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LETTER

Maximising return on conservation investment in the conterminous USA

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Abstract

Efficient conservation planning requires knowledge about conservation targets, threats to those targets, costs of conservation and the marginal return to additional conservation efforts. Systematic conservation planning typically only takes a small piece of this complex puzzle into account. Here, we use a return-on-investment (ROI) approach to prioritise lands for conservation at the county level in the conterminous USA. Our approach accounts for species richness, county area, the proportion of species' ranges already protected, the threat of land conversion and land costs. Areas selected by a complementarity-based greedy heuristic using our full ROI approach provided greater averted species losses per dollar spent compared with areas selected by heuristics accounting for richness alone or richness and cost, and avoided acquiring lands not threatened with conversion. In contrast to traditional prioritisation approaches, our results highlight conservation bargains, opportunities to avert the threat of development and places where conservation efforts are currently lacking.

Keywords

Benefit:cost ratio, conservation planning, economic cost, habitat protection, heuristic, land prices, reserve selection, resource allocation.

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INTRODUCTION

The global biodiversity crisis has made the timely acquisition, restoration and preservation of native habitats more important than ever. Existing protected areas, although important, miss 20% of threatened vertebrate species globally (Rodrigues *et al.* 2004). In addition, 38% of the world's terrestrial ecoregions are 'vulnerable' to 'critically threatened', due to a lack of protection in the face of habitat conversion (Hoekstra *et al.* 2005). Conservation funding is chronically limited and not surprisingly falls far short of adequately supporting a comprehensive global conservation programme (James *et al.* 1999). In light of these shortfalls, efficient and effective approaches for prioritising lands for conservation are essential.

Traditional conservation priority-setting approaches have sought to identify areas with the greatest value for conservation, including biodiversity hotspots, areas of high endemism and threatened ecoregions or habitats (for a summary see Brooks *et al.* 2006). These approaches take into account a measure of biodiversity (sometimes paired with threats to that biodiversity) and typically result in a list or ranking of areas of high priority for conservation (e.g. WWF's Global 200 ecoregions, Olson & Dinerstein 1998, 2002; Conservation International's biodiversity hotspots, Myers *et al.* 2000; critically endangered ecoregions, Hoekstra *et al.* 2005; BirdLife International's important bird areas, Devenish *et al.* 2009). However, such approaches ignore the economic costs of conservation, which vary widely within the same country or region (Ando *et al.* 1998; Fishburn *et al.* 2009).

More recently, researchers have developed a number of analyses that include an estimate of the cost of conservation to examine its impact on priority-setting approaches (Ando *et al.* 1998; Wilson *et al.* 2006; Murdoch *et al.* 2010). By explicitly considering conservation benefits and costs, we can maximise the return-on-investment (ROI), that is, the conservation benefit per dollar spent, and achieve more conservation with limited resources. Such approaches have also incorporated other factors important for assessing ROI such as: (1) *threats* to an area's biodiversity (e.g. the rate of conversion to unsuitable habitat, as in Wilson *et al.* 2006; or a risk index based on current patterns of human impacts, as in Murdoch *et al.* 2010), (2) *diminishing returns* to additional land acquisition through information about lands already protected in a given area (Wilson *et al.* 2006; Murdoch *et al.* 2007) and/or (3) *species complementarity* of the areas targeted for additional land acquisition, to avoid duplication of efforts (Underwood *et al.* 2008).

Until recently, including all of these different factors into a single ROI analysis for a large contiguous area has been precluded by a lack of fine-scale, continuous data sets for all factors. Such analyses are critical for setting conservation priorities at a national or continental scale. Here, we perform such an analysis for the contermi-

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nous USA using counties as a spatial unit of analysis and incorporating a conservation target (vertebrate species richness), a measure of diminishing returns to conservation effort (proportion of a county already protected, and proportion of each species' range already protected), a measure of threat (conversion of natural land cover), the species–area relationship (to account for variation in the size of counties) and an econometrically-derived estimate of land costs. We demonstrate a novel combination of these measures to produce an estimate of ROI for each county in the conterminous USA. In addition, we use a heuristic site-selection algorithm that uses ROI values to identify counties, and specific amounts of land within those counties, that together will protect a minimum percentage of the range of every species. Our approach can be used by conservation organisations working at ecoregional to continental scales to identify priority regions or counties for protection through the purchase of land or conservation easements, or through conservation incentive programmes such as the US Department of Agriculture Conservation Reserve Program.

