spatial grain combinations. Increasing this buffer distance is a spatial averaging process akin to aggregating species richness to the county level. As such, we expect diminished variation as well as the performance of benefit targeting across scenarios this sensitivity test.

As expected, increasing the buffer distance to 10 km reduced variation in parcel-level weighted species richness (CV=1.13) as opposed to a 5 km buffer (CV=3.08). The further aggregation of 10 km richness to a county-level species pool also substantially diminished variation in benefits (CV=1.01) in contrast with a 5 km buffer (CV=4.05). Furthermore, the reduction of variation in parcel-level benefits substantially reduced the performance of benefit targeting across all scenarios (Fig. 8). Although increasing the buffer criterion diminished the performance of benefit targeting, there were still combinations of spatial grain in where benefit targeting outperformed cost targeting for a complementarity objective (Fig. 8, scenario B2, compare open and grey symbols). As such, while the absolute performance of cost and benefit targeting in this sensitivity test was not consistent with our main text results, the apparent effectiveness of cost and benefit targeting still varied with the spatial grain of the underlying data being used (Table 5). For example, cost targeting was consistently less efficient than benefit

targeting in scenarios with fine-grain benefit data and a complementarity objective (scenarios A2 and B2), but this was reversed when coarse-grain benefit data were used (scenarios C2 and D2).

APPENDIX II

Table 2. Summary of model scenarios across spatial grains and conservation objectives

	Parcel data *TNC's parcel-level acquisition costs* & *Element occurrences of target species within a 5 km buffer*	Coarsen costs *Aggregate costs within each county*	Coarsen benefits *Aggregate element occurrences in buffer to county-level pool*	Coarsen both *Aggregate costs within each county* & *Aggregate element occurrences in buffer to county-level pool*
local richness	scenario A1	scenario B1	scenario C1	scenario D1
complementarity richness	scenario A2	scenario B2	scenario C2	scenario D2

Table 3. The average relative performance of cost, benefit, and ROI targeting across spatial grains and conservation objectives.

	Parcel data	Coarsen costs	Coarsen benefits	Coarsen both
local richness	C – B = 7% ROI – B = 33% ROI – C = 25%	C – B = 16% ROI – B = 59% ROI – C = 43%	C – B = -40% ROI – B = 27% ROI – C = 66%	C – B = 1% ROI – B = 52% ROI – C = 51%
complementarity richness	C – B = -10% ROI – B = 15% ROI – C = 24%	C – B = -30% ROI – B = 12% ROI – C = 42%	C – B = -12% ROI – B = 4% ROI – C = 17%	C – B = -25% ROI – B = 26% ROI – C = 50%

Table 4. The average relative performance of cost, benefit, and ROI targeting across all combinations of spatial grain and conservation objective in our easement sensitivity test.

	Parcel data	Coarsen costs	Coarsen benefits	Coarsen both
local richness	C – B = 12% ROI – B = 35% ROI – C = 23%	C – B = 17% ROI – B = 61% ROI – C = 43%	C – B = 9% ROI – B = 24% ROI – C = 15%	C – B = 15% ROI – B = 61% ROI – C = 46%
complementarity richness	C – B = 0% ROI – B = 20% ROI – C = 21%	C – B = -12% ROI – B = 29% ROI – C = 41%	C – B = 59% ROI – B = 72% ROI – C = 13%	C – B = 20% ROI – B = 64% ROI – C = 44%

Table 5. The average relative performance of cost, benefit, and ROI targeting across all combinations of spatial grain and conservation objective in our buffer sensitivity test.

