Contents lists available at ScienceDirect



# **Biological Conservation**

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



# The cost of buying land for protected areas in the United States



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# ARTICLE INFO

Keywords: Nature reserve 30 by 30 Site selection Conservation finance Philanthropy Private land

# ABSTRACT

Buying land to establish protected areas is a common conservation strategy, particularly in countries with strong private property rights. Accurately accounting for spatial heterogeneity in land cost could lead to large efficiency savings when planning future acquisitions. However, lack of data regarding actual acquisition costs faced by conservation organizations has led planners to rely on more readily available proxies, such as agricultural land value. Using data on nearly 36,000 parcels acquired for conservation by public agencies and land trusts in the continental U.S., we built a model predicting protected area acquisition costs. While costs of land for agriculture or development are useful predictors of variation in protected area acquisition costs, they are not, by themselves, good approximations of those costs. For example, using a more comprehensive combination of variables, our model explained almost four times as much variation in actual acquisition costs as those. We found that agricultural land value loses most of its explanatory power once other predictors are used, confirming that it acts as a partial proxy for actual acquisition costs. We then used an optimization model to compare prioritization recommendations with our new cost estimates to those suggested when relying on agricultural land values alone. Locations of highest conservation return on investment shifted from coastal regions toward the country's center, when using actual cost data. Cost estimates used in conservation planning should be based on actual protected area acquisitions, because the type of properties and motivations of buyers and sellers differ from those of other land transactions.

#### 1. Introduction

Protected areas have long been a primary strategy for conservation, especially in terrestrial systems (Haaland et al., 2021; Le Saout et al., 2013; Margules and Pressey, 2000; Watson et al., 2014). In the face of continued biodiversity erosion and limited funding (Lerner et al., 2007; McCarthy et al., 2012), conservation organizations have adopted systematic approaches to identify parcels for protection, relying on strategic work-flows to organize planning efforts and optimization tools when appropriate (Amundsen, 2011; McIntosh et al., 2017). Many of these methods aim to maximize the ecological return on investment (ROI) when selecting a set of areas to acquire (Moilanen et al., 2009). Conservation ROI has been defined in various ways, but most definitions are based around the ratio of the ecological benefit of a conservation action divided by the economic cost of the action (Boyd et al., 2015). When conservation costs were first included in large-scale planning studies, large efficiency savings were reported, suggesting more biodiversity could be protected for a given budget (Ando et al., 1998; Carwardine et al., 2008; Naidoo and Iwamura, 2007; Venter et al., 2014). ROI approaches, notably, promise large efficiency gains provided they can rely on reasonable estimates for both ecological benefits and economic costs of protection (Cullen, 2013).

In countries with strong private property rights, expansion of protected area networks often depends on buying or receiving donations of land from private landowners (Nolte, 2018). When purchases are involved, the cost of upfront land acquisition is a significant component of the overall cost of securing long-term conservation goals on a site (Le Bouille et al., 2022). Unfortunately, reliable data on the costs of protecting land are rarely available (Armsworth, 2014). Instead, many conservation studies rely on indicators of protected area acquisition costs, such as costs estimated from agricultural rental rates nearby (Lawler et al., 2020; Venter et al., 2014; Withey et al., 2012), gross margins of agricultural production (Adams et al., 2010; Chiozza et al., 2010; Jantke et al., 2004) or even GDP per capita (Eklund et al., 2011). However, protected parcels commonly include steeper terrain

https://doi.org/10.1016/j.biocon.2023.110138

Received 7 July 2021; Received in revised form 11 May 2023; Accepted 17 May 2023 Available online 6 July 2023 0006-3207/© 2023 Published by Elsevier Ltd.

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and higher elevation habitats than most agricultural lands (Sutton et al., 2016). In addition, dynamics associated with conservation transactions, such as motivations to buy and to sell between conservation organizations and existing private landowners, can be very different from those involved in conventional land sales (Armsworth, 2014; Clark, 2007; Knight et al., 2011).

Improving the accuracy of cost data promises further efficiency gains by avoiding costly misallocations of limited resources (Armsworth et al., 2020; Sutton et al., 2016). Indeed, priorities that emerge in conservation planning may be more sensitive to the cost data used than to particular biodiversity data (Kujala et al., 2018). Improved cost estimation is also necessary if we are to more accurately project what it will cost to deliver particular conservation objectives (Nolte, 2020). Improved data on land costs in the U.S. are becoming more readily available. For example, Nolte (2020) and Wentland et al. (2020) present new predictive models estimating the fair market value of individual land transactions from data collated by Zillow, a commercial real estate database company. However, for the reasons we mentioned above, land value for conservation may not reflect the full cost that would be faced by a commercial developer or other private purchaser. Instead, conservation organizations are often able to acquire land for less than fair market value, by way of a form of charitable donation on the part of sellers. With their focus on fair market value, Nolte (2020) and Wentland et al. (2020) used a different sample of transactions than we did. For example, Nolte validates his model against some of the same data we use here, but retaining only parcels sold at or close to (no more than 20 % discount) the estimated land's fair market value. In contrast, we focus on exploring variation in the actual acquisition costs faced by conservation organizations when protecting a property, not in the commercial real estate value of that land. For this reason, we use records of actual prices paid, including the portion of acquisition costs attributable to landowners selling to conservation organizations for below fair market value, i.e. land discounted or donated.

In this study, we sought to understand large-scale patterns in the costs of acquiring land to establish new protected areas (also often referred to as "fee simple acquisition"). We used statistical regression to relate the patterns we found to socioeconomic, geographical and ecological covariates. The resulting model produced a national map of protected area acquisition costs. We also compared our cost estimates to estimates of agricultural land value and urban land value used in past studies. Finally, we show how prioritizations for future protection change when relying on our new conservation cost estimates.

#### 2. Material and methods

#### 2.1. Acquisition cost data

We used data on 35,880 land transactions made to protect land in the continental U.S. These data include 31,332 land transactions made by local, state and federal governments across the U.S. that were collated by the Trust for Public Land (TPL) in their Conservation Almanac (The Trust for Public Land, 2019). Exact dates vary by states, but most states' records start in the 90's, with around one third starting in the 80's. The most recent records for most states are from 2014 or 2013. The data also include 4,548 additional land transactions made between 1980 and 2014 by The Nature Conservancy, the largest private land trust in the U. S. (Carr, 2006), which is another major contributor to expansions of the U.S. protected area network (Fishburn et al., 2013; LTA, 2015). We corrected the costs for inflation and reported them as 2016-dollars, using the Consumer Price Index (U.S. Bureau of Labor Statistics, 2019). Because we want to explore costs of acquiring land for protection as actually faced by conservation organizations, we retained sites that were fully or partially donated in our main analyses, but see below for relevant sensitivity tests.