MATERIALS AND METHODS

Data

We used counties as the spatial unit of analysis for assessing return on conservation investment for two reasons. First, counties are political units in the USA that are relevant to regional and local land-use planning. Second, we developed a new estimate of land costs that was based on county-specific economic data. We obtained county boundary files from the US Census Bureau and used names of Level I–III ecoregions (Omernik 1987) to refer to specific areas of the continent.[1]

We used terrestrial vertebrate species occurrences as a measure of biodiversity. Individual taxa often perform relatively poorly as surrogates for more general measures of biodiversity (McBride *et al.* 2007; Jetz *et al.* 2008); however, ROI analyses incorporating economic and other factors are typically robust to the choice of biodiversity surrogate (Bode *et al.* 2008b). Vertebrate distributions are currently the most comprehensive species data available for US counties at the continental scale (data for plants at the county level are incomplete and may provide a biased account of plant species occurrences). We tallied vertebrate species for each county using digital range maps from NatureServe for 339 mammals (Patterson *et al.* 2003), 452 birds (Ridgely *et al.* 2003) and 275 amphibians (data available online[2]), and included any overlap of the range map with the county as an occurrence. Using range maps rather than occurrence records specific to a county allowed us to calculate species richness consistently across the entire conterminous USA, but also created errors of commission (counting a species as occurring in counties where it in fact does not). The total number of species from all taxa occurring in a county is hereafter referred to as 'species richness'.

For information about protected areas in each county, we used the Conservation Biology Institute's database (CBI (The Conservation Biology Institute) 2010). We considered areas with GAP Status Codes of 1 or 2 to be protected, meeting the definition of 'protected' by the IUCN.[3] The median percentage of range already protected for the 1066 species included in our study is 8.6% (with a minimum of 0% to a maximum of 66%).

As a proxy for the threat of land conversion in each county, we used the National Land Cover Database (NLCD) 1992–2001 change product (Fry *et al.* 2009) and calculated the amount of natural land cover in 1992 (forest, grassland, shrubland or wetlands) that was converted to anthropogenic land cover (developed, cropland or pasture) by 2001. We also calculated the total amount of anthropogenic cover present in 2001 for each county, that is, lands already converted. We assume that levels of development in the immediate past are a good predictor of levels of development in the future.

Calculating land cost

We develop an economic model to estimate the cost of land acquisition. In a competitive market with full information, land price theoretically equals the present value of the returns to land over time. We assume that non-urban land in a particular use (pasture, cropland, forest or grass/shrublands) is kept in its current use until time T when it is converted to developed use. Let π_{Dc} represent the annual returns to land from development in county c, r be the interest rate and T_c be the assumed time of development in c (we assume T_c is the same across all land uses in county c). The present value of future returns due to development is $R_c = \int_{Tc}^{\infty} \pi_{Dc} e^{-rs} ds$. Let π_{jc} represent the annual returns to land in use j (pasture, cropland, forest or grass/shrublands) in county c. The price for land in use j in county c is then equal to:

$$P_{jc} = \int_0^T \pi_{jc} e^{-rs} ds + R_c \tag{1}$$

Plantinga *et al.* (2002) identify the two components of farmland prices using data from the US Department of Agriculture. To construct land-price estimates for each county and land use using eqn 1, we use their estimates of R_c, while annual net returns by use j and county c (π_{jc}) are provided by Lubowski *et al.* (2006). These estimates have been used previously for econometric modelling (Alig *et al.* 2010; Radeloff *et al.* 2012).

Using this method gave us land-price information by county and land use for 95% of the 3109 counties in the conterminous USA; we then calculated an average county land cost:

$$P_c = \sum_{j=1}^{4} P_{jc}(A_{jc}/L_c), \tag{2}$$

where P_{jc} is the cost (in US\$, hereafter \$) per hectare of land use j in county c, A_{jc} is the area of county c in land use j and L_c is the area of county c excluding urbanised lands and water.

Land costs for the remaining 154 counties could not be directly estimated because of missing data or the absence of agricultural land. We estimated land costs for these counties based on a weighted average of the use-specific land prices from counties with which the county shared a perimeter. We tested this approach by calculating such 'filled-in' land costs (F) for all counties with estimated price data (P, calculated using eqn 2), the county area (A) and the proportion of developed lands in the county (U). For U, we used the Freeman-Tukey arcsine-square root transformation suggested by Zar (1996). We estimated coefficients using ordinary least squares for the model $\log(P) \sim \alpha + \beta_1 \log(F) + \beta_2 \log(A) + \beta_3 (U) + \varepsilon$ ($R^2_{adj} = 0.73$, $P < 0.001$ with $n = 2955$ counties) and used those coefficients to predict land price P for 93 counties. We

[1]http://nationalatlas.gov/biology.html
[2]http://www.iucnredlist.org/technical-documents/spatial-data
[3]'A summary of the relationship between GAP status codes and IUCN definitions,' accessed at http://gapanalysis.usgs.gov/2011/06/21/iucn-definitions/

excluded 61 counties from this filling-in approach that were mostly developed, mostly water, island counties or peninsular counties, whose neighbours also lacked land-price data. Our final list included 3048 counties – 98% of the counties in the conterminous USA. Cost data and calculations are available from the first author.

