

Manuscript Title Optimal conservation outcomes consider donor geography and their willingness to support more distant projects

Abstract

Private donors are often willing to give more to support conservation activities, like protecting land, when these take place nearby. However, population centers in which most donors live may be far from conservation priority areas. Here we examine how conservation organizations can best balance pursuing high impact conservation projects with their need to raise funds. We develop general principles governing optimal protected area siting by representing distance decay in people's willingness to give to conservation as an increase in the effective cost of more distant projects. We illustrate these principles through applications to terrestrial vertebrate conservation and donation patterns to a private land trust in two U.S. states, California and North Carolina. In both states, we find a negative association between donation levels and conservation priorities, a pattern shaped by the lower cost of land protection in rural areas. A protected area strategy that gives some consideration to the distribution of donors while not compromising on protecting places that offer the highest conservation impact ensures the greatest improvement in biodiversity. This optimal strategy spreads spending on protected areas more than would have been optimal if ignoring spatial patterns in philanthropic giving. The optimal solution makes clear the value of integrating donation data and philanthropy staff earlier in the priority setting process. It emphasizes that the value of a conservation dollar depends on where it is donated, which suggests the need to cultivate local donor capacity in priority areas and persuade more distant donors to relax spatial restrictions on giving.

Keywords

Conservation finance, conservation planning, philanthropy, The Nature Conservancy, willingness-to-pay, 30 by 30.

Introduction

Recent national and international policies call for expanding the coverage of protected area networks (Haaland et al. 2021, CBD 2022) to help stem ongoing losses of biodiversity and ecosystem services (IPBES 2019). Spatial optimization tools can help conservation practitioners identify priority sites for expanding protection (Groves and Game 2016). Optimization methods now take into consideration the biodiversity found in candidate sites (Hamilton et al. 2022), the cost of protecting them (Nolte 2020), and threat of conversion they would face if left unprotected (Salgado-Rojas et al. 2020), along with other factors. Available approaches however typically assume that resources available to support establishment of new protected areas are free to move in space (but see Kark et al. 2009, Pouzols et al. 2014), something rarely true in practice. Instead, people's willingness to pay (WTP) to support environmental projects is often lower for projects that are located further away (Hanley et al. 2003, Schaafsma 2015). We examine the implications for protected area priorities if funding available to support conservation declines with distance.

Locations that promise the greatest gains for biodiversity when expanding protected area coverage are often concentrated in particular parts of the map (Armsworth et al. 2020). These are places rich in biodiversity, where land can be protected relatively cheaply and where habitats are at risk of conversion if left unprotected. The combined effects of these factors can be summarized in the conservation 'return-on-investment' (ROI) offered by investing in protected areas in a given locale (Boyd et al. 2015). Conservation ROI measures the gain in a given conservation objective per dollar spent. Locations where potential sources of support are most readily available to enable protected area establishment also tend to be concentrated in particular locations (Kroetz et al. 2014, Fovargue et al. 2019). Unfortunately, these are not the same places offering the greatest ROI in terms of conservation benefits (Armsworth et al. 2023). Most studies that examine the best places to protect ignore this spatial misalignment between protection priorities and conservation support and instead just assume funding for new protected areas is free to move anywhere in space. But this is not true for many sources of public and private funding for conservation.

NGOs active in conservation are major contributors to land protection in many parts of the world. For example, in the U.S., 1281 active land trusts have protected around 25 million

hectares of land, an area equivalent to 72% of the U.S. National Park system (LTA 2023, NPS 2023). The Nature Conservancy (TNC), an international NGO that operates a land trust like business model for some of its conservation activities in the U.S. (Birchard 2005), has itself helped protect over 50 million hectares of land worldwide (TNC 2023). The geographic context of resulting privately protected areas can be quite different from federally protected areas (Aycrigg et al. 2013, Jackson et al. 2021). NGOs typically depend on a mix of public and private funding to enable these protection efforts. Some funding given to NGOs active in land protection by private donors offers a degree of flexibility over where it can be used (Larson et al. 2016). However, surveys examining people's willingness to give to support environmental causes repeatedly document declines in what people would be willing to give with increasing geographic distance (Glenk et al. 2020, Yamaguchi and Shah 2020) and across administrative boundaries, such as national borders (Dallimer and Strange 2015, Haefele et al. 2019). Here we examine the effect on protected area priorities of a decrease in willingness to support conservation with geographic distance (see also Ando and Shah 2010). Elsewhere we have examined implications of donors placing restrictions on funding support crossing administrative boundaries (Armsworth et al. 2023; see also Erasmus et al. 1999, Kark et al. 2009, Pouzols et al. 2014).

Materials and Methods

We extend the spatial optimization framework and parameterization of Armsworth et al. (2020) so it can account for spatial decay in donors' willingness to pay for conservation. This formulation focuses on allocating conservation funding to counties within the conterminous U.S. to establish new protected areas. In the main text, we assume a conservation goal of maximizing the number of species that will persist by adding new protected areas to prevent future habitat conversion. The Supporting Information includes results for other conservation objectives. The framework accounts for species complementarity, existing protected areas, the ecological value of private land and spatial heterogeneous costs and threats.

Distance decay in WTP

We optimize the choice of how much additional protected area to establish in county i using funds from donors in county k . We denote this quantity x_{ik} . In Armsworth et al. (2020), we calculated optimal allocation vectors describing how much protection should take place in each county from a shared national budget. Here, we differentiate new protected areas based on where the funding for them originates and where projects take place.

We use y_k to indicate the total amount of funding donors in county k are willing to pay to establish protected areas in their home county. Possible funding allocations must satisfy

$$\sum_{i=1}^I c_i \varepsilon_{ik} x_{ik} \leq y_k \forall k \quad (1)$$

In this inequality, c_i is the cost per hectare of protecting land in county i . Meanwhile ε_{ik} represents the ‘effective cost’ of asking donors to support more distant projects instead of ones close by. We assume this leads to a reduction in what the donor would be willing to give, meaning less land can be protected. I.e., the effect is identical to what would happen if there were a cost to moving funds from one location to another, which is how we represent it here. With our assumptions, $\varepsilon_{ii} = 1$, $\varepsilon_{ik} > 1$ for $i \neq k$, and the effective cost of moving funding ε_{ik} gets larger the greater the distances involved. This term applies multiplicatively as it affects every dollar allocated from donors in county k invested in protecting land in county i .

In the main text, we assume people’s willingness to donate to conservation projects declines exponentially with distance and explore the impact of varying the decay rate, σ , in our analyses. To convert that exponential decay rate to our effective cost representation, we set

$$\varepsilon_{ik} = e^{\sigma \times \text{distance}(i,k)} \quad (2)$$

In the Discussion and Supporting Information, we consider the effects of assuming spatially heterogeneous decay rates or using an alternative functional form for distance decay in WTP.

We use the term ROI in the main text to refer to underlying ROI patterns before accounting for the effect of distance decay as a cost multiplier. We also report all results in terms of the potential funding available from each donor county before any distance decay is applied.

Expressing recommendations in this way makes it easier to compare how assuming low or high distance decay rates changes optimal allocation decisions.