We focus our analysis on the average cost per hectare of purchasing land for protected areas within a county. While recognizing other choices would also make sense, we chose to work at the county level for several reasons. First, based on conversations with practitioners, we believe counties provide a relevant spatial grain when deciding how to allocate conservation dollars and working over a large spatial extent. Organizations and government programs that conduct conservation planning to inform protection strategies over large spatial scales tend to leave the final decisions over just which parcels should be acquired to staff in local field offices — while the large-scale budget planning itself, deciding which parts of the country should be priorities for future investment, is conducted at coarser spatial units such as counties. Second, counties are a relevant administrative and political unit in the U.S. for regional and local land-use planning. Third, several of our chosen socioeconomic variables are available only at county-level. Finally, and partly for these other reasons, county-grain is also a scale at which many return on investment (ROI) based optimizations have previously been formulated, making it easier to compare our results with existing literature (Ando et al., 1998; Armsworth et al., 2020; Boyd et al., 2015; Dobson et al., 1997; Kroetz et al., 2014; Withey et al., 2012). That being said, county sizes vary across the U.S. In case that would affect any of the above, we included county area as one of our model's predictive variables. We used county boundaries as recorded by the U.S. Census Bureau (2015). The transactions in our dataset span 1927 counties, 63 % of the total number of counties in the continental U.S (Fig. 1).

#### 2.2. Covariates

The model we fit to explain variation in protected area acquisition costs included both ecological and socioeconomic covariates (Table 1). The choice of variables was based on hypotheses about factors that might explain cost variation. We first included measures of the value of alternative land uses, both agricultural land value (USDA-NASS 2012) and urban land value (Davis et al., 2021), because acquisition cost is likely to reflect the foregone value (opportunity cost) incurred when protecting land. For counties where these estimates were unavailable, we used the state average for the relevant variable.

The amount paid by a conservation organization to acquire a property also depends on the willingness of the landowner to sell below market value as a form of philanthropic donation to conservation (Clark, 2007). Unfortunately, most conservation organizations do not record fair market value at the time of a land purchase ( $\sim$ 87 % of the data we used in this analysis did not retain that information) making it difficult to quantify the prevalence and magnitude of partial donations. So, while one could estimate donation rates separately from fair market value and afterwards combine the two estimates to arrive at an overall estimate of conservation costs, we opt for the simpler approach of combining both processes within a single estimation. Others have found environmental philanthropy in the form of monetary donations to be associated with higher household incomes (Mount, 1996), higher levels of education (Greenspan et al., 2012), higher employment rates, urban living (Chen et al., 2011) and more prevalent left-leaning political beliefs (Fovargue et al., 2019). As such, we included poverty percentage (United States Census Bureau, 2021), education levels, as the percentage of adults with a bachelor's degree or more (United States Census Bureau, 2021), unemployment rate and population density (Friesenhahn, 2016), and democratic leaning, as the average proportion of votes for that party during presidential elections, since 2000 (MIT Election Data and Science Lab, 2018) as possible predictors of land donations.

We accounted for the proportion of the county already covered by protected areas with explicit mandates for biodiversity protection, using data from the Protected Area Database of the United States — GAP categories 1, 2 and 3 (USGS Gap Analysis Project, 2018). We also included the proportion of the county that had already been converted to either urban land, crop or pasture, as well as the proportion that is projected to be converted to these land cover types by 2030. We took these proportions from U.S. Forest Service's 2010 RPA assessment (Wear, 2011). We converted the later into an indicator of short-term



Fig. 1. Number of land parcels bought for protection, since 1980, in our dataset. Records for the Great Plains region are scarce, with many counties containing <5 land deals (grey), while the Lake region and both coasts are more densely represented (color scale).

conversion threat by calculating the ratio of additional converted area to the current total converted area within the county. We also obtained the mean elevation (NASA-JPL, 2013) for each county. Finally, we calculated how many vertebrate species that were evaluated by IUCN (2016) as being vulnerable to extinction or worse were present in the county.

Recognizing that there may be broad spatial patterns not accounted for by these variables, we also included categorical variables summarizing whether counties were located in particular parts of the country. We used ecoregional boundaries associated with broad biophysical attributes when specifying these categorical variables. Specifically, we included categorical variables describing whether a given county was included in one of 85 EPA-3 ecoregions (U.S. Environmental Protection Agency, 2015), which are mapped in Fig. S.I.-1. We tested two alternative specifications for categorical variables that focused on larger regions. For these, we used state boundaries and 8 EPA-1 ecoregions, but these more aggregated descriptors were not retained by our fitting procedure (S.I. Section I).

#### 2.3. Analyses

We used a regression approach to examine covariation between our socioeconomic and ecological variables and our acquisition cost data. We started with a simple linear regression model, weighted by the number of transactions in each county. The analysis was conducted in R (R Core Team, 2018), with packages MuMIn (Bartón, 2023), ImerTest (Kuznetsova et al., 2017), ape (Paradis and Schliep, 2019) and DMwR (Torgo, 2016). The average cost per hectare of buying land for conservation per county was log-transformed with an offset of 1 to reduce skewness while accounting for zeroes in the data. For the same reason as

well as for consistency, we also log-transformed the average urban and agricultural land values per hectare for each county. Our basic model structure was:

$$Y = \alpha + \sum_{i} \beta_i * X_i + \epsilon$$

where *Y* is the acquisition cost of a protected area of land and  $\beta_i$  are the coefficients to be estimated for each  $X_i$  covariate described above,  $\alpha$  is the intercept and  $\varepsilon$  is the error term. When generating a proximity matrix with all pairwise distances between counties and applying a Moran's test to the residuals weighted by those distances, some spatial autocorrelation in the error terms was found. The model fit was significantly improved, based on AIC comparison as well as thorough model validation (see S.I. section II for more model validation details), by retaining EPA-3 ecoregions but some spatial autocorrelation still remained. We then tried explicitly adjusting the model's error structure. We fitted the model once more, using generalized least squares, and compared the fits obtained when assuming five different autocorrelation structures (S.I. section I). While improving the model's AIC, they did not significantly decrease the remaining autocorrelation in the residuals. The covariate estimates were very similar across all model structures, which points to functional form of our model as being robust and correctly specified. Therefore, we proceeded with the base model, without a spatially autocorrelated error structure.

