Biological Conservation 161 (2013) 223–229

Contents lists available at SciVerse ScienceDirect

Biological Conservation

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

Changing spatial patterns of conservation investment by a major land trust

Isla S. Fishburn [a], Alison G. Boyer [b], Peter Kareiva [c], Kevin J. Gaston [a,1], Paul R. Armsworth [a,b,*]

[a] Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[b] Department of Ecology and Evolution, University of Tennessee, 569 Dabney Hall, 1416 Circle Drive, Knoxville, TN 37996-1610, USA
[c] The Nature Conservancy, Santa Clara University Project Office, Santa Clara, CA 95053, USA

ARTICLE INFO

Article history:
Received 2 August 2012
Received in revised form 7 February 2013
Accepted 11 February 2013
Available online 30 April 2013

Keywords:
Biodiversity
Economic cost
Conservation planning
Protected area
Land trust
The Nature Conservancy

ABSTRACT

While numerous scientific publications have used biological data and sometimes decision theory to identify where conservation funds should be invested, studies that examine where money for conservation actually has been spent and how investment patterns have changed through time are scarce. We analyze changing spatial patterns of spending on land protection, using investments by a major conservation organization, The Nature Conservancy (TNC), in the conterminous United States as a case study. We focus on investments in land protection made by TNC in four decades (1970–2009) using fee simple and easement acquisitions. During this period, TNC expanded and accelerated its investments in land conservation. We compare patterns of conservation investment in different states via two metrics: (1) the amount TNC spent to acquire land for protection, and (2) the overall area protected. The two metrics, while correlated, reveal different information about TNC's investment patterns. The amount of conservation activity TNC undertook in different states shows pronounced variation when measured either by the overall area protected or the cost of acquiring that area. We used a regression approach to relate variation in investment levels across states in each decade to a suite of biological and socioeconomic factors relevant to the effectiveness of conservation resource allocation decisions. Through time, these variables are able to explain greater spatial variation in the levels of investment into different states. The richness of native species per state showed the strongest association with overall investment levels. However, land costs also influenced investment patterns in recent decades but in ways that differed when measured by the overall area protected and by the money spent to protect it.

1. Introduction

Conservation scientists have long advocated adoption of systematic approaches for designing protected area networks (Margules et al., 1988; Pressey et al., 1993; Margules and Pressey, 2000; Pressey, 2002; Groves, 2003; Pressey and Bottrill, 2008; Moilanen et al., 2009). For example, recent academic writings have focused on how socioeconomic considerations, like the cost of establishing protected areas, should be factored into prioritization of future candidate sites for protection (Naidoo et al., 2006; Polasky et al., 2008; Withey et al., 2012) and on how levels of investment in different locations can most effectively be sequenced through time (Wilson et al., 2006, 2007; Visconti et al., 2010). However, empirical assessments of where funding for conservation actually has been spent lag behind these theoretical recommendations. Examinations of past financial investment in conservation typically operate at coarse spatial grains (e.g. countries or broad geographic regions), because of limited data (Balmford and Long, 1995; James et al., 1999; Castro and Locker, 2000; McKinney, 2002; Balmford et al., 2003; Halpern et al., 2006; Fishburn et al., 2009a; Brockington and Scholfield, 2010; Hickey and Pimm, 2011; but see Underwood et al. (2008)). Among these studies on conservation spending, almost no consideration has been given to how spatial patterns of investment have evolved through time (although see Abramovitz (1994) and Ahrends et al. (2011)).

When examining the spatial distribution of protected areas, we know more about their areal coverage than we do about spatial patterns of conservation spending. It is commonly argued that early protected areas were created in places where land was cheap

Abbreviation: TNC, The Nature Conservancy.

* Corresponding author at: Department of Ecology and Evolution, University of Tennessee, 569 Dabney Hall, 1416 Circle Drive, Knoxville, TN 37996-1610, USA. Tel.: +1 865 974 9748; fax: +1 865 974 3067.

E-mail addresses: alison.boyer@utk.edu (A.G. Boyer), pkareiva@tnc.org (P. Kareiva), k.j.gaston@exeter.ac.uk (K.J. Gaston), p.armsworth@utk.edu (P.R. Armsworth).

[1] Present address: Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9EZ, UK.

0006-3207/$ - see front matter
http://dx.doi.org/10.1016/j.biocon.2013.02.007

and largely unwanted for more productive, economic uses (Runte, 1983; Pressey, 1994). This resulted in disproportionate coverage of high elevation habitats and poor quality soils (Pressey et al., 1996; Hansen and Rotella, 2001; Scott et al., 2001; Jackson and Gaston, 2008) and poor coverage of species of conservation concern (Rodrigues et al., 1999, 2004; Andelman and Willig, 2003). Some authors have also examined how spatial patterns of protected area coverage have changed through time (Chape et al., 2003; Tuvi et al., 2011; Fisher and Dills, 2012), often finding that representation of communities and habitats has improved (Nilsson and Gotmark, 1992; Mendel and Kirkpatrick, 2002; Pressey et al., 2002).