Optimization problem

In our notation, we aim to maximize

$$\sum_j w_j P_j(S_j) \quad (3)$$

where j indexes species, S_j describes a landscape suitability score for species j across the conterminous U.S., $P_j(S_j)$ is the probability species j persists which is a function of S_j and w_j is a weight taking the value 0 or 1 depending on whether species j is a conservation priority. We use a smooth, saturating functional form to represent how persistence probabilities depend on the amount of a species range that is protected or unconverted, $P_j = 1 - e^{-\varphi_j S_j}$. Here saturation rate φ_j is a positive constant for each species. The landscape score for species j across the conterminous U.S. is the sum of ecological conditions for the species across individual counties,

$$S_j = \sum_{i=1}^I s_{ij} \quad (4)$$

The conditions for species j in county i are described by s_{ij} , a nonlinear function, of the total amount of new protected area established there,

$$s_{ij} = s_{ij} \left(\sum_{k=1}^K x_{ik} \right). \quad (5)$$

Here the total area protected in county i is summed across contributions from different donor counties and the functional form of s_{ij} is given by our land use change model described below.

With these assumptions, the conservation organization's spatial prioritization problem becomes

$$\max_{[x_{ik}]} \sum_j w_j P_j \left(\sum_{i=1}^I s_{ij} \left(\sum_{k=1}^K x_{ik} \right) \right) \text{ such that } \sum_{i=1}^I c_i \varepsilon_{ik} x_{ik} \leq y_k \forall k \text{ and } x_{ik} \geq 0 \forall i \text{ and } k \quad (6)$$

which must be solved subject to additional constraints described below that ensure funding allocations do not attribute more land to given uses than counties contain.

Land use change model

Remaining assumptions in our framework concern how we calculate the benefits in terms of improved conditions for a species (species j) that result from adding more protected areas into a county (county i), as represented by the county's contribution s_{ij} to the overall landscape suitability score, S_j , for that species. This land use component of the models is somewhat modular and Armsworth et al. (2020) compared two different sets of assumptions for it. Here we adopt their pessimistic assumptions, which assume protected areas sample a species range in each county in proportion to the amount of habitat being protected. With their formulation, land can either be converted, protected or left unconverted and unprotected. Converted areas are assumed no longer to contribute to species persistence, while those inside protected areas are assumed to offer the greatest value to enabling species persistence. Areas that remain in the unprotected but unconverted category are assumed to offer a portion of the ecological value for species offered by full protected areas. Armsworth et al.'s (2020) formulation also considers to what degree any new protected areas successfully target parts of a county that would otherwise have faced conversion and whether any of the conversion threat involved is displaced onto other areas. Dropping i, j , and k subscripts by focusing on a generic county for now and instead using subscripting in this land use change model description to denote time, so that subscripts 0, 1 and 2 distinguish these past, present and future activities, we use the following notations

a	is the area of the focal county
b_0	was the historical range area of the species found in that county before any conversion to development or intensive agriculture took place
d_0	was the area of habitat converted for development or intensive agriculture in the past

d_1	is the area that would be converted in the present if no further conservation action were taken today
r_0	is the area that was protected through past conservation actions
x	denotes the new area that will be protected today as a function of the amount of additional funding available to the county
$u_2(x)$	is the future area of suitable habitat left unprotected that will not be converted for development or intensive agriculture, after accounting for both past and present protection and conversion
$\alpha \in [0,1]$	weights the ecological value of a hectare of unprotected, unconverted habitat with $\alpha=0$ when this habitat makes no contribution to supporting species persistence and $\alpha=1$ when it is as valuable for supporting species as a hectare of protected area.
$\delta \in [0,1]$	indicates whether new protected areas target areas that would otherwise have been converted
$\gamma \in [0,1]$	indicates how much of that conversion pressure is displaced onto other unprotected sites as a result of establishing new protected areas, a form of leakage

The area of the focal county that ends up protected is $r_0 + x$. Meanwhile, the amount of converted habitat is

$$d_0 + d_1 - (1 - \gamma)\delta \min(x, d_1) \quad (7)$$

Finally, the amount of suitable habitat remaining on unprotected land in the future is the total area of the county minus the area protected or that will be converted

$$u_2(x) = a - (r_0 + x) - (d_0 + d_1 - (1 - \gamma)\delta \min(x, d_1)) \quad (8)$$

Our formulation assumes the three land uses cover species ranges in proportion to the area of range in the county, giving

$$s(x) = \frac{b_0}{a} (r_0 + x + \alpha u_2(x)) \quad (9)$$

We use this land use change submodel in the optimization formulation to quantify by how much adding protected area to a county will improve conditions there for each species. Adding back in i and j subscripts, extending them to the land use change model components, and accounting for the overall amount of protection in the county, we obtain

$$s_{ij} \left(\sum_{k=1}^K x_{ik} \right) = \frac{b_{0,i}}{a_i} \left(r_{0,i} + \sum_{k=1}^K x_{ik} + \alpha u_{2,i} \left(\sum_{k=1}^K x_{ik} \right) \right) \quad (10)$$

We can now formalize the upper bound constraint on the total amount of land protected in a county as

$$u_{2,i} \left(\sum_{k=1}^K x_{ik} \right) \geq 0. \quad (11)$$

Numerical Applications

We use two examples for our numerical applications, one focused on counties in California and the other on counties in North Carolina. These two states reflect broad East and West Coast contrasts relevant to land protection in the conterminous U.S. For example, counties in California tend to be larger, with a greater area already protected and a lower historical rate of land conversion than those in North Carolina (Table S1). Counties in both states tend to donate slightly larger amounts to conservation, to involve somewhat higher land protection costs, and to be places where habitat conversion is predicted at a somewhat higher rate, than the average county in the lower 48 (Table S1).

We consider how to allocate funding given by donors within each state to TNC to establish new protected areas where these are evaluated against how they will affect species persistence in 2040. When doing so, we account for the existing distribution of protected areas across the whole of the conterminous U.S. as well as any additional protected areas created with conservation funding being allocated in each focal state. We also assume funds from California

donors will be used in California and those from North Carolina donors will be used in North Carolina (but see Armsworth et al. 2023).

Donation data

To represent spatial variation in the availability of donations to support conservation, we rely on the estimation of Fovargue et al. (2019). That study used statistical models to explain spatial variation across zip codes in the conterminous U.S. in giving to TNC by donors who gave between \$1000 and \$100,000 between 2009 and 2014. This included 160,000 gifts totaling USD \$ 350 million. All dollar amounts in this paper were inflation corrected to 2016 U.S. dollars using the Bureau of Labor Statistics' Consumer Price Index (U.S. Bureau of Labor Statistics 2023).

We use the predicted values from these models to represent spatial variation in giving. Fovargue et al. (2019) used a hurdle model in their estimation that first predicts the probability of a gift being observed and then predicts the giving amount conditional on this outcome. We combined the two parts of their hurdle model to arrive at an overall expected gift amount per zip code by applying a threshold to identify zip codes likely to see gifts. To obtain an estimate of predicted giving by county, we took a population weighted average of the resulting predicted gift amounts by zip code. We used the distance between county centroids to calculate distance decay in potential donations.