We tested the robustness of the resulting fitted model in both time and space. We subjected our model to both an out of sample crossvalidation routine (repeated k-fold with 100 repeats of 10-fold random sets — Kohavi, 1995) and an in-sample validation check by fitting predicted values against observed values across our whole dataset

#### Table 1

Definition and distribution (given as the 25 %, 50 % and 75 % quartiles) for variables used in our model.

Acquisition cost	Quartiles	Description
Cost per hectare (parcel)	[1,923–8,649–35,522]	Purchase price per hectare across parcels
Cost per hectare (county)	[2,853–7,353–28,828]	Equal weight average of the purchase price for protected areas in a county (in dollar/ha)

Covariates	Quartiles	Description
County area	[113k–162k–242k]	County area, in ha
Average deal size	[22-50-128]	Average area of protected areas
		bought in this county, in ha
IUCN listed species	[3–3–4]	Number of vertebrate species listed
		as vulnerable or worse by IUCN
Elevation	[144-277-487]	Mean county elevation, in meter
Urban land value	[94k–148k–234k]	Urban land value, in dollar per
		hectare
Agricultural land value	[5k–7k–12k]	Agricultural land value, in dollar per hectare
Education	[15–19–25]	Percentage of 25+ year old adults
		with a bachelor's degree or above
Poverty	[11-14-18]	Percentage of people living below
		the poverty limit
Unemployment	[5–7–8]	Unemployment rate as percentage
Rate		of the total population
Population density	[0.07-0.18-0.44]	Density of population, per hectare
Proportion land	[0.19-0.38-0.64]	Proportion of the county area that is
converted		either urban, crop or pasture
Proportion land	[0.009-0.036-0.137]	Proportion of the county area
protected		protected under PAD-US cat. 1, 2 or
		3
Future conversion	[0.3-2.3-8.7]	Percent increase of the converted
threat		area projected by 2030
Democratic leaning	[0.3-0.4-0.5]	Proportion of total votes that were
		casted for the Democratic party
Ecoregion	NA (factor)	EPA-3 ecoregion denomination

#### 2.4. ROI prioritization

To illustrate how conservation recommendations would change when drawing on our new cost estimates, we used a spatial prioritization approach to identify future priority locations for establishing protected areas. Specifically, we used the prioritization model presented in Armsworth et al. (2020) that focuses on enhancing the protection of 1514 terrestrial vertebrate species (birds, mammals, reptiles and amphibians). This formulation accounts for ecological complementarity in the set of species being protected, conservation costs, existing protected areas, projected habitat conversion threats, contributions to species protection from unprotected private land, and a range of other factors. The conservation objective is assumed to be one of maximizing expected future species richness when considering the probability of a species persisting to be a function of the amount of protected area and unconverted private land found within the species range. Conservation funds allocated to a county are used to acquire new protected areas, thus changing future land cover and species persistence probabilities. Armsworth et al. (2020) compare different assumptions regarding subcounty siting of protected areas relative to species ranges. Here we adopt their "pessimistic" scenario where each hectare of additional protected area covers species ranges in proportion to their range area in the county. This prioritization approach and its assumptions are explored fully in that earlier Armsworth et al. (2020) paper. Here we focus on applying it as a demonstration of how the priorities one arrives at through a conservation planning process depend on the underlying cost data being used.

We compared the ROI offered by investing in each county when using our new cost estimate with the ROI estimate obtained when using average agricultural land value in the county, a proxy commonly used in past studies. We defined the return on investment in terms of the change in the number of species expected to persist across the conterminous US when allocating a small additional budget for land protection to each county over status quo protection levels. The ROI available from investing in further land protection in county *i* takes the form:



ROI county i

Cost per hectare of new protected area in county i

(Fig. 2a). Additionally, we repeated our model fitting when only using transactions from the most recent decade included in the dataset. We also checked for other possible temporal trends by calculating the difference between individual parcel cost and county land cost average and then testing for significant changes in this quantity through time; there was no significant trend in the spread of data points around the county averages over time (ANOVA, *P*-value = 0.458). Finally, some parcels within our dataset (15 %) were fully donated by the original landowner, meaning the cost per hectare was USD\$0. To examine whether our results were sensitive to their inclusion, we repeated our analyses omitting these fully donated transactions. In all cases, spatial and temporal, in and out of sample, with and without donations, parameters estimates and predictions of our model remained largely consistent (S.I. section III).

The summation in the numerator is taken across species, meaning counties with higher species richness tend to be higher priorities. The first term in the numerator represents the improvement possible in the future persistence probability for a species by improving conditions for it on the landscape by a small amount. While this term is positive for most species, the potential gains eventually dissipate for those common species for which conditions are sufficiently favorable across the landscape that their persistence is assured. The second term in the numerator focuses on the county being targeted for investment and indicates by how much ecological conditions for the species in the future would be improved in that county by creating an additional hectare of protected area today. This term tends to be larger for counties where future conversion threat would be higher, absent the additional protection and so the added value of new protected area is large. Finally, the denominator is just the cost per hectare in the county, which is the term we are most interested in here. All else being equal, lower cost counties have higher



#### (a) Comparison of Predictions against Observations

(b) Land Costs and Urban Land Value

(c) Land Costs and Agri. Land Value



**Fig. 2.** Observed average county purchase costs against model predicted average county purchase costs (a), urban land value (b) or agricultural land value (c). In all cases, costs are log-transformed (base e) and red points are counties where all acquisitions were fully donated. Lines are each models' fit (red) and y = x (orange). Intercepts are significantly different from 0 for regressions with urban (b) or agricultural (c) land values but is not for the regression observed against predicted estimates (a). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ROI values.

To focus attention only on top priority counties that reside in the upper tail of the ROI distributions, we reported the percent agreement between the top 5, 10 and 15 % of counties when ranked by ROI when assuming each cost dataset.

Finally, we pushed beyond ROI and calculated optimal budget allocations when using each cost estimate. When optimizing, we treated the conservation budget allocated to a county as a continuous control variable. We report the congruence in the optimized budgets, defined as the proportion of overall funding for which the two optimized strategies agree on the allocation. Additional details of our prioritization specification are given in the S.I. The optimization indicates the optimal funding allocation when considering species complementarity, which sometimes involves focusing investment into a relatively small number of priority counties. In contrast, a focus on ROI more broadly allows a comparison of spatial patterns across the whole landscape.