In Fishburn et al. (2009a), we compared the areal coverage of a protected area system with the financial cost of establishing these areas as complementary metrics of conservation effort, the first time such a comparison appears to have been offered. The two metrics of conservation investment that we consider (area protected and dollars spent to protect them) are obviously related, but they speak to different priorities. If cost is no object, then area is what matters. In contrast, if maximizing returns per dollar is what matters, then the economic investment is more illuminating. In that study, we focused on areas protected by a conservation nonprofit, The Nature Conservancy (TNC). By focusing on a single organization, we were able to examine a set of conservation investments made under a single broad, conservation mission and subject to consistent governance, operating procedures and reporting structures. Here, we use an updated dataset to examine how patterns of conservation investment by TNC, as revealed by the two different metrics, have changed through time. We also compare changing investment levels to changes in a suite of biological and socioeconomic variables argued in the literature to be relevant to effective conservation resource allocation decisions.

Since it was founded in 1951, TNC has grown to become the world's largest nonprofit focused on biodiversity conservation (Armsworth et al., 2012). As it has grown, the organization's mission and conservation strategies have evolved (Brewer, 2003; Birchard, 2005). We examine how the spatial pattern of investments in land conservation by TNC changed between 1970 and 2009. During this period, conservation planning theory widened its lens from an initial focus on the most effective design of small numbers of protected areas (Diamond, 1975; Higgs, 1981; Simberloff and Abele, 1982; Simberloff, 1988) to consider the most effective design of whole networks of protected areas (Margules et al., 1988; Pressey et al., 1993; Margules and Pressey, 2000; Pressey, 2002) and of spatial priorities more broadly (Olson and Dinerstein, 1998; Myers et al., 2000; O'Connor et al., 2003). This period also spans important changes in the practice of land conservation in the US, including: fast growth of the environmental nonprofit sector in general (Blackwood et al., 2008) and of land trusts, like TNC, in particular (Davies et al., 2010; LTA, 2011), and rapid uptake of conservation easements as a method for land protection (Fishburn et al., 2009b; LTA, 2011).

2. Methods

2.1. TNC land protection dataset

TNC is a worldwide organization that is structured into state and country chapters, where these are subject to organization-wide policies, priorities and reporting standards. While chapters work towards unified organization goals, they are given flexibility to turn these goals into specific, state-level conservation objectives and to prioritize actions, including land acquisition, to achieve these objectives.

There are different scales (extents and grains) over which one can examine TNC's conservation activities, ranging from the level of individual land parcels to the level of state chapters to national and international scales. For example, Fisher and Dills (2012) look within US states and assess whether land parcels acquired by each chapter fall within TNC's portfolio of priority areas for protection for that state; they do not consider financial costs of protecting these areas. The spatial resolution of the financial dataset that we use limits what is possible when investigating how funding has been invested in conservation. As such, we focus on whether some states have seen more conservation activity than others within the US when measured by area protected and costs to TNC of securing that protection, and how the patterns we find have changed through time.

TNC provided data on over 16,500 land transactions they undertook in the conterminous US using conservation easements or fee simple acquisition between 1970 and 2009. We compare patterns of conservation investment to a set of covariates (discussed below). To reflect the frequency with which these covariates are measured (e.g., every 10 years for US Census data), we aggregated land transactions into totals for each decade for analysis: 1970–1979, 1980–1989, 1990–1999 and 2000–2009. TNC undertook its first conservation land acquisition in the mid-1950s and was active in land conservation throughout the conterminous US by the 1970s.

We analyzed conservation investment using two measures. First we used the total area protected in each state during each decade. Then we used the upfront cost to TNC of acquiring that area. We do not have comparable data on other relevant costs, such as transaction costs or stewardship costs subsequently involved in managing these areas. Our two measures of investment provide distinct but related measures of conservation activity, and, as our results make clear, a richer understanding of conservation investment priorities is possible when comparing them. Land that was fully donated to TNC is only included in the analyses of the area protected; partially donated deals (i.e. land acquired by TNC at a fraction of its fair market value) are included in analyses for both the area protected and the sums invested. All dollar values were converted to 2010 equivalents using the Consumer Price Index (CPI, 2011).