	Parcel data	Coarsen costs	Coarsen benefits	Coarsen both
local richness	C – B = 27% ROI – B = 40% ROI – C = 13%	C – B = 47% ROI – B = 75% ROI – C = 28%	C – B = 27% ROI – B = 38% ROI – C = 11%	C – B = 40% ROI – B = 65% ROI – C = 25%
complementarity richness	C – B = 15% ROI – B = 26% ROI – C = 10%	C – B = -7% ROI – B = 18% ROI – C = 25%	C – B = 35% ROI – B = 43% ROI – C = 8%	C – B = 18% ROI – B = 39% ROI – C = 21%

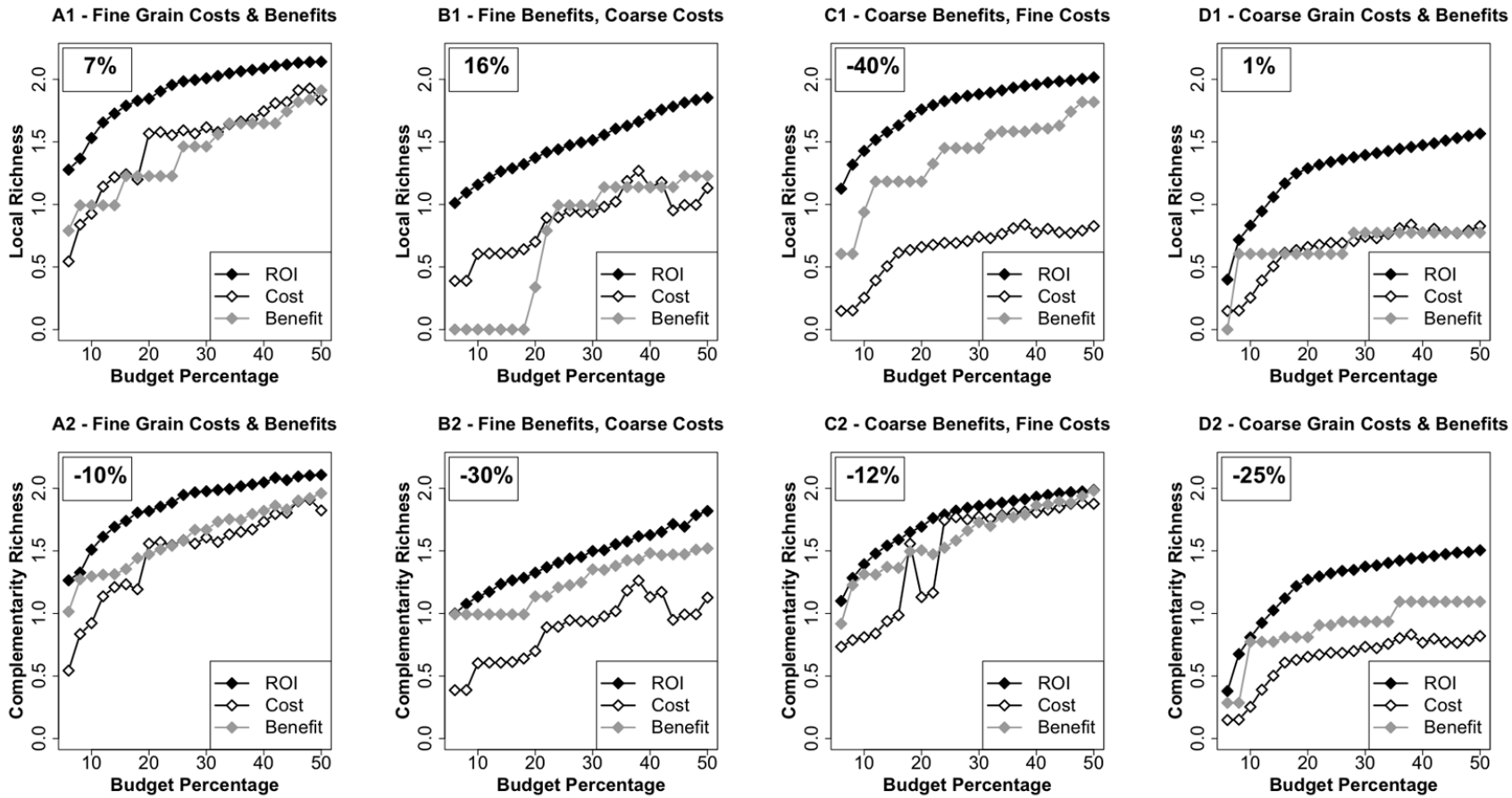


Figure 6. The apparent effectiveness of a cost targeting conservation strategy varies with grain for a local richness objective (top panels), but not for a more resolved complementarity objective (bottom panels). The average difference in relative performance of cost minus benefit targeting (Eq. 7) across all budgets is stated in upper left hand corner of each panel. Vertical axes in each panel represent the absolute value of our local or complementarity species richness estimates (Eqn. 6). Fine-grain cost data represent parcel-level acquisitions costs of protected areas, and benefit data are derived from the element occurrences of target species. Coarse data scenarios used the same datasets, but had been aggregated to the county level. We find the relative performance of cost and benefit targeting is generally equivalent at matched spatial grains (Scenarios A and D), but diverges more substantially at mismatched spatial grains (Scenarios B and C). This suggests combining data from different spatial resolutions, or relying on proxies for conservation cost, inflates the apparent effectiveness of an opportunistic conservation strategy.