#### 3. Results

The total cost per parcel, the cost per hectare and parcel size were all heavily skewed (Table 1). In general, transactions included in the dataset were for small parcels; >87 % of the parcels acquired were smaller than 100 ha. The prevalence of small area transactions in the dataset is to be expected, both given our focus on the individual transactions used to build protected areas and because, by number, most protected areas are small (Deguignet et al., 2014). There was also a great deal of spatial variability in the data. Even after averaging per county, cost per hectare and parcel size both varied by ~6 orders of magnitude across the U.S. (Table 1).

Among our covariates, urban land value is a significant predictor of protected area acquisitions costs, while agricultural land value is not (Table 2). All other covariates are positively associated with protected area acquisition costs except for average deal size in the county, which is negatively correlated to acquisition costs, denoting economies of scale

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#### Table 2

Estimated coefficients for the covariates used in the land value model to fit the log-transformed average purchase price per hectare, in 2016 U.S. dollars (n = 35,880). Covariates marked with x were log-transformed, when fitting the model.  $R^2 = 0.59$ , significance levels are marked as follow: . at 0.1, \* at 0.05, \*\* at 0.01 and \*\*\* at 0.001.

Covariates	Value	Std.error	<i>P</i> -value	Semi partial $R^2$ (× E-03)
(Intercept)	4.60	1.02	* * *	0.24
County area	5.12 E-08	7.79 E-08		5.04
Average deal size	-2.97 E-04	9.73 E-05	**	3.64
IUCN listed species	3.79 E-02	1.47 E-02	**	9.75
Elevation	9.07 E-04	2.14 E-04	***	22.56
Urban land value <sup>¤</sup>	0.41	0.06	***	0.93
Agricultural land value <sup>¤</sup>	-0.10	0.08		4.40
Education	1.63 E-02	0.57 E-02	**	0.19
Democratic leaning	-0.25	0.43		0.93
Population density <sup>II</sup>	0.55	0.04	***	76.90
Poverty	-2.27 E-02	1.16 E-02	•	2.09
Unemployment rate	0.14	0.03	***	12.31
Proportion land converted <sup><sup>xx</sup></sup>	1.37	0.40	***	6.46
Proportion land protected <sup>xx</sup>	1.19	0.32	***	7.36
Development threat	0.41	0.16	**	3.68
Ecoregions	Factor	Factor	***	213.96

that are still visible at county level. County size, poverty prevalence and political leaning do not have a significant (at *P*-value < 0.05) relationship with acquisition costs. The direction of most of these associations aligned with our a priori expectations. We did not, however, anticipate the positive associations with elevation, which is likely attributable to us employing a multiple regression approach. i.e., the positive association with elevation here describes the relationship after controlling for the effects of broad ecoregion, county size, etc., rather than a simpler bivariate association between elevation and protected area acquisition costs. Semi partial R<sup>2</sup> are one way of measuring effect size for parameters in a linear model, by calculating the portion of residual variance explained by adding a given covariate to the full model specified without it. In this model, ecoregions, urban land value, population density, and unemployment are the covariates that explain the largest proportion of unique shared variance between the predictors and the response

variable (Table 2).

In our sensitivity test of the model fitting procedure, parameter estimates and predictions of our model remained consistent across our different spatial specifications and our in and out of sample validation checks (S.I. section III-A). When refitting the model using only transactions from the most recent decade, the model estimates remained similar, though there was a slight loss in significance of some parameters as would be expected given the smaller sample sizes involved (S.I. section III-B). We also included a sensitivity test where we re-estimated the model when dropping any transactions that were fully donated. Our findings are that the results remain largely unaffected by this change, except for county area, which became a significant factor (S.I. section III-C).

While the value of both agricultural and urban land in a county might be expected to be a significant predictor of variation for protected area



Fig. 3. Complete map of predicted acquisition costs (in dollars/ha) for all counties of the conterminous U.S. using parameter estimates from our model, presented in Table 2.

acquisition costs, our hypothesis was that relying on either of these variables as a direct estimate of acquisition costs for protected areas would miss much of the relevant variation. In Fig. 2, we plotted simpler bivariate associations between actual average cost per hectare of acquiring land for conservation (y-axis) per county against average urban (Fig. 2b) or agricultural (Fig. 2c) hectare value per county. Note the difference of scale between x and y axes on each graph: urban land value and agricultural land value greatly under-represent the magnitude of the variation in observed costs. Also, urban land value and agricultural land value explain almost 4 times less variation in actual acquisition costs than does our model (comparing R<sup>2</sup> values in Fig. 2b and c with those in Table 2).

Fig. 3 maps the predicted land acquisition costs from our model, including extrapolating to counties where we did not observe transactions (standard errors for these predictions are mapped in Fig. S.I.-6). As would be expected, predicted costs of acquiring protected areas tend

to be higher in the North East, in coastal counties on the West Coast and Florida and around major conurbations in the interior U.S. (Chicago, Atlanta, Phoenix, etc.). In contrast, acquisition costs appear lower in rural counties in the interior of the U.S., particularly in the Great Plains (stretching from North Dakota and parts of Montana down into Texas and New Mexico), where admittedly, more extrapolation is involved. The model fit is highly significant (*P*-value < 0.0001) and it explains 59 % of the overall variation in protected area costs that we observe.

We used the prioritization framework from Armsworth et al. (2020) to illustrate how different cost data would affect conservation priorities. We compared the ROI offered by additional protection efforts in each county within the U.S., when using the two different cost datasets. The ROI estimates per county obtained with each cost dataset are positively correlated ( $R^2 = 0.29$ ,  $P \ll 0.001$ , n = 1918, after log transforming and dropping 9 counties where the ROI is zero for both cost datasets because species in those counties are already fully protected, Fig. 4a). This



(c) Change in ROI Ranks



**Fig. 4.** Patterns in ROI with new cost data and average agricultural land value. (a) Correlation of ROI estimates using each dataset ( $R^2 = 0.29$ ,  $P \ll 0.001$ , n = 1918, after log transforming and omitting 9 counties where the estimated ROI is zero) and (b) agreement levels over priorities with new cost data and average agricultural land value (grey bars show the percent agreement in the sets of counties that fall within the top 5, 10 and 15 % of counties by ROI with each cost dataset; no funding was allocated to the same counties for the fully optimized solution). (c) Comparison of ROI ranks per county (blue counties appear to be a relatively higher priority for protection when relying on average agricultural land value than our predicted purchase costs, while pink counties appear to be a relatively higher priority with the predicted purchase costs). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlation indicates that when relying on either source of cost data, conservation planners would broadly agree on the relative ranking to attribute to individual counties. However, there are still important changes in those ranks: the prevalence of blue in Fig. 4c on the North-East and West coasts indicates that these counties would present lower ROI, and as a result be ranked lower for investment, when relying on our new cost data. As a result, priority would overall switch toward the Great Plains, whose counties tend to rank higher for investment with the new cost data. These broad patterns reflect the underlying cost gradient reported in our cost data (Fig. 3).