2.2. Covariates

We used a multiple regression approach to relate the patterns of conservation activity that we find to a combination of biological and socioeconomic factors. Conservation planning writings debate just which factors should influence the spatial allocation of resources available to support conservation (Merenlender et al., 2009; Arponen et al., 2010). However, common suggestions include the amount of biodiversity found in a particular region; the threats facing that biodiversity, for example, from development; and the cost of acquiring land in that region for protection. We chose covariates that could reflect relative spatial variation among states in these factors. To measure variation in biodiversity across states, we used the total species richness of native species of vertebrates, invertebrates, and plants. We used native species counts recorded by NatureServe in each state in the middle of the final decade analyzed (NatureServe, 2006). The cost of land may constrain land protection in each state. We included the average price of agricultural land in each state during each decade as an independent indicator of relative spatial variation in rural land costs. We obtained these cost estimates from agricultural census data from the US Department of Agriculture (2009). To represent the threat to ecosystems from development of land and from degradation of habitats associated with human activities, we used the population density per state in each decade and also the rate of change in the number of households in each decade (US Census Bureau, 2010). Growth in the number of households is associated with the areal footprint of development and consumption of resources (Liu et al., 2003) and household number is associated with relative threats to biodiversity at the state-level in the US (Brown and Laband, 2006). Finally, we included the area of each state to reflect varying opportunities for conservation.

2.3. Statistical analyses

The response variables, total area protected and total dollars invested for each decade, were $\log_{10}$ transformed to meet the assumptions of normality. Where appropriate, covariates were also $\log_{10}$ transformed, but a more flexible Box-Cox transformation (Krebs, 1999) was applied for state area. All analyses were performed using the transformed data. Even with transformations, assumptions of normality could only be met once some states were omitted due to the very low number of investments that occurred in the earliest decade. For the area protected, three states were excluded from analyses: Delaware, Louisiana and North Dakota. For total dollars invested as the response variable, six states were excluded from analyses: Delaware, Kansas, Louisiana, North Dakota, South Dakota and Wyoming.

All analyses were performed using non-spatial modeling techniques. In Fishburn et al. (2009a), we found little evidence of spatial autocorrelation in state level investment patterns in a large subset of the data considered here (1970–2003) when using two different distance metrics. Moreover, were spatial dependency present for one decade and absent in another, results could not have been easily compared.

We checked for multicollinearity amongst the covariates for each decade. In most cases tolerance levels were acceptable (i.e. >0.1). However, the 1970s and 1990s values for population density were at the lowest recommended tolerance level (0.08 and 0.09, respectively). Similarly, we found low tolerance levels (0.10) for state area for the 1970s and 2000s data. The two covariates were retained for analyses to ensure comparability across decades.

We adopted an information theoretic approach to multiple regression to relate spatial patterns of investment each decade to our covariates. Just as the conservation planning literature contains debates over which factors should influence conservation prioritization, it also contains debates over what functional forms should be used to combine them. Here we follow the simple, parsimonious approach used by Yuan-Farrell et al. (2005), Miller et al. (2013) and others to describe spatial patterns of conservation investment using linear combinations of relevant covariates, as opposed to using a more richly specified structural model (see Armsworth et al., 2009 for relevant discussion). We did not include quadratic terms for any covariates because linear models in bivariate regressions always had lower AIC values. We also did not include interaction terms, because we had no a priori reason to privilege some of the many possible interactions over others. We compared all possible linear combinations of the five covariates using the package 'glmulti' in R v.2.11.1. We ranked models according to the small sample size AICc criterion and calculated the Akaike weights for each (Burnham and Anderson, 2002) using package 'AICcmodavg' in R. We constructed a set of parsimonious models for each decade, defined as those having an AICc value within two points of the minimum for any model. We estimated model-averaged parameters over this set of parsimonious models.

3. Results

3.1. Overall trends in investment

During the forty years examined, TNC protected over 3.9 million ha of land and TNC spent USD $8.1 billion either to buy fee titles or easements covering this area. Conservation effort by TNC increased over time. The total area protected by TNC from 1970 to 1979 was about 400,000 ha; between 2000 and 2009, it had increased to 1.6 million ha. Over USD $1.3 billion was spent on land acquisition costs by TNC in the 1970s. This total reduced by a quarter during the 1980s but increased again in subsequent decades, with a total expenditure of USD $3.7 billion from 2000 to 2009.

The amount of funding invested and the overall area protected in different states varied by 2–3 orders of magnitude in each decade. There was a strong positive correlation between the area protected and dollars invested by TNC in each state during the past four decades (Fig. 1).

Investment levels into different states were also positively correlated through time, a signal that was stronger for the area protected in each state than for the dollar amounts invested to protect it (Fig. A1). Despite this consistent overall pattern, investment levels in individual states varied through time (Fig. 2). For example, some states saw large increases in the area of land protected in each decade while levels of financial investment grew more slowly (e.g. Connecticut; CT). In other states, expenditures increased dramatically but the amount of land protected during each decade stayed relatively constant (e.g. New York; NY, 1970s–