Data informing conservation ROI estimates

We use the same approach to parameterize the biodiversity optimization models here that we took in Armsworth et al. (2020). Importantly, that earlier work along with subsequent analyses (Yoon et al. 2022, Armsworth et al. 2023, Le Bouille et al. 2023) includes extensive sensitivity tests to model assumptions and parameters. Briefly, we focused on protecting terrestrial vertebrate species. We used range map data for mammal, amphibian and reptile species from IUCN (2016) and for bird species from Birdlife and Handbook of the Birds of the World (2016). In the main text, we include scenarios focused on protecting species evaluated as being vulnerable to extinction or worse by IUCN by setting $w_j=1$ for these species and $w_j=0$ for others. In the Supporting Information, we provide results when focused on protecting all species

regardless of their vulnerability status. In the California application, we included 707 species of which 48 were vulnerable to extinction or worse. The North Carolina application included 515 of which 19 were vulnerable to extinction or worse.

With function P_j the contribution that protecting an additional hectare of habitat makes to increasing the persistence probability for species j decreases the greater the area within the species range that is already protected or remains unconverted. We use species specific saturation rates, φ_j , in this function based on the procedure laid out in Armsworth *et al.* (2020). These saturation rates were chosen such that large range species have a high persistence probability once 10% of their total range is fully protected, whereas small range species need their entire range to be protected to have high persistence probabilities. We assume four hectares of unconverted land that remains in private ownership makes an equal contribution to ensuring species persistence as each hectare of protected areas. Also, we assume the combined effects of imperfect subcounty targeting of protected areas and of leakage is such that for every two hectares of land protected, one hectare that would have faced conversion and one that would have remained unconverted now would be protected. When evaluating the contribution of any new protected areas in California and North Carolina, we focus on persistence throughout a species range. To do so, we account for existing protected areas and predicted habitat changes throughout the lower 48. Following Armsworth *et al.* (2020), we also include an ‘ecological subsidy’ for species with ranges reaching outside the conterminous U.S. to reflect the contributions to ensuring their persistence made by protected areas and unconverted habitats outside the lower 48 states.

We used GAP 1 and 2 protected areas from the flattened version 1.4 of the data from the Protected Area Database of the United States (2018) to account for existing protected areas before considering where additional protected areas should be added. We used the predicted protected area acquisition costs per county of Le Bouille *et al.* (2023). These estimates are based on a regression model fit to acquisition costs for 36,000 parcels of land protected between 1980 and 2014 by TNC or state and federal agencies within the U.S. We used land cover change projections produced by USFS to estimate spatial variation in the threat of habitat conversion if areas remain unprotected. We used land cover change projections for 2040 per county from the

A2 growth scenario in Wear (2011). When assessing the ecological value of the landscape for species, we treated areas predicted to be covered by urban, crop or pasture in 2040 as having been converted and those covered by rangeland and forest as remaining unconverted. Armsworth et al. (2020), Yoon et al. (2022) and Le Bouille et al. (2023) explore the effects of these assumptions relative to other ways of representing spatial variation in biodiversity benefits, costs and threats on protected area priorities.

From our assumptions, we can derive a baseline persistence probability for species when accounting for existing protected areas and projected land cover change by 2040, before considering how investing in new protected areas could improve species persistence. With our assumptions and parameters, the median persistence probability for all species in California is 0.95 and that for vulnerable species in the state is 0.44. The median persistence probability for species in North Carolina with these assumptions and parameters is 0.90 for all species and 0.37 for vulnerable species. Our analyses of ROI patterns and optimization solutions focus on the improvement over these baseline persistence probabilities made possible by further investment in protected areas.

The future land conversion predictions we rely on are not available for the small, heavily urbanized City and County of San Francisco in California. We exclude this county when considering targets for potential conservation investment in California, although include donations from it when considering funding for conservation. After dropping this county, 57 counties are candidates for conservation investment in California and 100 in North Carolina.

Analysis

We obtain insights into the behavior of the optimal solution by forming the relevant Lagrangian for the optimization problem in Eqn. (6) and calculating the first order necessary conditions for an optimal solution. To do so, we augment the objective with relevant constraints using Lagrangian multipliers and slack variables.

To find numerical solutions for our optimization problem, we use Matlab's nonlinear programming solver, `fmincon` (Matlab version 2019B). We rely on a sequential search strategy,

given the size of the control space. Specifically, we optimize the funding allocation from counties one at a time, while keeping allocations from other counties constant, proceeding through all counties in a randomized order three times, by which point no further changes in allocation occur. We repeated this process 100 times for randomly assigned starting guesses and orderings of counties, selecting the solution giving the highest objective score. Convergence was excellent across the solution sets generated with this method. We also compared the performance of this search strategy to two other solution methods. Additional details of our optimization approach are provided in the Supporting Information.

The underlying model formulation quantifies conservation ROI from investing in any county, not just the optimal set of counties. As well as shaping the optimal solution, these ROI values provide informative summary statistics in their own right by describing patterns of spatial variation in conservation opportunities. ROI measures the gain in the overall conservation objective when a small amount of additional protected area is created in a county divided by the cost of protecting that additional area (i.e., it measures the marginal benefit to cost ratio). Within our model, ecological complementarity implies that the ROI from investing in some county is a function of investment levels into every county and not a constant. However, displaying and describing spatial patterns in these values is easier when assuming a particular underlying investment pattern. As such, when producing maps of ROI, we start from the existing distribution of protected areas today and show the ROI on offer from the first dollar invested in making new, additional protected area in a county while assuming no further new investment is made elsewhere on the landscape.

We use Spearman's rank correlations to examine covariation between predicted donations available to support conservation and the ROI offered on the first dollar invested into each county. We also provide correlations between this ROI score and components that comprise it (cost, threat, etc.) and between donations and factors explaining variation in donation rates. We evaluate the significance of these correlations while accounting for spatial autocorrelation. We use Moran spectral randomization to maintain the global level of spatial autocorrelation while randomly resampling from each variable using R package *adespatial* (Dray et al. 2023). Because Moran spectral randomization is sensitive to linear trend (Wagner and Dray 2015), we first

removed spatial trends based on latitude and longitude from the relevant variables before applying significance tests to the detrended residuals. As a robustness check, we compared coefficients and significance levels to those obtained when making other test assumptions, namely: not controlling for spatial autocorrelation, not detrending first, or assuming alternative distance measures to define neighborhoods. We provide additional details of these steps in the Supporting Information.

Sensitivity tests

To explore the sensitivity of our results to assumptions we made, we repeat some analyses for a larger geographic extent (the conterminous US); two other conservation objective choices (one focused on protecting all species regardless of their vulnerability status and one focused on protecting vulnerable species while also providing recreational benefits to people); alternative representations of distance decay; an alternative representation of conservation donations; and alternative numerical optimization methods (Supporting Information).

Results

Analytical optimization results

The first order necessary conditions for an optimal solution reveal how including distance decay in donations changes optimal recommendations regarding protection priorities. These conditions require funds from county k be only allocated to counties that provide large marginal benefit to effective cost ratios for dollars donated from county k . Moreover, funds are shared in such a way that these marginal benefit to effective cost ratios are equalized across counties receiving funding (an “equimarginal” principle) and all potential funds from county k are fully allocated.