Focusing more narrowly on only those counties offering the highest ROI with each cost dataset, we find that agreement levels over priorities depend on how many counties are being considered. Fig. 4b shows the percent overlap in counties that would appear priorities when focusing on the top 5, 10 or 15 % in terms of ROI with cost dataset. The more focused the spatial targeting with each dataset, the less they agree on priorities. Pushing further to compare optimal budget allocations that result, the two optimized recommendations disagree on where funding should be allocated Fig. 4b). If relying on the average agricultural land value data, the optimization recommends concentrating investment into Arizona (notably, Gila County) and New Mexico (Hidalgo County), marked with red points in Fig. 4a. When relying on our new cost estimates, the optimal solution favors investment in Texas and coastal Louisiana (including the counties marked with blue points in Fig. 4a). It also favors a more dispersed investment strategy with 11 counties each receiving more than \$30 M to enable large projects in the Gulf Prairie and Marshes, South Texas Plains, Edwards Plateau, and Trans Pecos ecoregions (Texas Parks and Wildlife Department, 2022).

#### 4. Discussion

Ongoing losses of biodiversity and ecosystem services (Millennium Ecosystem Assessment, 2005; Pimm et al., 2014) and limited resources for conservation mean there is a pressing need to allocate what resources are available optimally (Le Saout et al., 2013; Waldron et al., 2013). This requires having a good understanding of how much conservation will cost in different places. However, conservation costs are often poorly documented. We examined what parameters drive acquisition costs of protected areas, used that knowledge to better predict protected area acquisition costs across the conterminous U.S. and then examined the consequences this would have on prioritization analyses.

The model we present provides insight into some of the factors that consistently make some acquisitions more expensive than others. First, we hypothesized that social-economic factors usually associated with environmental philanthropy, in the form of monetary donations, could also be associated to land donations, partial or total, during land transactions for conservation. This would effectively result in decreased acquisition costs. However, our model finds the effect of those parameters is either not present or associations are different when considering land acquisitions. In particular, selling land at a lower cost is more common in less densely populated areas, with lower education levels and where unemployment remains low. In contrast monetary donations for conservation are concentrated in and around cities, which are often characterized by having higher education and unemployment levels (Chen et al., 2011; Greenspan et al., 2012). Second, we also found that a higher proportion of already converted land, as well as a higher threat of further conversion were both associated with higher land acquisition costs. Past and future land conversion trends can correlate with land trusts' willingness to buy, pushing them to accept less favorable pricings (Boyd et al., 2015; Murdoch et al., 2007). Similarly, protected area acquisitions cost per hectare was positively associated with the number of species listed as endangered by the IUCN. This increasing effect on land cost possibly indicates a greater willingness to pay for protected areas in these locations, by conservation organizations. The presence of species of interest might also offer leverage to landowners for driving prices up (Lennox and Armsworth, 2013) or act to reduce conservation

organizations flexibility to seek out low cost parcels. Finally, higher density of already existing protected areas was associated with increased cost of securing new deals in that county. This might be a consequence of the lowest cost opportunities within a given county already having been protected. However, while the role of these covariates was consistent across our different spatial specifications, we found several associations were no longer significant when we only considered areas protected within the most recent decade, likely reflecting the smaller sample size involved.

Market-based (agricultural or urban) land value are common proxies that have often been used as direct estimates of protected area acquisition costs. While our model found urban land value to be positively associated with protected area acquisition costs, the predictive power of agricultural land value seems to have been almost completely picked up by the other covariates. In either case, we would caution against using either of those in isolation as proxy for land value, in the context of conservation. Protected area acquisition costs across the U.S. proved to be extremely variable and also highly skewed (see also Davies et al., 2010). Capturing that high degree of variability is important when evaluating the potential efficacy of conservation programs. Schöttker et al. (2016), for example, found that more variation in land prices across the landscape would increase the efficiency of buying land, as opposed to contract easements. Yet, observed variation in the cost of land for conservation is under-represented when substituting agricultural or urban land value for conservation land value (Fig. 2b and c).

Using a prioritization framework, we further investigated how conservation recommendations could be affected by using our predicted costs versus using agricultural land value as a proxy for these costs. The conclusions one would draw about the sensitivity of priorities to the cost data used would depend on whether someone focused on only the best opportunities for conservation or on broad patterns in ROI across the country. In particular, the top sites and optimized budget allocation that emerged when using our new cost data are quite different to that obtained when relying on agricultural land values to approximate costs. Different counties are prioritized and different sets of species would benefit. At the same time, agreement levels improve with less stringent targeting (Fig. 4b), something to be expected given the overall correlation in ROI we find when considering all of the counties. Also, even if no longer optimal, counties picked by the optimization when assuming one cost dataset still offered a very good ROI when evaluated against the other cost dataset (e.g., colored points in Fig. 4a). Optimization tends to be more demanding about the underlying data, responding as it does to the upper tail of the ROI distribution only. In contrast, our correlation statistic summarizes patterns across all of the counties, most of which would not be in consideration for investment under an optimized strategy. This suggests that analyses considering policy interventions that would apply across many counties (e.g., large-scale payment programs to private landowners, Lubowski et al., 2006) may be less sensitive to the underlying cost data used than those seeking to inform more concentrated conservation investments, like protected area acquisition programs. Other aspects of the optimal funding allocations and ROI distributions can be understood by considering the interaction of the cost datasets with the other relevant input variables. For example, that both optimized allocations favor southern counties reflects the latitudinal gradient in species richness across the US, while the shift further from the East and West Coasts with the new cost data reflects the longitudinal pattern in costs in Fig. 3.