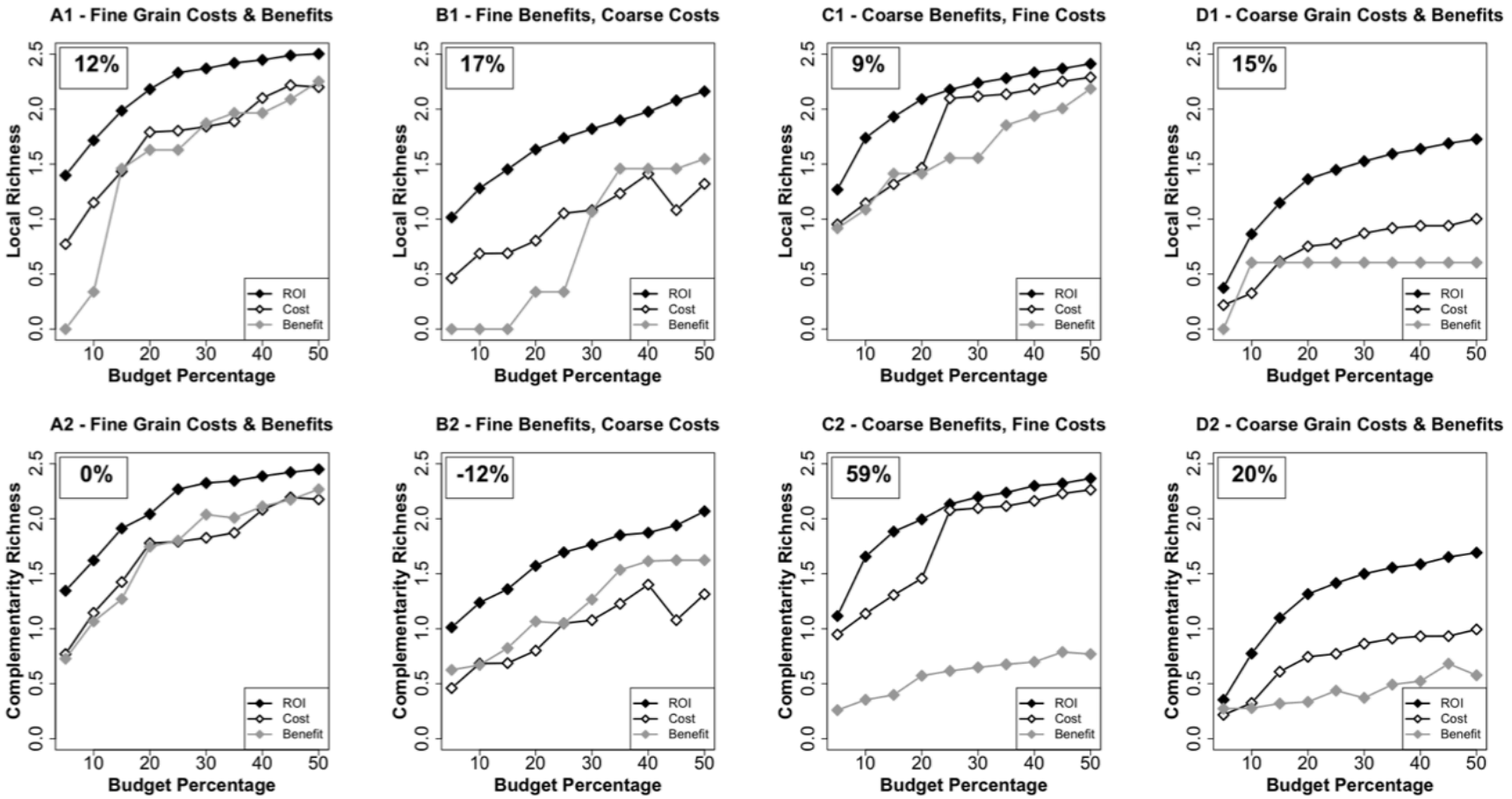


Figure 7. When easements are minimally weighted (w=0.95), the relative performance of an opportunistic conservation strategy still varies with spatial granularity. The average difference in relative performance of cost minus benefit targeting (Eq. 7) across all budgets is stated in upper left hand corner of each panel. All main text scenarios come from weighting species richness in easements at half the value of fee-simple acquisitions (w=0.5). As a sensitivity test, we repeated model simulations for a minimally weighted scenario (w=0.95) at 5% budget intervals across all combinations of spatial grain. Altering our easement weighting diminished variation in the benefits of protected areas, and as a result cost targeting outperformed benefit targeting across all combinations of spatial grain for a local richness objective. However, we still find the apparent effectiveness of an opportunistic conservation strategy was sensitive to spatial grain for a complementarity objective