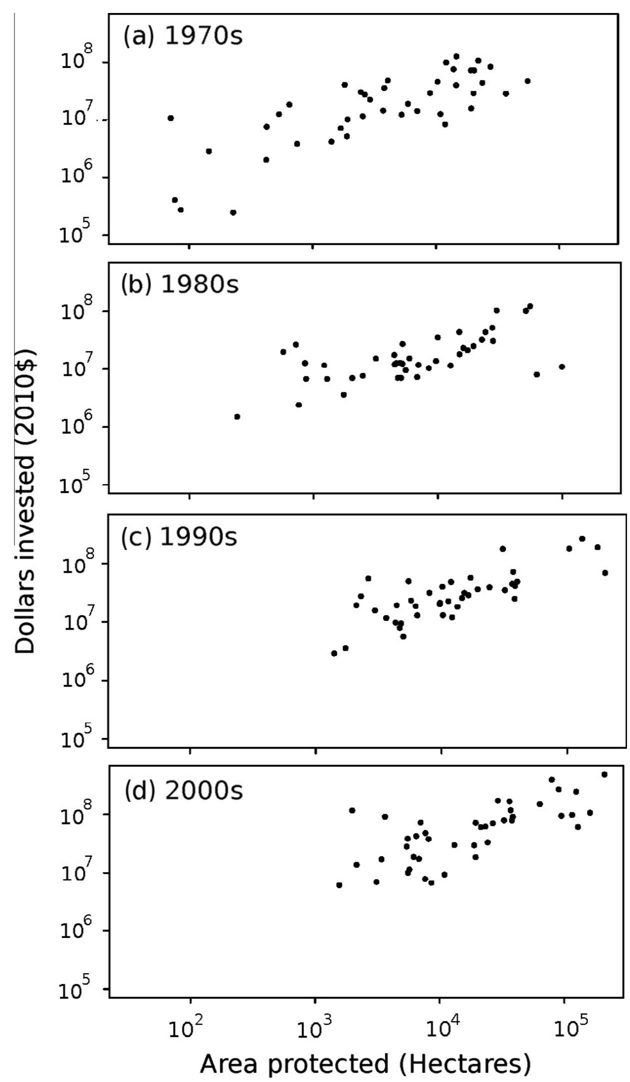

Fig. 1. Relationships between the area protected and dollars invested by The Nature Conservancy in each US state ($n = 42$) for the past four decades. (a) 1970s (Pearson correlation coefficient, $r = 0.79$, $p < 0.001$); (b) 1980s ($r = 0.64$, $p < 0.001$); (c) 1990s ($r = 0.77$, $p < 0.001$); (d) 2000s ($r = 0.72$, $p < 0.001$).

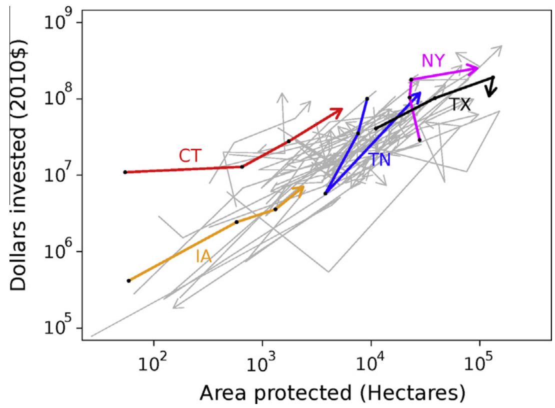

Fig. 2. Temporal trends in the total area protected by The Nature Conservancy and the cost of acquiring that area. Data for all states each decade are illustrated by gray arrows. Data for five example states are shown with colored arrows and black points represent total area and dollar investments for each decade: 1970s, 1980s, 1990s, and 2000s. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1990s). Other states witnessed a steady increase in both measures of conservation investment over time (e.g. Iowa; IA). Finally, some states experienced periods of decline in investment during the four decades studied (e.g. Tennessee; TN and Texas; TX), although most such declines were followed by rebounds.

3.2. Covariation with biological and socioeconomic factors

The set of parsimonious models relating variation in the overall area protected by TNC in different states in each decade to biological and socioeconomic factors relevant to conservation contained between 2 and 9 different models (Table 1). The model averaged partial r^2 is greatest for the richness of native species, which through time became consistently the best predictor of overall area protected in different states (Table 1). In the 1990s, the cost of land also showed an association with the overall area protected in different states with less area protected in states where land was expensive. However, in the most recent decade, this signal was no longer present and land cost showed little association with the overall area protected. The explanatory power of the models for overall protected area increased from the 1970s peaking in the 1990s at 47%. However, the explanatory power of these models decreased in the most recent decade, due to the diminished importance of land costs as a predictor of the overall area protected in different states.

Next we examined how well the same set of covariates could explain variation in levels of financial investment allocated to acquire land for protection in different states. This time the set of parsimonious models included 2–6 models for each decade (Table 2). The model average r^2 value improved steadily through time from 6% in the 1970s to 37% in the most recent decade. Species richness was again the most consistent predictor of overall levels of investment becoming increasingly important through time. However, in the most recent decade, the cost of land in different states also influenced where TNC allocated financial resources. In the last decade, TNC spent more in states where land was expensive. The remaining covariates explained little of the variation in either the area protected or the cost of securing that protection in any of the four decades.