The relevant marginal benefit to effective cost ratio for dollars donated from county k is

$$\lambda_k = \frac{\sum_j w_j \frac{dP_j}{dS_j} \frac{\partial S_{ij}}{\partial x_{ik}}}{c_i \varepsilon_{ik}} \quad (12)$$

where λ_k is the Lagrangian multiplier on that county’s budget constraint. The numerator here summarizes the change in the overall conservation objective (how many species will persist) as a

function of adding a hectare of new protected area to county i . The numerator is greater for counties with more species (the summation is over species). The dP_j/dS_j ensures these species are not already well-protected, while the $\partial s_{ij}/\partial x_{ik}$ term favors counties where adding new protected area does more to improve outcomes for them (e.g., counties where conversion threats are higher). The c_i in the denominator favors counties where land can be protected relatively cheaply. The ε_{ik} adjusts this cost of protection to reflect the effective cost of moving funds from county k to county i , because of the distance decay in donors' WTP. It is this ε_{ik} term that drives differences between optimal solutions for different severities of distance decay. There are as many of these Lagrangian multipliers as there are donor counties.

Figures 1 and 2 near here

We illustrate the behavior of the optimal solution with and without distance decay for a hypothetical three county application in Figs. 1 and 2. The three counties are located at different distances from one another. They also differ in the cost of establishing new protected areas (grey bars in Fig. 1a) and improvement in conservation goals that results from doing so. The initial improvement is shown by black bars in Fig. 1a, but this improvement will decline as more funding is allocated to a county to establish additional protected areas, as reflected in the tan downward sloping marginal benefit to cost ratios for each county in Fig. 1b. For ease of illustration in Figs. 1 and 2, we did not include interaction effects caused by species complementarity across the counties, but we account for these fully in our derivations and numerical applications.

If there were no distance decay in donations (Fig. 1b), funding would be pooled ($y_1+y_2+y_3$ represents the summed donations from the three counties combined) and allocated in the optimal solution only to counties offering the highest marginal benefit to cost ratio (here counties 1 and 2). All available funds would be divided between counties 1 and 2 in such a way as to equalize these marginal benefit to cost ratios. This allocation is illustrated by the horizontal blue line segments.

When adding distance decay in donations (inset in Fig. 2a), the optimal allocation changes. Now we must consider the marginal benefit to effective cost ratios offered when seeking to allocate funds donated by each individual county (Figs. 2abc). The marginal benefit to effective cost ratio of keeping funds in the same county where they were donated is unchanged (solid tan line in Fig. 2a, dashed tan in Fig. 2b and dotted tan in Fig. 2c). But the effective cost of protecting land in more distant counties is now higher, because of the distance decay in donors' WTP for conservation. This moves the marginal benefit to effective cost ratios for more distant counties downwards (as indicated by the mini-plots and yellow arrows). A similar equimarginal principle applies but this time is applied to dollars donated by each county individually. For example, in Fig. 2c, funding from county 3, the largest donor county (length of magenta line segment), is divided between counties 2 and 3 in such a way as to equalize the marginal benefit to effective cost ratio available in each location. County 1, which had been a top investment priority when no distance decay applied (Fig. 1b), no longer offers a good investment when considering donors in county 3, because of the large distance decay in donations that would result.

The characteristics of the optimal solution revealed by first order necessary conditions and illustrated in Fig. 2 indicate two important properties.

1. *the value of a dollar for conservation depends on where it is donated.* The potential improvement in conservation outcomes offered by an additional donation in each county are illustrated by the horizontal line segments in Figs. 2a-c and measured by these Lagrangian multipliers, λ_k . While these are equalized between counties receiving funds from county k , they differ among donor counties. In our illustrative example, conservation dollars donated from county 3 are worth only 60% of dollars donated from county 1 when measured in terms of conservation gain.
2. *priority targets for investment are different for donors in different places.* When no distance decay applies (Fig. 1b), protection priorities are the same for donors everywhere. However, when distance decay in donation is considered, donors in different locations should be asked to support different projects. E.g., in our illustration, donors in counties 1 and 2 should be asked to support their local protected areas, whereas those in county 3 should be asked to support projects in both counties 2 and 3.

The illustrations in Figs. 1 and 2 also make clear the behavior of the optimal solution in extreme cases when there is no distance decay rate or where this rate is very large. Fig. 1b illustrates the case where the distance decay rate is zero; this is the situation explored in Armsworth et al. (2020). In the optimal solution for this case, funds flow to the highest marginal benefit to marginal cost opportunities regardless of where they were donated and tend to be quite concentrated in space (Armsworth et al. 2020). In contrast, as the decay rate becomes very large, the dynamic illustrated in Fig. 2a-c in which marginal benefit to effective cost curves for distant counties move downwards, would be greatly accentuated. In this situation, moving funding in space becomes prohibitively expensive and conservation funds should just be spent in the counties where they were donated. More interesting questions lie in understanding when and how solutions transition between these two extremes, something that depends on the particular distributions of donations and conservation opportunities on the landscape as we now explore in our numerical applications.

Spatial variation in donations and in ROI patterns

The total predicted donation amount for California counties is USD \$46.2 M, while that for North Carolina is \$9.7M. The distribution of giving in both states is highly skewed (Table S1); the top 10% of counties in each state account for the bulk of predicted donations (60.8% for California and 74.0% for North Carolina). In California, counties predicted to give most are clustered around the San Francisco Bay Area and coastal areas near Los Angeles (Fig. 3a). In North Carolina, high predicted donation areas include the region in the center of the state containing the cities Raleigh, Durham, Greensboro and Winston-Salem and the counties containing the cities of Charlotte and Asheville (Mecklenburg County and Buncombe County respectively; Fig. 3d). Counties predicted to donate more in each state tend to have higher population sizes, higher median income levels, and a greater proportion of individuals holding a bachelors degree or above (Table S2).

Figure 3 near here

The distribution of ROI is also heavily skewed. When focused on improving conditions for vulnerable vertebrate species in California, investments in additional protected areas in a set of

counties in the interior of the state offers the greatest ROI (including Kern, Mariposa and Riverside counties; Fig. 3b). In North Carolina, the highest ROI is offered either by a set of coastal counties (including Tyrrell and Hyde counties) or by counties in the southern Appalachian Mountains in western North Carolina (including Swain and Burke counties; Fig. 3e). Examining the change in the persistence probabilities of individual species that drives changes in ROI makes clear that high ROI counties are ones where new protected areas can benefit small range species (e.g., small range endemics, including many amphibians and small mammals, or species that have undergone acute range contractions, such as red wolf, *Canis rufus*).