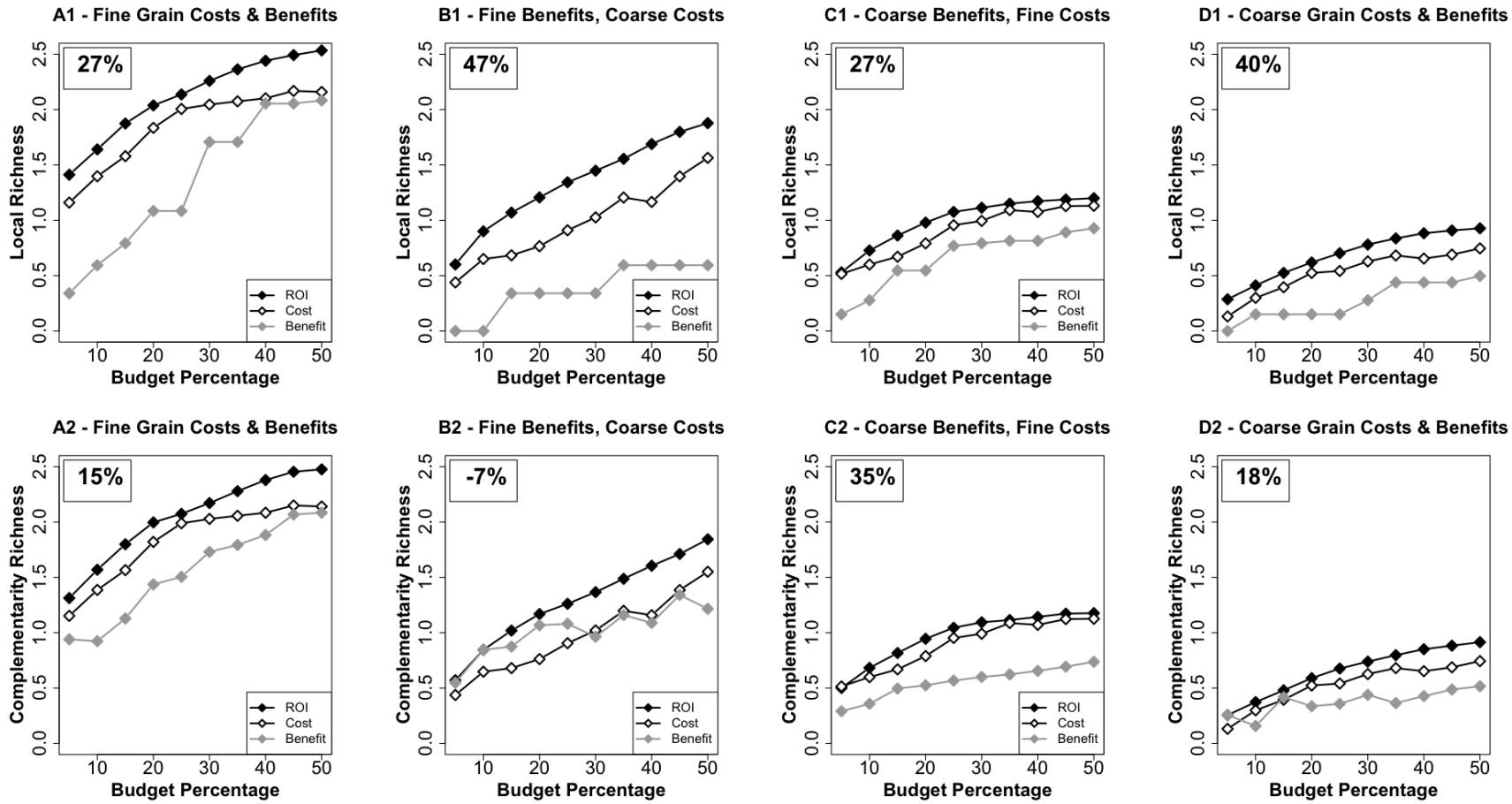


Figure 8. When we double the radius of our buffer criterion for biodiversity benefit to 10 km, the relative performance of an opportunistic conservation strategy still varies with spatial grain. The average difference in relative performance of cost minus benefit targeting (Eq. 7) across all budgets stated in upper left hand corner of each panel. All main text scenarios comes are represented by the known element occurrences of species richness within a 5 km buffer. As a sensitivity test, we repeated model simulations for a larger 10 km buffer at 5% budget intervals across all combinations of spatial grain. Increasing our buffer criterion is a spatial averaging process that reduced variation in species richness between protected areas; consequently, the cost targeting outperformed benefit targeting across all grain combinations for a local richness objective. However, we still find the apparent effectiveness of an opportunistic conservation strategy was sensitive to spatial grain for a complementarity objective

CONCLUSION

It is widely recognized there is insufficient representation of ecological systems in the current distribution of protected areas, and in response the academic conservation community has developed tools to more systematically prioritize scarce resources for biodiversity protection. However many of these assessments have fallen short in realizing the promise of cost-effective conservation, and in this study, we provide two examples of how uncertainty in socioeconomic data drives a wedge between the theory and practice of conservation planning.

In Chapter 1, we used a case study of recent protected areas to demonstrate how uncertainty due to spatial averaging and proxy choice affected the prioritization of areas for protection. We first demonstrated how average agricultural land values had little predictive capacity for acquisition costs at fine and aggregated spatial grains. This supported the hypothesis that downscaling errors were attributable to