Here we focus on the role that different covariates play when operating in combination. Results of bivariate regressions of the two response variables against each covariate individually are given in the Supplementary material (Tables A1 and A2).

4. Discussion

Despite how much has been written advocating where conservation organizations should target most conservation effort, we know surprisingly little about how conservation investment patterns actually have evolved when measured by money spent on

Table 1
The set of parsimonious models (ΔAICc $\leqslant$ 2 compared to the best model) explaining variation in the total area (in hectares) protected by The Nature Conservancy in different states of the conterminous USA (n = 45) in each of four decades.

Decade	Model	Parameter estimates ± 1SE					Partial R^2					Model R^2	AICc	Model weight (rescaled)
		Spp. rich.	Land cost	Popn. dens.	Growth in households	State area	Spp. rich.	Land cost	Popn. Dens.	Growth in households	State area			
1970s	1	–	−0.58 ± 0.37	–	0.83 ± 0.29	–	–	0.05	–	0.16	–	0.17	102.73	0.16
	2	–	–	–	0.68 ± 0.28	–	–	–	–	0.12	–	0.12	102.84	0.15
	3	2.17 ± 0.93	–	–	–	–	0.11	–	–	–	–	0.11	103.13	0.13
	4	–	–	–	0.55 ± 0.29	0.03 ± 0.02	–	–	–	0.07	0.04	0.16	103.19	0.13
	5	–	–	0.46 ± 0.25	–	0.08 ± 0.03	–	–	0.07	–	0.16	0.16	103.23	0.13
	6	–	–	−0.22 ± 0.19	0.82 ± 0.31	–	–	–	0.03	0.14	–	0.15	103.83	0.09
	7	1.23 ± 1.26	–	–	0.43 ± 0.39	–	0.02	–	–	0.03	–	0.14	104.25	0.08
	8	–	–	–	–	0.04 ± 0.02	–	–	–	–	0.09	0.09	104.38	0.07
	9	–	−0.82 ± 0.80	0.82 ± 0.43	–	0.07 ± 0.03	–	0.02	0.07	–	0.15	0.18	104.62	0.06
Average		0.38	−0.14	0.09	0.42	0.02	0.02	0.01	0.02	0.07	0.04	0.14	–	–
1980s	1	2.31 ± 0.76	–	–	–	–	0.17	–	–	–	–	0.17	85.52	0.72
	2	2.22 ± 0.78	–	−0.11 ± 0.16	–	–	0.16	–	0.01	–	–	0.18	87.44	0.28
Average		2.28	0.00	−0.03	0.00	0.00	0.17	0.00	0.00	–	–	0.18	–	–
1990s	1	2.11 ± 0.53	−0.56 ± 0.16	–	–	–	0.20	0.15	–	–	–	0.47	50.39	0.71
	2	2.00 ± 0.54	−0.91 ± 0.43	0.24 ± 0.28	–	–	0.17	0.06	0.01	–	–	0.48	52.15	0.29
Average		2.08	−0.66	0.07	0.00	0.00	0.19	0.12	0.00	–	–	0.47	–	–
2000s	1	2.11 ± 0.64	–	–	–	–	0.20	–	–	–	–	0.20	69.97	0.37
	2	2.05 ± 0.64	–	−0.17 ± 0.14	–	–	0.19	–	0.03	–	–	0.23	70.66	0.26
	3	1.55 ± 0.83	–	–	–	0.02 ± 0.02	0.06	–	–	–	0.02	0.22	71.16	0.20
	4	1.95 ± 0.66	−0.19 ± 0.20	–	–	–	0.16	0.02	–	–	–	0.22	71.43	0.18
Average		1.95	−0.03	−0.04	0.00	0.00	0.16	0.00	0.01	–	0.00	0.21	–	–

Table 2
The set of parsimonious models (ΔAICc $\leqslant$ 2 compared to the best model) explaining the variation in total monetary sums invested by The Nature Conservancy to acquire land in different states of the conterminous USA (n = 42) in each of four decades.