All else being equal, we would expect counties where costs of land protection are lower, habitats are at a greater risk of conversion and there are more vulnerable species, to be higher priorities for investment. The negative association between ROI and cost is clear in both states (Table 1). There is also a significant positive association between ROI and the number of vulnerable species in North Carolina (Table 1). However, the association of ROI with threat does not conform to the basic expectation (Table 1). The reason lies in correlations between different components of ROI. Land protection costs are strongly positively correlated with conversion threat in both states, setting up a trade-off between cost and threat for determining where higher ROI values will be found. The cost signal appears to dominate in both states. Table S3 provides a comparable correlation table for all counties in the lower 48 states, showing that similar patterns apply across larger spatial scales in the U.S. as well.

Table 1 near here

The consequence of these patterns is that predicted donations to conservation are negatively correlated to ROI opportunities in both states (Table 1). Predicted donations tend to be higher in more urbanized areas, while the higher ROI opportunities in each state are found in more rural counties, where land costs are lower (Fig. 3). A similar negative association between conservation donations and ROI applies across the lower 48 (Table S3).

Our finding of a negative association between predicted donations and conservation ROI in these applications depends on our assumed conservation objective. In Table S5, we provide similar results for two alternative conservation objectives, one focused on conserving all species regardless of vulnerability status and one that both seeks to protect vulnerable species and also provide recreational benefits to people (Supporting Information). We find even stronger negative associations between donations and conservation ROI when pursuing the first of these alternative objectives, but no association between the two when pursuing the second (Table S5).

Numerical optimization results for California and North Carolina

The numerical optimization results for our CA and NC applications parallel the theoretical expectation for the extreme cases. Very low distance decay rates lead to spending all being directed to the same place, while very high distance decay rates favor funding just being spent in donors' home counties. More interesting is the transition between these extremes, as illustrated by the examples in Figures 4 and 5. For clarity of display, these figures only show part of the full optimal solution focused on the allocation of funding from the fifteen counties predicted to give most in each state (our analyses use the full optimal solution). The skewed nature of the distributions of conservation ROI and predicted donations mean that values displayed in the figure account for between 77% and 87% of the overall conservation gain achieved by the full optimal solution across the four scenarios shown, despite only accounting for 0.45% (NC) to 1.3% (CA) of the overall control set. As noted in the Materials and Methods, the optimal allocations in Figs. 4 and 5 are shown in terms of potential dollars available from a donor county when accounting for a particular distance decay rate but before that distance decay has been applied. The actual dollars that would reach a recipient county that was far away would be lower once that decay rate was applied. Showing things in terms of potential dollars from donor counties in this way aids visual comparison of plots that assume distance decay rates of differing severity.

Figures 4 and 5 near here

In California, a low rate of distance decay favors funding being concentrated in the highest ROI county (Kern county, Fig. 4ab), which contains habitats for a number of vulnerable species (e.g.,

Nelson's antelope squirrel, *Ammospermophilus nelsoni*; White eared pocket mouse, *Perognathus alticola*). At a higher rate of distance decay however (Fig. 4c-f), funding from counties in northern California, particularly around the Bay Area, should shift to protect parts of Mariposa county in the foothills of the Sierra Nevada Mountains, and donors in Riverside county should fund local projects. This shift in funding allows additional species to benefit (e.g., Sierra Nevada yellow-legged frog, *Rana sierrae*).

Fig. 5 shows how similar shifts play out in optimal solutions for North Carolina as a higher decay rate is assumed. Funding should be concentrated into projects at the eastern and western extremes of the state if there is a low level of distance decay in donors' willingness to support conservation projects (Figs. 5a-c). Specifically, Tyrrell county on the coast should receive the most funding allowing protection of coastal species. Meanwhile, funding from Charlotte, Asheville, Boone (Mecklenburg, Buncombe, Watauga counties) and other areas nearer to the Appalachians should be used for projects protecting mountain species (e.g., Cheoah Bald salamander, *Plethodon cheoah*) in Swain county on the edge of the Great Smoky Mountains National Park. At a higher decay rate, we again see a shift in the optimal funding allocation with a third funding priority emerges that is more centrally located and draws funding away from these more distant counties (Figs. 5d-g). Specifically, in that case, funding from some more central counties shifts to Burke County that covers parts of the Eastern Blue Ridge Mountains.

We chose the particular decay rates used in Figs. 4 and 5 to illustrate how transitions in optimal funding allocations play out. The decay rates at which donors in Santa Clara in California and Mecklenburg in North Carolina would become indifferent between closer and more distant projects falls between the low decay rate in Figs. 4ab and 5a-c (willingness to give halves after 500 km) and high decay rate in Figs. 4c-f and 5d-g (willingness to give halves after 100 km). We review in the Discussion how these values compare to empirical estimates of distance decay rates in people's willingness to give to conservation projects.

Overall, the greater the distance decay in donors' willingness to support conservation projects the less effective conservation can be at protecting vulnerable species (Figure 6a). Accounting for distance decay in willingness to support conservation also changes optimal solutions in other

ways. For example, conservation funding appears to be dispersed across more counties the greater the distance decay in donors' willingness to give to projects (Figure 6b). This increased spreading of funds means a greater diversity species and ecosystems will see some benefit from conservation actions, even if aggregate benefit will not be improved as much (Fig. 6a).

Figure 6 near here

The distance decay rates shown in Figures 4 and 5 are not great enough to favor keeping all projects in donors' home counties, as would maximize conservation income. Instead, conservation organizations should accept some reduction in overall donations if it allows them to pursue high ROI opportunities. Indeed, for the particular decay rates shown, only pursuing projects in donors' home counties and not moving funds at all in order to maximize income would greatly reduce overall conservation efficacy (Figure 6c). Simply pursuing the highest ROI opportunities and ignoring distance decay altogether would also come at some cost in terms of conservation outcomes, albeit not as large a cost as seeking to maximize conservation income for the particular decay rates shown (Figure 6d). How the optimal solution balances these two competing forces (maximizing donations versus maximizing ROI from projects) depends on the severity of the distance decay rate (Figures 4 and 5).

Conclusions

Empirical evidence suggests the amount people are willing to give to support environmental projects declines with distance (Bateman et al. 2006, De Valck and Rolfe 2018). Here we examined consequences for protected area priorities of distance decay in the willingness of private philanthropic donors to support conservation projects. We developed an optimization approach that can account for different forms of distance decay and derived general characteristics describing optimal solutions. We also examined patterns of covariation between philanthropic giving to conservation and spatial protection priorities in two U.S. states and applied numerical optimization to reveal optimal funding allocations at different distance decay rates. We find that ignoring the distribution of donors and any spatial distance decay in their willingness to support projects when identifying protection priorities will reduce conservation's potential impact on vulnerable species. Our results also suggest the value of finding ways to

integrate donors' interests during priority setting while, at the same time, not compromising on pursuing the highest conservation return opportunities.