Calculating return on investment (ROI)

We used the data and county attributes described above to calculate an ROI value for each county that took into account vertebrate richness, land area of the county, diminishing returns due to already-protected lands, the threat of land conversion and land costs. Dividing species richness by area produces species density, but this assumes a linear relationship between species and area that is not observed empirically (Rosenzweig 1995). Instead of dividing by area, we incorporated the species–area relationship itself ($S = cA^z$) into our calculation of return. We assumed that in a given county, there are a certain number of species protected by existing reserves, and others that occur on lands that are not threatened with conversion (Fig. 1). To make land acquisition as effective as possible, we wanted to know what the potential is for newly protected lands to avert species losses, which we calculated as follows.

We calculated the county-specific constant in the species–area relationship, c_c from each county's species richness (S_c) and area (A_c), setting $z = 0.2$. For mainland plants and animals, reported z values are generally between 0.1 and 0.3 (Rosenzweig 1995). We chose 0.2 as the midpoint of this range, and to be consistent with other ROI analyses (Murdoch *et al.* 2007; Underwood *et al.* 2009). Recent work also suggests that the results of ROI analyses similar to ours are not sensitive to the value of z (Bode & Murdoch 2009; Murdoch *et al.* 2010).

For each county, we calculated an annual rate of land conversion from natural to anthropogenic lands from the NLCD 1992–2001 change product (see *Data*, above): k_c = ln(natural land cover in 2001/natural land cover in 1992)/9. Threat was calculated over a 100-year time period as follows:

$$T_c = 1 - e^{(k_c * 100)} \quad (3)$$

where T_c varies from 0 (no land conversion) to just under 1 (nearly all lands converted). We used a 100-year time horizon for calculating threat common to other conservation planning applications, for example, to help determine species' extinction risk (IUCN 2011) or to analyse minimum viable population size (Flather *et al.* 2011). The area of land threatened with conversion in a county was therefore

$$AT_c = A_c * T_c \quad (4)$$

under the constraint $AT_c \leq A_c - (PA_c + AC_c)$, where all variables are as shown in Fig. 1, and T_c is calculated using eqn 3. The constraint in eqn 4 prevents the area of land threatened with conversion from exceeding the total amount available, that is, lands not already protected (PA_c) or already converted (AC_c).

The county-specific variables described above were then used to calculate the number of species in each county, whose loss could be averted by acquiring 1000 hectares of land for conservation (Fig. 1). We made the starting point of new land acquisition, where lands were threatened with conversion, that is, excluding existing protected area, PA_c, and lands not threatened with conversion, AN_c (Fig. 1). Using this starting point, the number of species whose loss could be averted on 1000 ha in county c, SAV_c, was calculated:

$$SAV_c = c_c(PA_c + AN_c + 1000)^{0.2} - c_c(PA_c + AN_c)^{0.2} \quad (5)$$

One thousand hectares was selected as the minimum amount of new land acquisition to be neither too large (it did not exceed the minimum area of land available for conservation in all counties) nor too small (it was in the 33rd percentile of the land area currently protected, in counties with protected areas). For 383 counties, there were no unthreatened lands ($AN_c = 0$), which occurred due to high values of threat, large amounts of land already converted and/or large amounts of existing protected areas.

Finally, we divided our return, averted species loss, by the county's estimated price of land acquisition to get a county-specific ROI value:

$$ROI_c = SAV_c/(1000P_c) \quad (6)$$

where SAV_c is calculated with eqn. 5, P_c is calculated with eqn 2 and 1000 hectares is the amount of land targeted for acquisition. ROI_c represents the number of species, whose loss is expected to be averted per dollar spent.

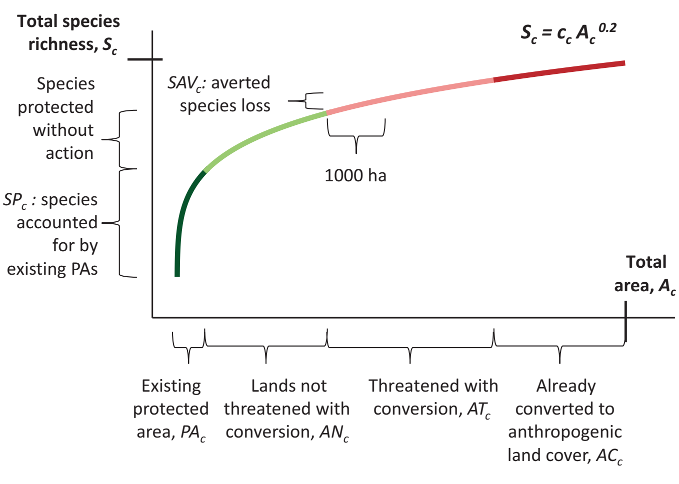

Figure 1 Components of the species–area curve for county c, as calculated from $S_c = c_c A_c^z$ with $z = 0.2$, used in our approach to calculating the return on investment. In the figure, SP_c is the number of species accounted for in existing protected areas, PA_c. The area of the county already converted to anthropogenic land cover is AC_c and the area threatened with conversion is AT_c. The number of species whose loss would be averted by land acquisition, SAV_c, is calculated from the species–area curve based on 1,000 ha of land acquired starting at the point shown on the figure (PA_c plus any lands not threatened with conversion, AN_c).