uncertainty due to proxy choice, or the substitution of agricultural land values for the acquisition costs of protected areas. We then compared model conservation plans based on different sets of socioeconomic information. While we found the effect of spatial averaging varied with our conservation objective, errors due to proxy choice consistently overestimated the costs of biodiversity protection across coverage constraints.

We further investigated these prediction errors due to spatial averaging in Chapter 2 by manipulating the spatial grain of our biological and socioeconomic data in concert. Then, we demonstrated the conclusion of a classic debate between cost and benefit targeting was sensitive to the spatial grain of the data being used. Specifically, we found that combining data over different spatial grains inflated the apparent effectiveness of a cost targeting strategy. These results are relevant to other studies not only because they shed light on the relative importance of socioeconomic and biological data, but also because they demonstrated how spatial averaging can alter even the basic conclusion of a classic debate in conservation planning.

Given the tradeoffs between the extent and resolution of available socioeconomic data, we are not suggesting that plans must be conducted at a finer resolution to be useful to conservation practitioners. Instead, we believe there is scope to better inform localized action if *uncertainty* in socioeconomic data is more transparently handled in systematic conservation planning. We suggest that future studies manage this uncertainty by i) matching the spatial grain of their socioeconomic data, biological data, and planning units, ii) focusing on the collection of socioeconomic data that represents the actual costs of the conservation actions a plan is meant to inform, and iii) utilizing cross-scale modeling approaches that can transmit uncertainty from the underlying data sources into a resulting prioritization.

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