In this study, we made choices and assumptions that should be kept in mind when interpreting our results. First, we conducted this analysis at the county level which we maintain is a relevant unit of aggregation for large-scale spatial planning. But we also recognize that fine-grain information is lost when doing so. Nolte (2020), for example, focuses on parcel-grain prediction. Sub-county variation of acquisition costs can translate into potential additional low-cost opportunities for conservation (Sutton and Armsworth, 2014). But we should note that such variations would also be missed by using county averages of agricultural or urban land values, as has previously been done. Sub-county variation still play an important role in translating larger scale plans, as we addressed here, into local measures (Pressey et al., 2013) and there is a need to harness that potential in conservation planning (Gotway and Young, 2002; Holzkämper and Seppelt, 2007).

Second, we have little information regarding acquisition costs for several states in the central U.S. For example, we only have ~75 land transactions or less for Kansas, North and South Dakota (Fig. 1). These tend to be states where land protection approaches other than fee ownership are more prevalent, particularly term contract agreements made as part of the U.S. Farm Bill's Conservation Reserve Program (Farm Service Agency (USDA), 2019; Jackson et al., 2021). We favored a linear regression, as opposed to a more flexible regression structure such as that presented by Nolte (2020), in part out of concerns about possible errors that could result from highly nonlinear specifications when extrapolating costs to parts of the country where we have little to no data.

Third, although our model explains roughly four times as much variation in acquisition costs as substituting agricultural land values did, it still leaves a non-negligible amount of variation unexplained. One reason the explanatory power of the model might be lower than it otherwise might be is because we chose to focus on how much it costs a conservation organization to protect land, instead of only focusing on predicting fair market value. Conservation organizations are often able to acquire properties for less than fair market values via a form of donation by the original landowner. In extremis, land may be fully donated, but partial donations where some cost is incurred but less than would be the case for a commercial buyer are also common. Factors affecting the tendency of private landowners to make such donations are also likely characterized by spatial variability and securing such donations may be easier for conservation organizations in some counties than others. To accommodate this in our model, we included covariates we hypothesized were associated with donation behavior alongside factors we hypothesized would be associated with setting fair market values. Our results however suggest we may not yet be predicting the donative component of conservation costs as well as we are aspects tied to fair market value. For example, Fig. 2a shows that full donations of land (in red) encompass the whole range of predicted values. Also, regression fits produced larger R<sup>2</sup> values in a sensitivity test where we excluded fully donated parcels, which again only represent a fraction of the overall amount of donation activity that is going on (Table S.I.-6). Thus, a deeper investigation of when and how much landowners are willing to donate when selling for conservation, including both full donations and partial donations, would be warranted.

Coomes et al. (2018) called for improved access to land cost data. They argue that such data should be a public good and is vital to the future of global change science and policy at large. Understanding and being able to predict the cost of land bought for conservation, in particular, are necessary conditions for the development of useful and reliable optimization tools. In the face of ever-increasing threats to biodiversity and the limited resources available to conservation organizations, such tools are urgently needed. With this work, we are providing a national map of protected area acquisition costs to empower national scale conservation planning exercises for the U.S., such as the  $30 \times 30$  initiative (Haaland et al., 2021) Beyond the U.S. context, our findings are also relevant to conservation researchers examining costs in other settings. For example, our results highlight the importance of focusing research effort directly on estimating the costs that conservation organizations face when implementing conservation actions, instead of on costs associated with other types of land use. Focusing on the costs faced by conservation organizations is important because the factors influencing costs they face may be different to those shaping costs with competing land uses.

#### CRediT authorship contribution statement

DLB: Conceptualization, Methodology, Investigation, Data curation, Software, Formal analysis, Validation, Writing - original draft + review & editing, Visualization.

PRA: Conceptualization, Methodology, Investigation, Writing - original draft + review & editing, Visualization, Resources and Funding acquisition, Supervision.

JF: Conceptualization, Writing - review & editing, Data access and Funding acquisition.

# Funding

DLB was supported on a graduate research assistantship from the National Institute for Mathematical and Biological Synthesis, an institute sponsored by the National Science Foundation through NSF Award #DBI-1300426, with additional support from The University of Tennessee, Knoxville. NSF had no involvement in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; or in the decision to submit the paper for publication.

#### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: We use data provided by a conservation organization (The Nature Conservancy) and one of the coauthors works for that organization. We do not consider this arrangement unusual among conservation papers, but it might not be appropriate from someone from that organization, or from The Trust for Public Land (who also contributed data and guidance) to be considered among the referees.

# Data availability

We are unable to make the raw cost data publicly available, but we have created a repository at https://github.com/dlebouille/Le-Bouille-et-al.-BC2023 containing supplemental material, including the code used, our model outputs and additional maps.

#### Acknowledgements

We thank The Nature Conservancy for information on their protected area acquisitions, the Trust for Public Land for information on land acquisitions collated in The Conservation Almanac and D. Wear for information from the U.S. Forest Service RPA assessment. We thank J. Welch and A. DuMoulin from TPL for feedback on this study. We thank D. Mahoney, H.B. Jackson, R. Fovargue and A. Benefield for help with data collation.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110138.

#### References

- Adams, V.M., Pressey, R.L., Naidoo, R., 2010. Opportunity costs: who really pays for conservation? Biol. Conserv. 143, 439–448. https://doi.org/10.1016/j. biocon.2009.11.011.
- Amundsen, O., 2011. Strategic conservation planning module. In: Land Trust Alliance Publications. Land Trust Alliance. Washington, DC.
- Ando, A., Camm, J., Polasky, S., Solow, A., 1998. Species distributions, land values, and efficient conservation. Science (80-.) 279, 2126–2128. https://doi.org/10.1126/ science.279.5359.2126.
- Armsworth, P.R., 2014. Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions. Ann. N. Y. Acad. Sci. 1322, 61–76. https://doi. org/10.1111/nyas.12455.
- Armsworth, P.R., Benefield, A.E., Dilkina, B., Fovargue, R., Jackson, H.B., Le Bouille, D., Nolte, C., 2020. Allocating resources for land protection using continuous

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optimization: biodiversity conservation in the United States. Ecol. Appl. 30, 1–13. https://doi.org/10.1002/eap.2118.

Bartón, K., 2023. MuMIn: Multi-model Inference.