Using ROI to efficiently allocate conservation resources

Our ROI calculation provides a value for each county, allowing for a national ranking of counties. However, such a measure does not provide a means of prioritising counties for conservation action based on the complementarity of counties, that is, accounting for species that occur in multiple counties (Vane-Wright *et al.* 1991). To account for complementarity, we used a greedy heuristic algorithm. Each time we ran the algorithm, the heuristic calculated ROI for all counties (eqn 6) and selected the county with the highest ROI. We then added 1000 ha to the lands protected in that county, and to the protected area within the range of all species that occur in that county. To consider a species in need of more protection, as opposed to already protected (and therefore taken off the list of species considered by the heuristic), we also set a target for the minimum percentage of every species' range that is protected. For example, if we set the protection target at 10%, 605 species were on the list at the outset of running the heuristic (the other 461 already have $\geq$ 10% of their range in protected areas). At each step of the heuristic, the top-ranked ROI county is selected and 1000 ha is added to protected lands – and therefore counted as additional protection in the range of the species that occur there. If that pushes any species over the 10% target, the species is taken off the list for additional steps of the heuristic, which reduces c_c in the counties in which that species occurs. Our greedy heuristic allows for multiple 1000 ha selections within the same county, but only if that county continues to have the highest-ranked ROI value even after adding the 1000-ha selection to its protected area (i.e. PA_c increases by 1000 ha). With this approach, different amounts of land were targeted for conservation acquisition in different counties. We ran the greedy heuristic with targets from 1% to 20% (at increments of 1%) and calculated the total estimated cost and number of species on the list for additional protection for each target.

To assess the potential added value of including diminishing returns and the threat of land conversion in the ROI estimate, we ran the greedy heuristic using two simpler ways of calculating ROI: 'richness alone', based on species richness and county area only, and 'richness/cost', based on richness, county area and land cost. The heuristic used the same rules, but rather than selecting the top county based on eqn 6, we used $c_c\ (1000)^{0.2}$ for richness alone, and $c_c\ (1000)^{0.2}/(1000P_c)$ for richness/cost. We used the same protection targets (1–20%) for the two alternative approaches and based the consideration of complementarity on the same principle of reaching the protection target across all species' ranges.

To compare the results of the three heuristics using different criteria, we (1) summed the total area identified for acquisition across all counties and summed the cost of that land, (2) calculated the averted loss of species on lands acquired by the heuristic based on the county-specific species–area relationship, (3) divided averted losses by the cost of the land acquired in that county to calculate averted losses/$ spent, (4) calculated the amount of overprotection in a county as the total amount of land acquired that would occur on lands not threated by conversion within 100 years (i.e. if land acquired > AT_c) and (5) calculated the portion of overprotection that would necessarily include areas that are already protected (i.e. if land acquired > (AN_c + AT_c) and PA_c > 0, see Fig. 1).

RESULTS

A county's ROI represents the conservation benefit per dollar spent to acquire land (Fig. 2). Counties with high ROI values can be found throughout the Great Plains and in parts of the Eastern Temperate Forest ecoregion, especially the Midwestern USA. Comparing ROI to its two main components, species richness and land cost (Fig. S1), shows that the highest ROI values can be found in counties where richness is either high (e.g. selected counties in New York, Wisconsin or Minnesota), or low (e.g. most of the Great Plains), but not where land costs are particularly high (e.g. most coastal counties). The ROI calculated in a single step for all counties was positively correlated with the threat of land conversion and existing anthropogenic land cover in a county and negatively correlated with species richness, average land cost and the proportion of the county already protected (Table 1).

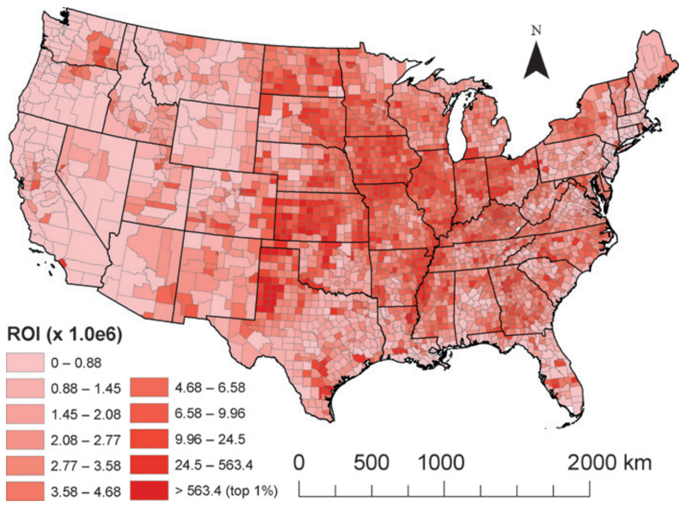

Figure 2 The return-on-investment (ROI_c) calculated for each county in the conterminous USA. The units are species/$, where species are those whose loss is averted by the acquisition of 1000 ha of land (SAV_c, eqn 6 and Fig. 1). Values shown in the legend are ROI $\times$ 10^6 for clarity and are separated by 10% quantiles, except for the bin with the highest ROI value (> 563.4), which is the top 1% of counties.