In our applications to land protection in California and North Carolina, we find a negative correlation between where donors are located who support conservation and where the highest conservation priorities are to be found. Top giving locations are not conservation priorities, while top priority locations are rarely those where donation amounts are particularly high. This disconnect poses a challenge when donors' willingness to support conservation declines with distance. Whether a negative or positive association between donations and conservation ROI should be expected more generally will depend on the particular geography, conservation objective, and source of funding. In terms of geography, we anticipate our findings of a negative correlation between predicted donations and conservation ROI in California and North Carolina may be quite common. For example, in Table S3, we show that equivalent associations across the whole of the conterminous U.S. again display a similar, negative correlation. For both individual states and for the lower 48, the negative association between conservation ROI and predicted donations arises, because costs exert a strong role in shaping overall ROI patterns (Table 1, S3). Conservation ROI is higher in more rural areas where costs of land protection are lower, but predicted donations are higher in urbanized areas where land is expensive. We observed greater sensitivity in the relationship between ROI and predicted donations when we compared across alternative conservation objectives. Table S5 shows correlation statistics between ROI and predicted donations when pursuing two alternative conservation objectives, one focused on protecting all species and one that balances protecting vulnerable species with providing recreational benefits to people. Again, conservation costs play a central role, because some conservation objectives give rise to ROI patterns that are more cost dominated (our all species example) and some less so (our recreation example; Table S5). Associations between sources of conservation funding and conservation priorities also depend on the type of funding involved. Here we focused on funding to a major national NGO, but the tendency for higher giving to be associated with larger population centers seems likely to apply to many other sources of conservation revenue (membership based funding, public funding tied to local tax revenues, compensatory mitigation funding tied to local development, etc.) Different types of

conservation funding will also differ in how much flexibility to move funding in space they offer.

To understand how distance decay in donors' willingness to support conservation projects shapes optimal protected areas strategies, we developed an approach that analogizes the effect of distance decay to an expanded conservation cost term. We refer to this expanded cost representation as the effective cost of supporting a project in one location when relying on funding from somewhere else. Using this formulation, we are able to derive conditions that an optimal protected area strategy must satisfy. This effective cost method is very flexible and can accommodate more complicated patterns in willingness-to-pay for conservation (Johnston and Ramachandran 2014). For example, we show ROI patterns for an alternative functional form for distance decay in willingness to support conservation in Table S6, one that allows funding to be moved flexibly in a region close to where it was donated but not further (Figure S1). We also consider situations where patterns in willingness to pay for conservation are better described using spatially heterogeneous decay rates (Glenk et al. 2020). In the Supporting Information, we discuss examples where decay rates vary based on characteristics of the population donating funds and of the location receiving conservation investment.

The functional form for distance decay we rely on for the numerical example in the main text is exponential decay. In Figs. 4-6, we display characteristics of the optimal solutions at two different decay rates (willingness to support conservation halves at 100 km and 500 km) where we chose these values because they sit either side of a transition in the behavior of the optimal solution. These decay rates are slightly larger than those observed in empirical studies. For example, in the stated preference studies reviewed in Loomis (2000), the highest decay rates involve people's willingness-to-pay for conservation programs to conserve Mexican spotted owl halving at around 500 miles (800 km), with other estimates decaying more slowly. In terms of our results, if decay rates this low also characterize revealed giving behavior, then concerns about distance decay should not prevent conservation organizations developing programs in locations offering the highest ROI for biodiversity. Indeed, as we describe below, TNC has been able to invest in high ROI counties even though these are further from peak giving locations. At

the same time, over larger scales limitations on how freely the organization can move donations are also apparent (Larson et al. 2016).

Skewed conservation ROI distributions in our applications favor concentrating investment in just a few locations, while distance decay in donors' willingness to support project favors dispersing funding a little more widely. Conservation ROI distributions are typically very skewed, reflecting the multiplicative nature of ROI formulae (Vijay et al. 2022, Yoon et al. 2022). At the budget levels we consider, ecological complementarity considerations are not sufficient to overcome the concentration this skewed distribution favors in optimal funding allocations. However, accounting for distance decay in donors' willingness to support conservation can lead to greater dispersion of conservation funds if decay rates are high enough, a trend continued if we consider even more aggressive forms of distance decay (Table S6). Ando and Shah (2010) also modeled the effect of spatial decay in people's willingness to support conservation on protection priorities and showed that optimally sited protected areas may be more fragmented and closer to population centers than would be expected if prioritizing based on ecological considerations alone.

Actual conservation spending also tends to be quite concentrated in space. For example, during the same period covered by our data, TNC concentrated spending to acquire land via fee simple acquisition or easements into just five counties in California and six in North Carolina. Moreover, in both states, counties that we identified as offering the greatest conservation ROI saw the largest expansion of protected area from this funding. Tyrrell County had as much new land protected as the rest of North Carolina combined during this period, while new protected areas TNC acquired in Kern County accounted for a much larger area than those acquired in the rest of California. TNC has also continued its investment into both counties subsequently, as part of a continuing project to protect the Tehachapi Range in California and a collaborative effort to protect North Carolina's coastal wetland ecosystems.

As with any modeling study, we had to make assumptions in our analyses. Here, we highlight three assumptions that are particularly relevant to how we combined conservation prioritization with information on donations. We refer readers more interested in the assumptions behind either

piece in isolation, either how we estimated donations or how we estimated conservation ROI, to earlier work (Fovargue et al. 2019, Armsworth et al. 2020, Yoon et al. 2022, Le Bouille et al. 2023). To examine how distance decay changed conservation priorities, we focused on priorities within state boundaries. TNC has a federated structure with fund-raising activities and land protection decisions being organized at the state level (Fishburn et al. 2013). At the same time, while much funding stays in-state, some movement of funds between states also occurs (Larson et al. 2016). For our North Carolina application, for example, ecosystems in the southern Appalachians emerged as one priority for investment. Land trusts working in that region often draw upon donors in the Atlanta area in Georgia and our analyses would miss these state to state transfers. We also based our analyses on spatial patterns in giving that had been observed (Fovargue et al. 2019) and not on the hypothetical level of giving that could have been realized had alternative conservation projects been presented to donors. An initial exploration suggests the patterns we find will not be particularly sensitive to this assumption (Supporting Information). We also did not yet consider richer specifications in which, for example: investing in protected area creation leads to greater donation levels in the future (Larson et al. 2016, Cazalis and Prevot 2019, Pinnschmidt et al. 2021); different sources of conservation support are combined (Kroetz et al. 2014); or multiple conservation organizations interact when protecting land (Harding et al. 2023, O'Bryan et al. 2023).

Our results have several implications for conservation NGOs and the donors who support them. For example, we show that the value of a conservation dollar depends on where it is donated when donors' willingness to support conservation declines with distance and is highest near priority areas for conservation investment. This finding emphasizes the importance of NGOs cultivating donors and building local capacity in locations that are top conservation priorities. Our approach also provides a means of quantifying for donors the potential improvement in conservation outcomes possible if they were to allow greater spatial flexibility over where funds could be used (Fig. 6a). Our optimization approach makes clear that donors located in different places should be asked to fund different projects. At the same time our results suggest when doing so, conservation organizations not compromise on top conservation priorities, even if this might mean accepting a smaller gift than a donor might be willing to give for a nearer project more personal to them. Obviously, that requires a careful balance. In our experience, many

philanthropy staff at NGOs manage this trade-off implicitly. They build relationships with potential donors, seek to understand their preferences, and offer them potential projects that might appeal, where these are drawn from a larger set of priorities already identified from examining ecological and other data. Our models try to capture some spatial aspects of this interaction, albeit in broad-strokes. Our results emphasize the advantages of an integrated approach that engages philanthropy staff in the process of conservation priority setting, rather than only after the fact. Doing so would allow priority recommendations to be delivered in ways that would be more helpful to philanthropy teams. For example, regionalized products tailored to donor interests may be more helpful to philanthropy teams and donors than a single large-scale priority map. Armsworth et al. (2023) provide an example of what tailored products could look like focused on interstate transfers of funding. The analyses we present here offers the potential to support similar products tailored to donors' preferences within state boundaries.