Decade	Model	Parameter estimates ± SE					Partial R^2					Model R^2	AICc	Model weight (rescaled)
		Spp. rich.	Land cost	Popn. dens.	Growth in households	State area	Spp. rich.	Land cost	Popn. dens.	Growth in households	State area			
1970s	1	–	–	–	0.52 ± 0.27	–	–	–	–	0.09	–	0.09	84.88	0.45
	2	1.50 ± 0.85	–	–	–	–	0.07	–	–	–	–	0.07	85.48	0.33
	3			(Intercept only)			–					2×10^{-16}	86.30	0.22
Average		0.50	0.00	0.00	0.23	0.00	0.02	–	–	0.04	–	0.06	–	–
1980s	1	1.26 ± 0.54	0.47 ± 0.18	–	–	–	0.11	0.14	–	–	–	0.19	41.30	0.29
	2	–	–	–	0.26 ± 0.11	–	–	–	–	0.12	–	0.12	42.17	0.19
	3	–	0.25 ± 0.17	–	0.23 ± 0.11	–	–	0.04	–	0.09	–	0.17	42.46	0.16
	4	1.05 ± 0.52	–	0.26 ± 0.11	–	–	0.09	–	0.12	–	–	0.16	42.76	0.14
	5	–	0.074 ± 0.28	–	–	0.03 ± 0.02	–	0.15	–	–	0.08	0.15	43.19	0.11
	6	–	–	0.13 ± 0.11	0.22 ± 0.12	–	–	–	0.03	0.08	–	0.15	43.20	0.11
Average		0.51	0.18	0.05	0.11	0.00	0.04	0.07	0.02	0.05	0.01	0.16	–	–
1990s	1	2.05 ± 0.50	–	0.19 ± 0.11	–	–	0.29	–	0.05	–	–	0.30	40.51	0.28
	2	2.59 ± 0.69	–	–	–	−0.02 ± 0.01	0.25	–	–	–	0.04	0.29	41.01	0.22
	3	1.84 ± 0.05	–	–	–	–	0.25	–	–	–	–	0.25	41.07	0.21
	4	1.81 ± 0.53	−0.49 ± 0.40	0.47 ± 0.26	–	–	0.20	0.03	0.06	–	–	0.33	41.49	0.17
	5	2.03 ± 0.54	0.18 ± 0.18	–	–	–	0.27	0.02	–	–	–	0.27	42.46	0.11
Average		2.08	−0.07	0.14	0.00	0.00	0.26	0.01	0.03	–	0.01	0.29	–	–
2000s	1	2.50 ± 0.58	0.66 ± 0.19	–	–	–	0.29	0.20	–	–	–	0.37	49.58	0.72
	2	2.65 ± 0.62	0.95 ± 0.42	−0.22 + 0.29	–	–	0.30	0.08	0.01	–	–	0.38	51.52	0.28
Average		2.54	0.74	−0.06	0.00	0.00	0.29	0.17	0.00	–	–	0.37	–	–

conservation. We examined investments in land conservation made by TNC, the world's largest biodiversity conservation non-profit, between 1970 and 2009 as a case study in conservation investment. TNC grew rapidly during this period and greatly expanded its investment in protecting land. The combined area protected in our dataset is equivalent to greater than 50% of the coverage of US National Parks in states in the study.

We contrasted the area of land protected and upfront cost to TNC of protecting these areas as alternative measures of conservation effort. As one might expect, the two measures of conservation activity were correlated. However, the correlations, while strong and positive, left 38–59% of the variation in investment patterns unexplained, indicating that the two measures of conservation activity contain distinct information about conservation investment patterns.

We compared overall investment levels in different states to a suite of biological and socioeconomic variables that it has been argued should be important for determining the effectiveness of conservation resource allocation decisions (Wilson et al., 2009; Moilanen et al., 2009; Withey et al., 2012). We included variables representing the biological value of different states, opportunities for conservation in those states (cost of land and overall land area) and the threats to biodiversity from development and human uses. The strongest patterns of covariation were between conservation investment levels and our biodiversity indicator, the richness of native species. This variable was responsible for most of the explanatory power of the models and its influence was greater in later decades than earlier ones, whether focusing on the overall area protected or the money spent to establish these protected areas.

The other important covariate of conservation investment levels was the average cost of agricultural land in each state. The associations with land cost demonstrate the value to using contrasting metrics (hectares protected and dollars invested) when examining conservation investment patterns. The increase in explanatory power of the models examining the overall area protected in each state (Table 1) for the 1990s (47%) over that offered the 1980s (18%) is due to the importance of land costs. In the 1990s, TNC protected less land in states where land was more expensive. However, the association between land costs and the area protected was no longer apparent after 2000. In contrast, when seeking to explain patterns of variation in the amount of money spent on land conservation, the average cost of land per hectare grew in influence after 2000. Moreover, average agricultural land cost was positively associated with levels of spending on conservation in this most recent decade; TNC spent more money protecting land in states where, on average, agricultural land was more expensive.

The obvious question becomes what is driving these patterns of covariation between TNC's investment in different states and factors thought important to effective resource allocations in conservation, like biodiversity value. One possibility is that the associations we find are causally linked and signify increasingly strategic resource allocation among states by TNC in later decades. This would be consistent with a common narrative in conservation writings that, while early protected areas were set up in locations poorly suited to meet conservation goals, over the past 3–4 decades, conservation organizations and agencies have adopted more systematic approaches and tools for the design of protected area networks (Pressey, 2002; Pressey and Bottrill, 2008; Moilanen et al., 2009; but see Prendergast et al., 1999; Knight et al., 2008). If there were an increasingly strategic pattern to investments, the explanatory power of the models should increase through time. However, the role of the covariates also matters. If most of the explanatory power were accounted for by land costs with more investments in places where land is cheaper, this would suggest a more ad hoc or opportunistic approach, and if state area had particularly large predictive capacity this would be more consistent with a null model for conservation investment. The results of our regression analyses are broadly consistent with an increasingly strategic signal to conservation investment patterns through time. In the past two decades, the models are able to explain more of the variation in the allocation of investments across states than in earlier decades. This pattern is clearest when focusing on the total dollars invested to protect land where the amount of variation explained by the models increased monotonically from 6% to 37%. That our biodiversity indicator is responsible for most of the explanatory power of the models and that its influence increased over time is also suggestive of a strategic alignment of TNC with conservation priorities.