Efficiently allocating conservation resources

At the lowest protection target, at least 1% of each species' range protected, the heuristic selected small amounts of land to acquire, and only selected counties in certain parts of the country, whereas at the highest targets, the lands selected were spread out to include at least some area in nearly all counties (Fig. 3). At the 1% target, only small amounts of land were necessary because only 27 species did not initially meet this target, and the target itself is low. Most of the counties selected for land acquisition to meet the 1% target had high initial ROI values (in the top 10%, Fig. 2) and were in the South Central Semi-Arid Prairie ecoregion of the Great Plains. With higher targets, however, more species did not meet the criteria (e.g. 978 species or 92% of the total do not have at least 20% of their range in protected areas – see full range of protection target results in Table S1) and the heuristic selected progressively more area in more counties (Fig. 3). Requiring additional protection for species while accounting for species complementarity led to the selection of counties with high land costs and therefore low initial ROI values

Table 1 Correlations between the return-on-investment (ROI) calculated using eqn 6 (*Methods*) and input variables for 3048 counties in the conterminous USA

County attribute (units)	Transformation (if any)	Pearson's *r*
Species richness (n)	None	−0.16
Area (ha)	None*	−0.03
Land cost ($/ha)	Logarithmic	−0.13
Proportion of county that is protected area	Freeman-Tukey[†]	−0.12
Proportion of county that is anthropogenic land cover	Freeman-Tukey[†]	0.15
Rate of land conversion (k_c)	$(-k_c)$[‡]	0.32

*Pearson's *r* for log-transformed area was nearly identical to that shown for untransformed area.
†Zar (1996).
‡The negative decay rate was used to show that ROI is positively correlated with threat.