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Tables

Table 1. Spearman's rank correlations on detrended data. Significance levels calculated with Moran's spectral randomization; * $p < 0.05$, ** $p < 0.01$.

CA, n=57	ROI for vul species	cost	threat	No. vul. species
Donations	-0.37**	0.50**	0.43**	0.39*
ROI for vul				
species		-0.56**	-0.21	0.18
cost			0.59**	0.21
threat				0.24
NC, n=100	ROI for vul species	cost	threat	No. vul. species
Donations	-0.34**	0.72**	0.59**	-0.05
ROI for vul				
species		-0.38*	-0.48**	0.78**
cost			0.68**	-0.07
threat				-0.31

Figure captions

Figure 1. Three county illustration of characteristics of optimal solution with no distance decay.

(a) Counties differ in benefits (black bars show benefit on the first dollar invested) and costs (grey bars) of protected areas, in location (horizontal axis), and in donation amounts (y_i for $i=1-3$ shown by length of magenta line segments). (b) Optimal solution with no distance decay. Tan line segments show marginal benefit to cost ratios which start at the ratio of black to grey bars in (a) but then decrease with additional investment into each county. Optimal allocation of spending (blue line segments, offset in plot for visual clarity) gives funding only to highest marginal benefit to cost ratio counties (1 and 2), equalizes these ratios across counties receiving funding, and fully allocates the total funds donated from the three counties (summed length of magenta line segments equals summed length of blue line segments).

Figure 2. Three county illustration of how distance decay changes optimal allocation recommendation. Benefits and costs of protected areas, county locations, and donation amounts same as in Figure 1. Optimal allocation of funds from counties (a) 1, (b) 2 and (c) 3 when distance decay in donations applies (inset in (a)). Marginal benefit to effective cost ratios reduced for distant counties (tan lines shift downwards as indicated by yellow arrows in mini-plots). Optimal allocation (blue line segments) targets donations from each county only to highest marginal benefit to effective cost ratio counties for that donor county; equalizes these ratios across places receiving funding from that donor county (blue line segments in (c) offset for visual clarity); and fully allocates funding from that donor county (length of magenta line segment for each donor county equals summed length of blue line segments showing spending allocation of funds from that donor county).

Figure 3. (ad) Predicted donations to conservation and (be) conservation return-on-investment (ROI) in terms of improving the persistence probability of vulnerable terrestrial vertebrate species by acquiring additional protected areas from counties in (ab) California and (de) North Carolina, with locations of these states in the conterminous U.S. shown (inset). Data shown as ranks and compared in scatters in (cf). Redder counties predicted to offer higher donation levels

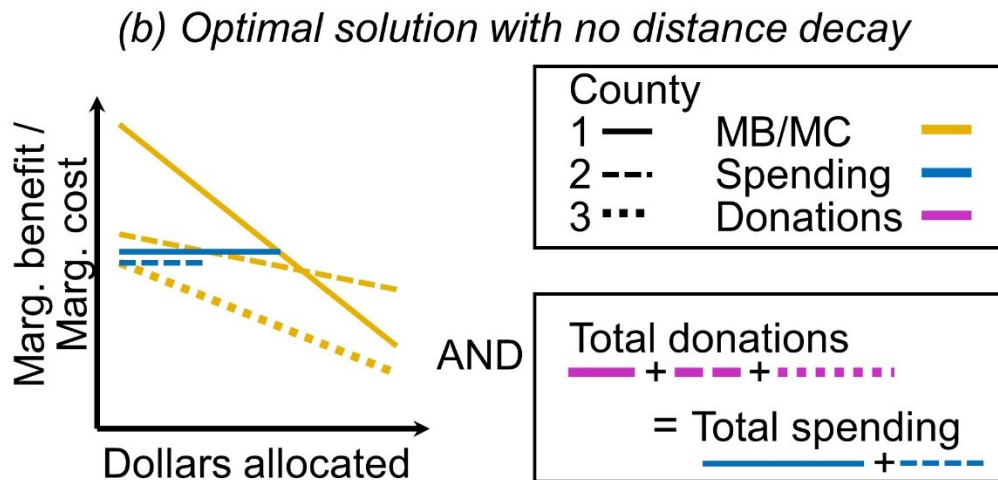
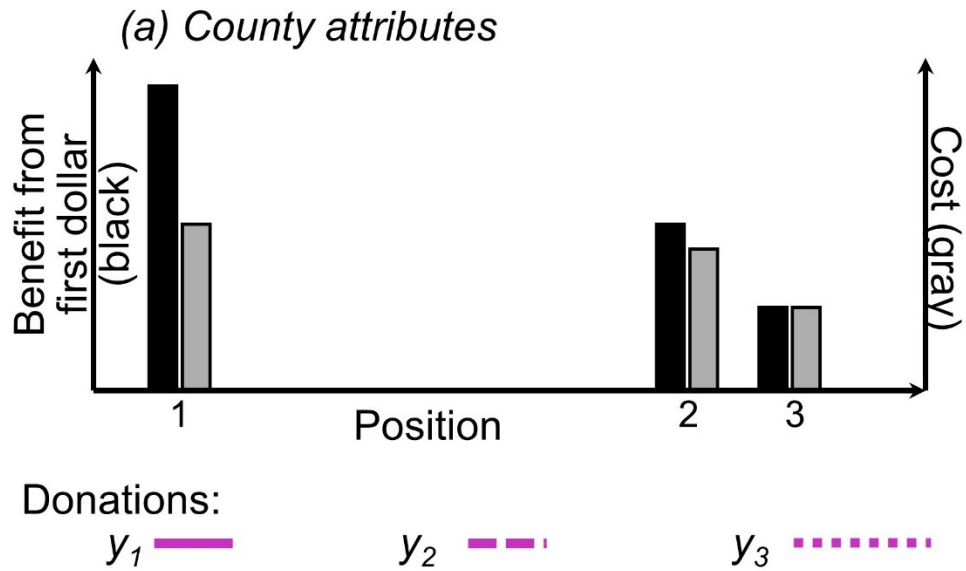
(ad) or higher priorities for protection (be). Scale bars in be) indicate 250 km. Return-on-investment in this plot is calculated before considering distance to decay in willingness to pay.

Figure 4. Optimal budget allocation when seeking to protect vulnerable vertebrate species through land acquisition in California for a (ab) low and (c-f) high distance decay rate in donors' willingness to support conservation projects. Bars show potential dollar amounts donated from 15 highest donation counties that are allocated to those counties receiving most funding. Potential dollar amounts shown before distance decay has been applied, which allows easier visual comparisons between low and high decay rate cases. Inset maps in (bf) show locations of these counties using same color coding as bars. Counties shown with thick border are those receiving funding from similarly shaded donor counties. Donors' willingness to support conservation assumed to halve at a distance of (ab) 500 km and (c-f) 100 km, with these distances indicated by scale bars.