- Boyd, J., Epanchin-Niell, R., Siikamäki, J., 2015. Conservation planning: a review of return on investment analysis. Rev. Environ. Econ. Policy 9, 23–42. https://doi.org/ 10.1093/reep/reu014.
- Carr, A.F., 2006. Book Review: Nature's Keepers: The Remarkable Story of How the Nature Conservancy Became the Largest Environmental Organization in the World, 1st ed. In: Science Communication. Jossey-Bass. https://doi.org/10.1177/ 1075547006292272.
- 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, 11446–11450. https://doi.org/ 10.1073/pnas.0707157105.
- Chen, X., Peterson, M.N., Hull, V., Lu, C., Lee, G.D., Hong, D., Liu, J., 2011. Effects of attitudinal and sociodemographic factors on pro-environmental behaviour in urban China. Environ. Conserv. 38, 45–52. https://doi.org/10.1017/ S037689291000086X.
- Chiozza, F., Boitani, L., Rondinini, C., 2010. The opportunity cost of conserving amphibians and mammals in Uganda. Braz. J. Nat. Conserv. Res. Lett. Nat. Conserv. 8, 177–183. https://doi.org/10.4322/natcon.00802012.
- Clark, S., 2007. A Field Guide to Conservation Finance. Island Press.
  Coomes, O.T., Macdonald, G.K., De Waroux, Y.L.P., 2018. Geospatial land price data: a public good for global change science and policy. Bioscience 68, 481–484. https://doi.org/10.1093/biosci/biy047.
- Cullen, R., 2013. Biodiversity protection prioritisation: a 25-year review. Wildl. Res. 40, 108–116. https://doi.org/10.1071/WR12065.
- Davies, Z.G., Kareiva, P., Armsworth, P.R., 2010. Temporal patterns in the size of conservation land transactions. Conserv. Lett. 3, 29–37. https://doi.org/10.1111/ j.1755-263X.2009.00091.x.
- Davis, M.A., Larson, W.D., Oliner, S.D., Shui, J., 2021. The price of residential land for counties, ZIP codes, and census tracts in the United States. J. Monet. Econ. https:// doi.org/10.1016/j.jmoneco.2020.12.005.

Deguignet, M., Juffe-Bignoli, D., Harrison, J., Macsharry, B., Burgess, N., Kingston, N., 2014. 2014 United Nations List of Protected Areas. UNEP-WCMC, Cambridge, UK.

- Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. Science (80-.) 275, 550–553. https://doi.org/10.1126/science.275.5299.550.
- Eklund, J., Arponen, A., Visconti, P., Cabeza, M., 2011. Governance factors in the identification of global conservation priorities for mammals. Philos. Trans. R. Soc. B Biol. Sci. 366, 2661. https://doi.org/10.1098/RSTB.2011.0114.

Farm Service Agency (USDA), 2019. Current CRP Enrollment - 2019.

- Fishburn, I.S., Boyer, A.G., Kareiva, P., Gaston, K.J., Armsworth, P.R., 2013. Changing spatial patterns of conservation investment by a major land trust. Biol. Conserv. 161, 223–229. https://doi.org/10.1016/j.biocon.2013.02.007.
- Fovargue, R., Fisher, M., Harris, J., Armsworth, P.R., 2019. A landscape of conservation philanthropy for U.S. land trusts. Conserv. Biol. 33, 176–184. https://doi.org/ 10.1111/cobi.13146.
- Friesenhahn, E., 2016. Nonprofits in America: new research data on employment, wages, and establishments. Monthly Labor Rev. https://doi.org/10.21916/mlr.2016.9.
- Gotway, C.A., Young, L.J., 2002. Combining incompatible spatial data. J. Am. Stat. Assoc. 97, 632–648. https://doi.org/10.1198/016214502760047140.
- Greenspan, I., Handy, F., Katz-Gerro, T., 2012. Environmental philanthropy: is it similar to other types of environmental behavior? Organ. Environ. 25, 111–130. https://doi. org/10.1177/1086026612449339.
- Haaland, D., Vilsack, T.J., Raimondo, G.M., Mallory, B., 2021. Conserving and Restoring America the Beautiful.
- 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. https://doi.org/10.1016/j.biocon.2006.11.011.
- IUCN, 2016. IUCN red list of threatened species. Choice Reviews Online. https://doi.org/ 10.5860/choice.49-6872.
- Jackson, H.B., Kroetz, K., Sanchirico, J.N., Thompson, A., Armsworth, P.R., 2021. Protected area, easement, and rental contract data reveal five communities of land protection in the United States. Ecol. Appl. 31 https://doi.org/10.1002/EAP.2322.
- 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. https://doi.org/10.1017/S0376892912000331.
- Jantke, K., Schneider, U.A., 2011. Integrating land market feedbacks into conservation planning—a mathematical programming approach. Environ. Model. Assess. 16, 227–238. https://doi.org/10.1007/s10666-010-9242-2.
- 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. https://doi.org/10.1016/ j.biocon.2011.07.013.

Kohavi, R., 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection. Proceedings of the 14th International Joint Conference on Artificial Intelligence 2, 1137–1145.

- Kroetz, K., Sanchirico, J.N., Armsworth, P.R., Spencer Banzhaf, H., 2014. Benefits of the ballot box for species conservation. Ecol. Lett. 17, 294–302. https://doi.org/ 10.1111/ele.12230.
- Kujala, H., Lahoz-Monfort, J.J., Elith, J., Moilanen, A., 2018. Not all data are equal: influence of data type and amount in spatial conservation prioritisation. Methods Ecol. Evol. 9, 2249–2261. https://doi.org/10.1111/2041-210X.13084.

- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. ImerTest package: tests in linear mixed effects models. J. Stat. Softw. 82 https://doi.org/10.18637/jss.v082. i13.
- Lawler, J.J., Rinnan, D.S., Michalak, J.L., Withey, J.C., Randels, C.R., Possingham, H.P., 2020. Planning for climate change through additions to a national protected area network: implications for cost and configuration. Philos. Trans. R. Soc. B Biol. Sci. 375 https://doi.org/10.1098/rstb.2019.0117.
- Le Bouille, D., Fargione, J., Armsworth, P.R., 2022. Spatiotemporal variation in costs of managing protected areas. Conserv. Sci. Pract. https://doi.org/10.1111/ CSP2.12697.
- Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T., Rodrigues, A.S.L., 2013. Protected areas and effective biodiversity conservation. Science (80-.). https://doi.org/10.1126/ science.1239268.
- Lennox, G.D., Armsworth, P.R., 2013. The ability of landowners and their cooperatives to leverage payments greater than opportunity costs from conservation contracts. Conserv. Biol. 27, 625–634. https://doi.org/10.1111/cobi.12039.
- Lerner, J., Mackey, J., Casey, F., 2007. What's in Noah's wallet? Land conservation spending in the United States. Bioscience 57, 419–423. https://doi.org/10.1641/ B570507.