But could TNC allocate resources across states in the way this inference assumes? TNC are structured hierarchically with state chapters making the primary resource allocation decisions over just which parcels of land to prioritize for acquisition and being limited primarily by revenues generated within state. Also, as a recent study showed, even if down-scaling the question and focusing on variation within states, conservation priorities only exert so much influence on which parcels of land to acquire (Fisher and Dills, 2012). However, we would maintain that there is plenty of scope for TNC to influence resource allocation among states over the time-scales considered in our study (40 years). Institutional support in the early decades for the emergence and strengthening of state chapters in locations important for biodiversity or other aspects of the organization's conservation mission would result in increased activity of those state chapters today, even if that activity was now funded from revenue generated within state. Another mechanism by which national priorities can steer resource allocation across states concerns the shift by TNC towards allocating a disproportionate share of conservation funding to very large land deals in the past two decades (Davies et al., 2010). These large deals are too expensive for individual state chapters to undertake on their own and are only made possible through a system of internal loans from TNC centrally to individual chapters. TNC's ability to make such loans is obviously limited and priority likely would be given to conservation projects that align with the organization's national conservation objectives. Many of the larger conservation transaction require major donations that can be encouraged by the senior executives and CEO of TNC, and the executive leadership of TNC is well versed in science-based conservation priorities.

An alternative explanation is that the relationships we find between levels of conservation investment in different states and the biodiversity and land cost covariates are not causal but instead are sourced in some other variable we have not considered. One important factor that the models do not include is the differing ability of state chapters to generate funds for conservation. At this time, data on differential fund-raising by TNC states are not available. In Fishburn et al. (2009a), we tried to include fund-raising potential by using grant income to TNC from charitable foundations obtained from GuideStar (2006), but found these data to have little predictive capacity for either the overall area protected by TNC or the cost of protecting it. However, it is unclear whether this is due to limitations on the data, which would reflect only a small proportion of a state chapter's income, or to a lack of any such association. We also tried to use gross state product (GSP) as an indicator of the relative wealth of different states, which could impact state chapter's fund-raising ability. However, GSP was very tightly correlated with one of our threat indices (rate of change of number of households in a state) and we chose to proceed with only one of the two variables (rate of change of households) in multiple regressions to avoid diluting out their potential influence as explanatory factors. A fruitful area for future study would be to quantify better fund-raising potential in different locations and the limitations this imposes on large-scale resource allocation strategies in conservation.

A common concern in the literature is that conservation planning research sees less application than might be hoped (Knight et al., 2008). One way that conservation planning tools and approaches can become more relevant to conservation organizations is if their design reflects more closely the strategic decisions that individual organizations take and how these evolve as an organization grows and changes. For that to happen, we need to understand better, and ideally quantify, aspects of conservation organizations' decision-making. Case studies of the type we present can help in this regard. Our results highlight the importance in such analyses of disaggregating data on conservation investments through time and of examining multiple aspects of investment decisions. Here we included two measures of conservation effort, the area protected and the cost of acquiring that area, that when taken together provided richer insights into TNC's land protection strategy than would be obtained when considering either measure in isolation.

Acknowledgments

We thank The Nature Conservancy for providing us with access to their investment data. The Natural Environment Research Council, the British Ecological Society, the Nuffield Foundation and the University of Tennessee funded this study.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.02.007.