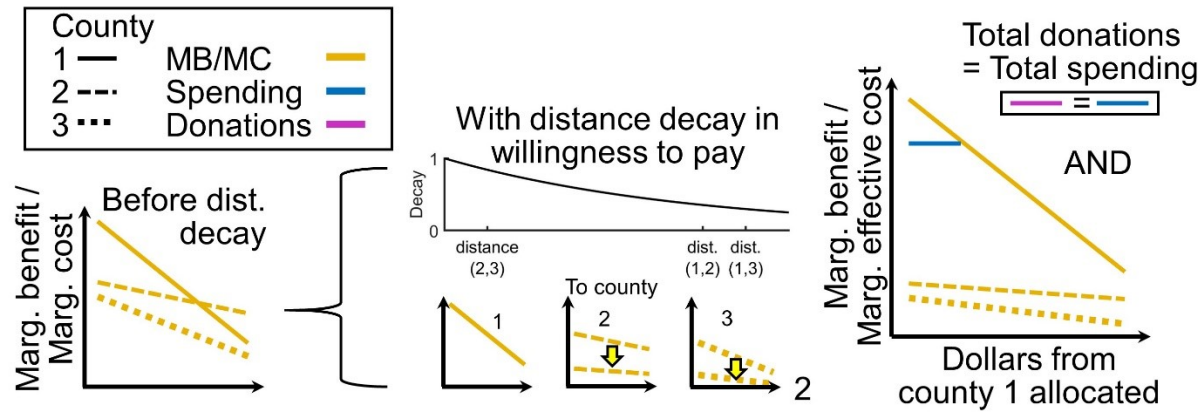
Figure 5. Optimal budget allocation when seeking to protect vulnerable vertebrate species through land acquisition in North Carolina for a (a-c) low and (d-g) high distance decay rate in donors' willingness to support conservation projects. Bars show potential dollar amounts donated from 15 highest donation counties that are allocated to those counties receiving most funding. Potential dollar amounts shown before distance decay has been applied, which allows easier visual comparisons between low and high decay rate cases. Inset maps in (ae) show locations of these counties using same color coding as bars. Counties shown with thick border are those receiving funding from similarly shaded donor counties. Donors' willingness to support conservation assumed to halve at a distance of (ab) 500 km and (c-f) 100 km, with these distances indicated by scale bars.

Figure 6. Characteristics of the optimal budget allocation when seeking to protect vulnerable vertebrate species through land acquisition shown for California (black) and North Carolina (gray) for a low (donations halve at 500 km) and a high distance decay rate (donations halve at 100 km) in donors' willingness to support conservation projects. (a) Effect of distance decay on conservation outcomes shown as proportion of hypothetical biodiversity gain predicted had no distance decay applied that is achieved by the optimal solution when donations are subject to

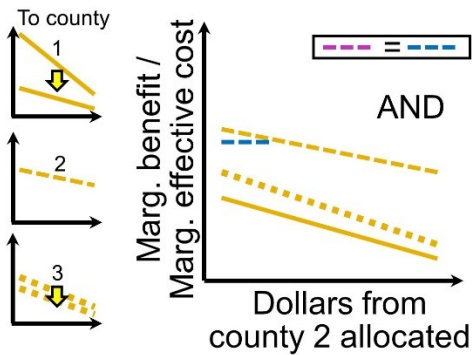
distance decay. (b) Number of counties accounting for at least 2% of overall potential funding in the optimal solution. Proportion of the optimal biodiversity outcome when accounting for distance decay that is achieved if instead (c) maximizing donations by spending funds in the county where they were donated to avoid any distance decay in donations or (d) ignoring the distance decay in donations and simply allocating funding to counties offering the highest ROI on the first dollar invested.



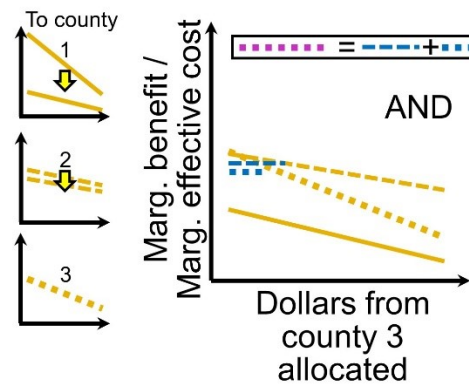
(a) Optimal solution with distance decay of funds from county 1



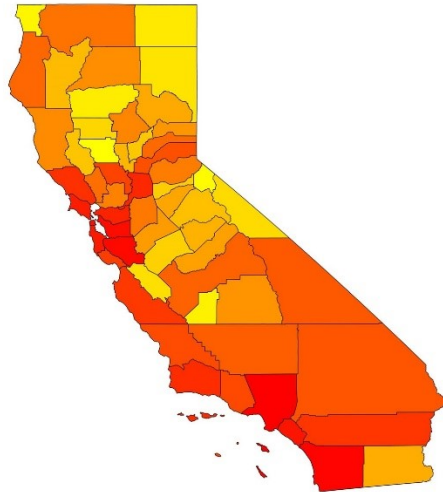
(b) from county 2



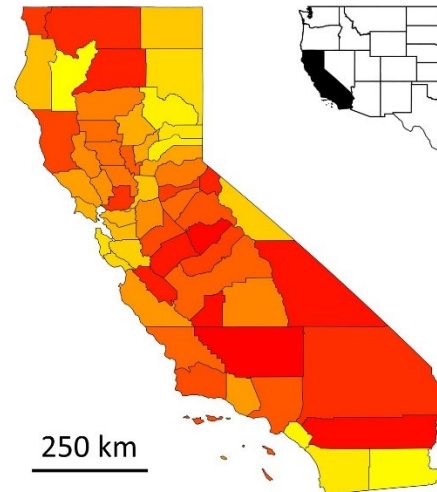
(c) from county 3



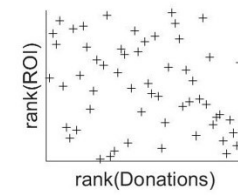
(a) Donations in California



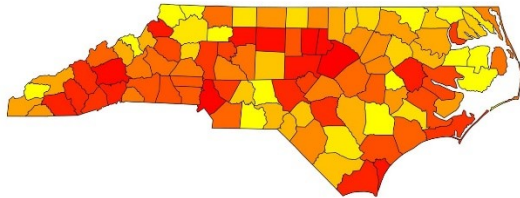
(b) ROI in California



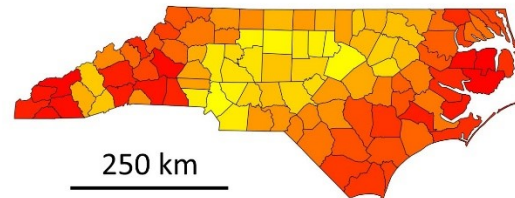
(c) Comparison in California



(d) Donations in North Carolina



(e) ROI in North Carolina



(f) Comparison in North Carolina