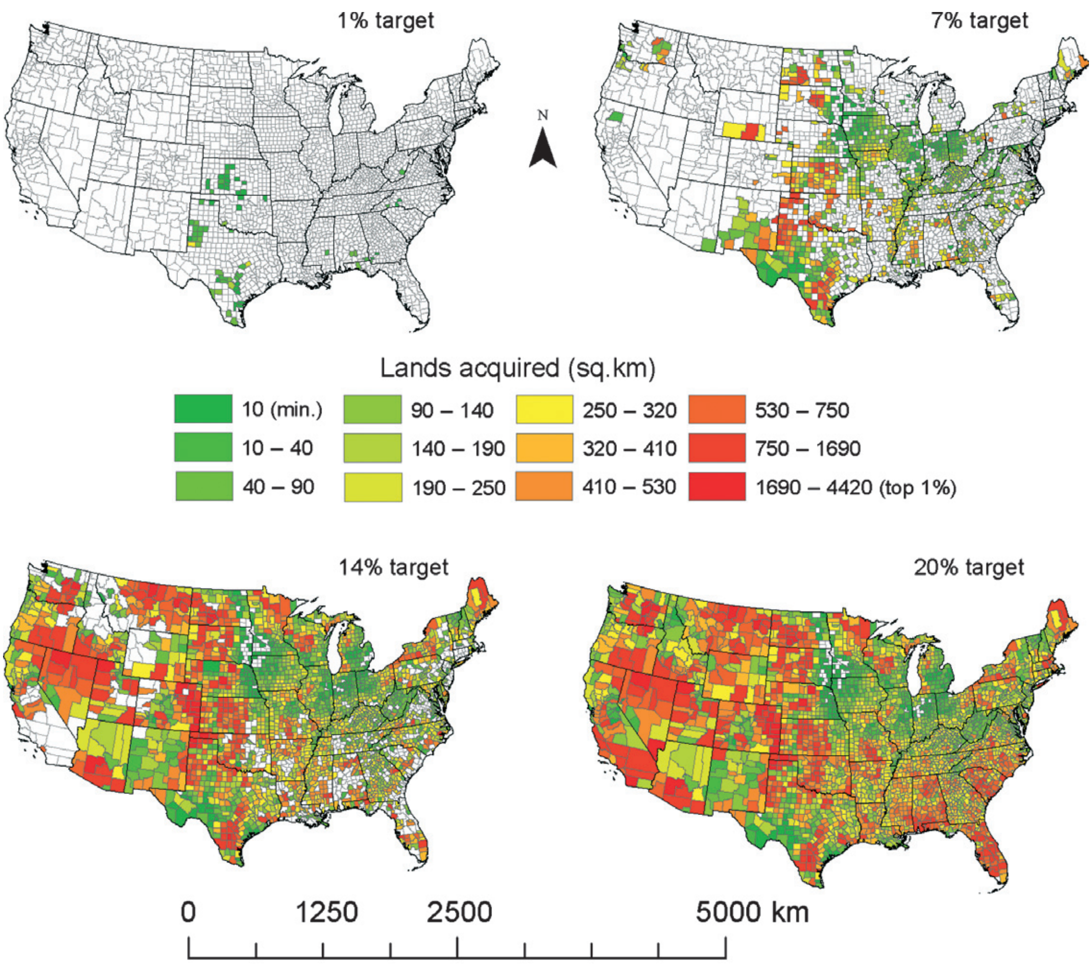

Figure 3 The area selected in each county by the greedy heuristic using our ROI approach for four protection targets (the minimum percent protected across every species' range) chosen to illustrate a range of targets: 1%, 7%, 14% and 20%. Separate categories in the legend include the minimum area selected (10 km^2), the top 1% of area selected (> 1690 km^2) and 10 categories that correspond with the 10% quantiles for the area selected.

(e.g. counties along the West Coast, the Intermountain West and South Florida). The total amount of lands selected in specific counties by the heuristic represented the most cost-effective means of adding lands for the particular species still on the list, until those species reached the protection target.

Some regions of the continent had very little area selected, even at high targets for species protection. These include the Temperate Prairie, Central USA Plains and Central Appalachian ecoregions (Fig. 3). Other regions required much more protection: more land area was selected in counties throughout the western USA, including both forested (Western Cordillera) and Cold and Warm Desert ecoregions, as well as Semi-Arid Prairies (West Central and South Central), and the Southeastern USA and Coastal Plains ecoregions.

The estimated cost of acquiring lands increased exponentially from low (1%) to high (20%) protection targets (Fig. 4, cost ~ target$^{1.79}$, where cost of lands acquired to reach each target for all species are measured in $B, and the target is the minimum per cent protected across every species' range, $R^2 = 0.95$, $P < 0.001$). The increase in costs was a function of both more land area and higher average land costs, as the heuristic was required to select more land area for more species with increasing targets of protection.

Using the information included in the full ROI approach on diminishing returns and the threat of land conversion was more

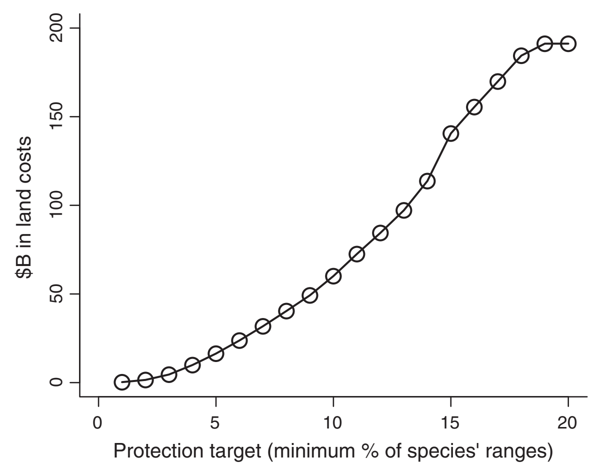

Figure 4 The cost of lands identified for acquisition by the heuristic at different protection targets. The target is the minimum percent protected area across every species' range, and land costs were calculated for targets of 1–20%, by increments of 1%.

effective in terms of averted species loss than using a richness/cost or richness alone approach (Fig. 5a, b). Even as values were more similar at higher targets, these differences were both statistically