LTA, 2015. National Land Trust Census Report. Land Trust Alliance Publications. Lubowski, R.N., Plantinga, A.J., Stavins, R.N., 2006. Land-use change and carbon sinks: econometric estimation of the carbon sequestration supply function. J. Environ. Econ. Manage. 51, 135–152. https://doi.org/10.1016/j.jeem.2005.08.001.

Luck, G.W., Rickettst, T.H., Daily, G.C., Imhoff, M., 2004. Alleviating spatial conflict between people and biodiversity. Proc. Natl. Acad. Sci. U. S. A. 101, 182–186. https://doi.org/10.1073/PNAS.2237148100/ASSET/7E76F46C-8D1E-4EBC-A476-DD0B7A329897/ASSETS/GRAPHIC/ZPQ0260333230004.JPEG.

- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253. https://doi.org/10.1038/35012251.
- McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D. A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science (80-.) 338, 946–949. https://doi.org/10.1126/science.1229803.
- McIntosh, E.J., Pressey, R.L., Lloyd, S., Smith, R.J., Grenyer, R., 2017. The impact of systematic conservation planning. Annu. Rev. Environ. Resour. 42, 677–697. https://doi.org/10.1146/annurey-environ-102016-060902.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

- MIT Election Data and Science Lab, 2018. County Presidential Election Returns 2000–2016. Harvard Dataverse.
- Moilanen, A., Wilson, K.A., Possingham, H.P., 2009. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. New York, NY.
- Mount, J., 1996. Why donors give. Nonprofit Manag. Leadersh. 7, 3–14. https://doi.org/ 10.1002/nml.4130070103.
- 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. https://doi.org/10.1016/j.biocon.2007.07.011.
- Naidoo, R., Iwamura, T., 2007. Global-scale mapping of economic benefits from agricultural lands: implications for conservation priorities. Biol. Conserv. 140, 40–49. https://doi.org/10.1016/j.biocon.2007.07.025.
- NASA-JPL, 2013. NASA Shuttle Radar Topography Mission Global 1 arc second number. Nasa Lp Daac. https://doi.org/10.5067/MEaSUREs/SRTM/SRTMGL1.003.
- Nolte, C., 2018. Buying forests for conservation: contours of a global trend. Curr. Opin. Environ. Sustain. https://doi.org/10.1016/j.cosust.2018.05.003.
- Nolte, C., 2020. High-resolution land value maps reveal underestimation of conservation costs in the United States. Proc. Natl. Acad. Sci. U. S. A. 117, 29577–29583. https:// doi.org/10.1073/pnas.2012865117.
- Paradis, E., Schliep, K., 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528. https://doi.org/10.1093/ bioinformatics/bty633.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science (80-.) 344, 1246752. https://doi. org/10.1126/science.1246752.

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. https://doi.org/10.1016/j.biocon.2013.06.025.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput.

- Schöttker, O., Johst, K., Drechsler, M., Wätzold, F., 2016. Land for biodiversity conservation — to buy or borrow? Ecol. Econ. 129, 94–103. https://doi.org/ 10.1016/j.ecolecon.2016.06.011.
- 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. https://doi.org/10.1111/cobi.12405.
- Sutton, N.J., Cho, S., Armsworth, P.R., 2016. A reliance on agricultural land values in conservation planning alters the spatial distribution of priorities and overestimates the acquisition costs of protected areas. Biol. Conserv. 194, 2–10. https://doi.org/ 10.1016/j.biocon.2015.11.021.
- Texas Parks & Wildlife Department, 2022. Texas Ecoregions [WWW Document]. Texas Park. Wildl. Dep. Website. URL https://tpwd.texas.gov/education/hunter-educati on/online-course/wildlife-conservation/texas-ecoregions (accessed 2.6.23).

The Trust for Public Land, 2019. The Conservation Almanac [WWW Document]. URL. https://www.conservationalmanac.org/ (accessed 11.21.19).

- Torgo, L., 2016. Data mining with R: learning with case studies, second edition. In: Data Mining with R: Learning with Case Studies, Second Edition, 1st ed. CRC Press. https://doi.org/10.1201/9781315399102.
- U.S. Bureau of Labor Statistics, 2019. CPI (Consumer Price Index) Inflation Calculator.
- U.S. Census Bureau, 2015. TIGER/Line Shapefiles.
- U.S. Environmental Protection Agency, 2015. ArcGIS- Ecoregions of North America [WWW Document]. URL. http://www.arcgis.com/home/webmap/viewer.html?we bmap=69e678375433435eabf537cc020e03a6 (accessed 6.12.20).
- United States Census Bureau, 2021. American Community Survey, Chicago [WWW Document]. URL. https://www.ers.usda.gov/data-products/county-level-data-sets/ download-data/ (accessed 11.21.19).

United States Department of Agriculture (USDA), 2012. Land Values - National Agricultural Statistics Service (NASS).

- USGS Gap Analysis Project, 2018. Protected Areas Database of the United States (PADUS) Version 2.0. https://doi.org/10.5066/P955KPLE.
- Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H.P., Rondinini, C., Smith, R.J., Venter, M., Watson, J.E.M., 2014. Targeting global protected area

expansion for imperiled biodiversity. PLoS Biol. 12, e1001891 https://doi.org/ 10.1371/journal.pbio.1001891.

- Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T., Gittleman, J.L., 2013. Targeting global conservation funding to limit immediate biodiversity declines. Proc. Natl. Acad. Sci. U. S. A. 110, 12144–12148. https://doi.org/10.1073/pnas.1221370110.
- Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature. https://doi.org/10.1038/nature13947.
- Wear, D.N., 2011. Forecasts of county-level land uses under three future scenarios: a technical document supporting the Forest Service 2010 RPA Assessment. In: Gen. Tech. Rep. SRS-141., Gen. Tech. Rep.
- Wentland, S.A., Ancona, Z.H., Bagstad, K.J., Boyd, J., Hass, J.L., Gindelsky, M., Moulton, J.G., 2020. Accounting for land in the United States: integrating physical land cover, land use, and monetary valuation. Ecosyst. Serv. 46, 101178 https://doi. org/10.1016/j.ecoser.2020.101178.
- 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, 1249–1256. https://doi.org/10.1111/j.1461-0248.2012.01847.x.