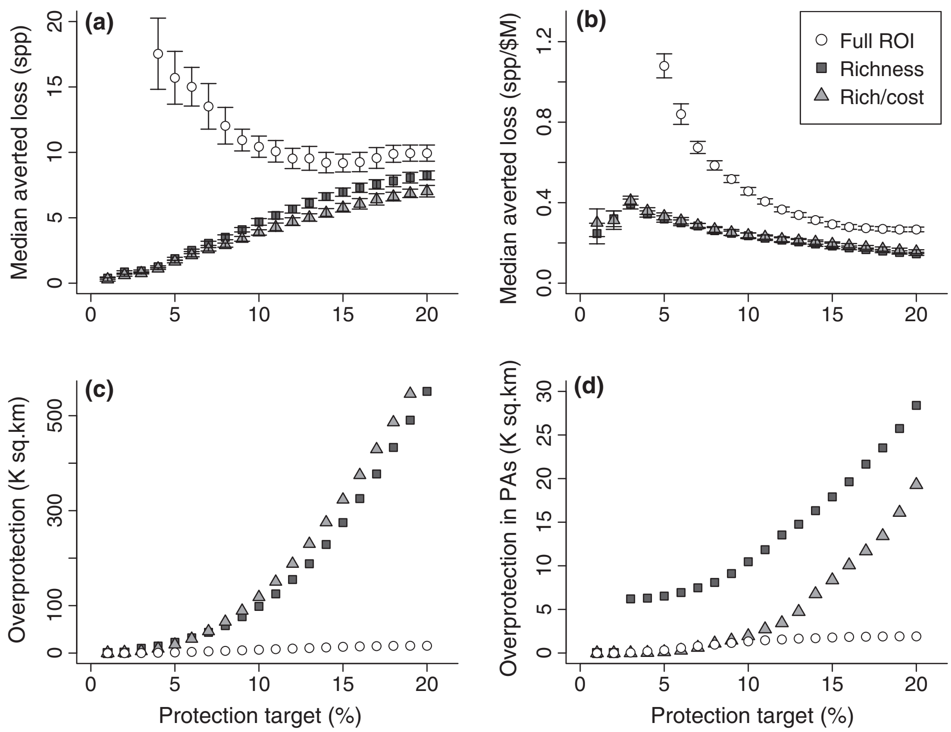

Figure 5 Results from the greedy heuristic for protection targets of 1–20%, using three different approaches: our full ROI (open circles), richness alone (closed squares) and richness/cost (grey triangles). (a) The median averted species loss of all counties; (b) the median averted species loss per $US million in land costs; (c) the area of land acquired that would occur in lands not threatened by conversion ('overprotection', in thousands of km^2); (d) the subset of overprotection that would necessarily include areas already protected (thousands of km^2). The 95% confidence intervals around the medians are based on Olive (2005). The values of the full ROI for 1–3% targets are all > 20 in (a) and all > 3.0 in (b).

significant (using the 95% confidence interval around the median) and demonstrated the potential for greater species conservation using ROI: the minimum difference in the median of averted species losses was 1.7 for ROI vs. richness alone and 2.9 for ROI vs. richness/cost (Fig. 5a). The total area of land acquired by each heuristic that was considered to be overprotection, or would necessarily include existing protected areas, was also much higher for richness alone and richness/cost approaches, especially at targets > 10% (Fig. 5c, d). Overprotection for the greedy heuristic using our full ROI approach was non-zero only because the minimum amount of lands acquired at each step was 1000 ha.

DISCUSSION

Although previous studies have demonstrated the importance of including costs or other individual factors into conservation prioritisations, our results clearly demonstrate that analyses that do not simultaneously account for costs, diminishing returns and threats will be inefficient in terms of dollars spent, and ineffective in terms of lands acquired. As others have shown in the past, accounting for land costs can substantially alter conservation prioritisations (Ando *et al.* 1998; Wilson *et al.* 2006; Murdoch *et al.* 2010). Nonetheless, a simple accounting of species protected per dollar spent, although typically an improvement over the consideration of richness alone, does not avoid wasting dollars on overprotection. Including the threat of land conversion provides a means for targeting those lands at the highest risk of being lost to development, and therefore averting species losses on those lands, while leaving more secure – even if highly biodiverse – lands to be addressed at a later date.

Using our ROI heuristic can potentially reduce costs and improve the effectiveness of conservation efforts by providing alternatives to areas selected based on richness or richness/cost alone. In some areas, there are few options for adding protection for certain species – especially at high targets for protection – and thus, prioritisations using different approaches may identify the same spatial units and areas for protection. However, the full ROI heuristic also highlights specific areas of the country, where it is possible to protect species on lands that are cheaper, more threatened and/or currently less-well protected. Even though the richness/cost approach identifies areas that in total cost less than the full ROI, many of those lands are not threatened and therefore represent overprotection (Fig. 5c, Table S1). Although we do not suggest that actual land purchases would take place in protected areas, our analysis shows that other approaches target lands already protected (Fig. 5d, Table S1) in addition to large amount of lands with no conversion threat.

The ROI values calculated in a single step (Fig. 2) should not, of course, be used in isolation for making land-acquisition decisions. Many of the counties in the Great Plains have high ROI values because land prices are quite low, not because there are rare species or high species richness – in fact, a county's richness is negatively correlated with its ROI value (Table 1). Although counter-intuitive, this result reflects the fact that our return is not simply overall richness, but the number of species whose loss can be averted, that is, taking into account threat and diminishing returns in a county, as well as its richness. For purposes of prioritisation for land acquisition, addressing species complementarity as through the greedy heuristic analysis applied here (Fig. 3), or through optimisation approaches that use integer programming methods (e.g. Ando *et al.* 1998; Önal 2003; Wilson *et al.* 2011), is much more important than calculating ROI for spatial units and simply ranking them. For example, together Figs. 2 and 3 show areas of the conterminous USA that have high initial ROI values, but have little area selected (e.g. the Midwest), or low initial ROI values, but many areas selected at higher targets (e.g. the Southwestern USA and Northern Rocky Mountains). In addition to our approach, we encourage practitioners to consider the use of methods such as stochastic dynamic programming (Costello & Polasky 2004; Strange *et al.* 2006) or optimal control theory (Bode *et al.* 2008a) for their specific applications.

The greedy heuristic algorithm is an example of a myopic heuristic that proceeds step-by-step and is a path-dependent. Such an approach does not guarantee finding an optimal solution. We used the heuristic and not an optimisation method so that after each selection of 1000 ha in a county, we could add those lands to PA_c before re-calculating ROI for all counties (Fig. 1, eqn 6). Of course, other applications of ROI could prioritise finding a true global optimal solution using fixed values over the dynamic calculation of returns. However, a majority of counties are selected by the heuristic at protection targets of at least 9%, but only for small amounts of land acquisition: the heuristic finds that ROI is higher in other counties and selects those for larger areas to acquire (Fig. 3). We therefore know that the heuristic considers acquiring lands in most counties, at least at higher targets, but finds the best conservation value in only some of them – hence, greater area selected in certain counties.

Given a threat horizon of 100 years, the estimated outlay for land acquisition in the conterminous USA identified by the full ROI approach (up to $190 billion, Fig. 4) roughly coincides with real outlays for conservation: e.g. $177 million/year by various sources over a 16-year period in California alone (Underwood *et al.* 2009), or $100 million/year spent in land acquisition just by The Nature Conservancy over a 50-year period (Fishburn *et al.* 2009). However, we also recognise that private land acquisition does not occur instantaneously and the biodiversity value of specific land parcels (especially in the face of climate change), their costs, and/or the availability of the parcel for purchase may change during the acquisition process (McDonald-Madden *et al.* 2008).

Our land-cost estimate is innovative, because it includes a variety of land-use types (pasture, cropland, forest and grass/shrublands) and the cost estimate also reflects the potential for development. At the same time, it does not capture all factors that influence the market price of land, as it excludes the value of capitalised amenity values. Other factors and approaches related to the investment portion of ROI that may be important to consider include the following: transaction uncertainty, either through specific land parcels becoming unavailable or through the cessation of conservation funding (McBride *et al.* 2007), ongoing management costs and the likelihood of management success (Joseph *et al.* 2009) or optimal allocation schedules of dollars spent over extended periods of time (Costello & Polasky 2004; Wilson *et al.* 2006, 2007; Bode *et al.* 2008b).

Our ROI analysis required a number of decisions that could reasonably be made differently for an ROI with different priorities. Vertebrate and plant richness are only moderately correlated in many areas (Murdoch *et al.* 2007), so a separate analysis for plants, or an analysis which defines benefit in terms of ecosystem type (Murdoch *et al.* 2010), would be useful. The approach we present here could be also applied only to species considered globally or nationally endangered, rather than all vertebrates. By calculating our return of averted species losses using the species–area relationship, we have not accounted for which species are actually found in the protected areas of a given county or region. In addition, using species range maps to indicate occurrences at the county level creates errors of commission, especially for narrow-ranged, specialist species (Jetz *et al.* 2008). We accepted these generalisations to calculate ROI values in over 3000 counties including over 1000 species. However, a finer-scale application, such as one based on ecological systems, hydrological units or sub-county boundaries, could use species distribution models such as those used by the USGS GAP analysis program[4] (e.g. Polasky *et al.* 2012) to account more precisely for which species are found where, and thus, more accurately address which species are adequately protected and which are in need of additional protection.

The use of a rigorous ROI approach will not only enable organisations to maximise the conservation benefit per dollar invested but also help to increase the funding available for conservation by demonstrating that donor or taxpayer dollars are being used as efficiently as possible. Clearly, not all conservation decisions are made with the goal of maximising regional or national contributions to biodiversity conservation, and this approach should not threaten local conservation initiatives being pursued in any geography. Nevertheless, it can bolster conservation efforts being pursued in regions that would provide the most cost-effective conservation investments.

The ROI estimates presented here provide simple, transparent estimates of conservation value that take land costs, diminishing returns and the threat of land conversion into account. Until recently, much of the information needed to make such estimates was absent and still is for many regions of the globe. However, where data exist on land values, the lands and species already protected and the threat of land conversion, taking such factors into account will greatly improve the efficiency and effectiveness of conservation efforts by maximising the averted loss of species and minimising overprotection.

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AUTHOR CONTRIBUTIONS

JL, SP, PK and WR designed the study and developed the initial approach for analysing results. JW, EN, CW, CS, TN, AR and JR collected and processed data sets, tested approaches to calculating ROI, wrote and refined code for the greedy heuristic algorithm and developed new ideas for analysis. AP developed the land-cost estimates and wrote that section of the Methods. JW wrote the first version of the complete manuscript. All co-authors contributed to interpreting early results as well as suggesting changes to the approach and making revisions to the manuscript.

[4]http://gapanalysis.usgs.gov/

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