References

Abramovitz, J.N., 1994. Trends in Biodiversity Investments: U.S.-based Funding for Research and Conservation in Developing Countries, 1987–1991.. World Resources Institute, Washington, DC.
Ahrends, A., Burgess, N.D., Gereau, R.E., Marchant, R., Bulling, M.T., Lovett, J.C., Platts, P.J., Kindemba, V.W., Owen, N., Eibleis, F., Rahbek, C., 2011. Funding begets biodiversity. Divers. Distrib. 17, 191–200.
Andelman, S.J., Willig, M.R., 2003. Present patterns and future prospects for biodiversity in the western hemisphere. Ecol. Lett. 6, 818–824.
Armsworth, P.R., Gaston, K.J., Hanley, N.D., Ruffell, R.J., 2009. Contrasting approaches to statistical regression in ecology and economics. J. Appl. Ecol. 46, 265–268.
Armsworth, P.R., Fishburn, I.S., Davies, Z.G., Gilbert, J., Leaver, N., Gaston, K.J., 2012. The size, concentration and growth of biodiversity conservation nonprofits. Bioscience 62, 271–281.
Arponen, A., Cabez, M., Edlund, J., Kujala, H., Lehtomaki, J., 2010. Costs of integrating economics and conservation planning. Conserv. Biol. 24, 1198–1204.
Balmford, A., Long, A., 1995. Across-country analyses of biodiversity congruence and current conservation effort in the tropics. Conserv. Biol. 9, 1539–1547.
Balmford, A., Gaston, K.J., Blyth, S., James, A., Kapos, V., 2003. Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. Proc. Natl. Acad. Sci. USA 100, 1046–1050.
Birchard, R., 2005. Nature's Keepers: The Remarkable Story of How the Nature Conservancy Became the Largest Environmental Organization in the World. Jossey-Bassey, San Francisco, CA.
Blackwood, A., Wing, K.T., Polak, T.H., 2008. The Nonprofit Sector in Brief. Facts and Figures from the Nonprofit Almanac 2008 Public Charities, Giving, and Volunteering. The Urban Institute, Washington, DC.
Brewer, R., 2003. Conservancy: The Land Trust Movement in America. Dartmouth College Press, Lebanon, NH.
Brockington, D., Scholfield, K., 2010. Expenditure by conservation nongovernmental organizations in sub-Saharan Africa. Conserv. Lett. 3, 106–113.
Brown, R.M., Laband, D.N., 2006. Species imperilment and spatial patterns of development in the United States. Conserv. Biol. 20, 239–244.
Burnham, K.P., Anderson, D., 2002. Model Selection and Multi-Model Inference, second ed. Springer, New York.
Castro, G., Locker, I., 2000. Mapping Conservation Investments: An Assessment of Biodiversity Funding in Latin America and the Caribbean. Biodiversity Support Program. World Wildlife Fund, Washington, DC.
Chape, S., Blyth, S., Fish, L., Fox, P., Spalding, M., 2003. 2003 United Nations List of Protected Areas. IUCN, UNEP-WCMC, Cambridge, UK.
CPI (Consumer Price Index), 2011. Inflation Calculator. US Department of Labor, Bureau of Labor Statistics. <http://data.bls.gov/data/inflation_calculator.htm> (accessed February 2011).
Davies, Z.G., Kareiva, P., Armsworth, P.R., 2010. Temporal patterns in the size of conservation land transactions. Conserv. Lett. 3, 29–37.
Diamond, J.M., 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol. Conserv. 7, 129–146.
Fishburn, I.S., Kareiva, P., Gaston, K.J., Armsworth, P.R., 2009a. State level variation in conservation investment by a major non-governmental organization. Conserv. Lett. 2, 74–81.
Fishburn, I.S., Kareiva, P., Gaston, K.J., Armsworth, P.R., 2009b. The growth of easements as a conservation tool. PLoS ONE 4, e4996.

Fisher, J.R.B., Dills, B., 2012. Do private conservation activities match science-based conservation priorities? PLoS One 7, e46429.

Groves, C.R., 2003. Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity. Island Press, Washington, DC.

GuideStar, 2006. <http://partners.guidestar.org> (accessed 23.09.06.

Halpern, B.S., Pyke, C.R., Fox, H.E., Haney, J.C., Schlaepfer, M.A., Zaradic, P., 2006. Gaps and mismatches between global conservation priorities and spending. Conserv. Biol. 20, 56–64.

Hansen, A.J., Rotella, J.J., 2001. Biophysical factors, land use, and species viability in and around nature reserves. Conserv. Biol. 16, 1112–1122.

Hickey, V., Pimm, S.L., 2011. How the World Bank funds protected areas. Conserv. Lett. 4, 269–277.

Higgs, A.J., 1981. Island biogeography theory and nature reserve design. J. Biogeogr. 8, 117–124.

Jackson, S.F., Gaston, K.J., 2008. Incorporating private lands in conservation planning: protected areas in Britain. Ecol. Appl. 18, 1050–1060.

James, A.N., Green, M.J.B., Paine, J.R., 1999. A Global Review of Protected Area Budgets and Staffing. WCMC, World Conservation Press, Cambridge, UK.

Knight, A.T., Cowling, R.M., Rouget, M., Balmford, A., Lombard, A.T., Campbell, B.M., 2008. Knowing but not doing: selecting priority conservation areas and the research-implementation gap. Conserv. Biol. 22, 610–617.

Krebs, C.J., 1999. Ecological Methodology, second ed. Addison-Welsey Educational Publishers, Inc., Canada, pp. 551–554.

Liu, J., Daily, G.C., Ehrlich, P.R., Luck, G.W., 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421, 530–533.

LTA (Land Trust Alliance), 2011. 2010 National Land Trust Census Report: A Look at Voluntary Land Conservation in America. Land Trust Alliance, Washington, DC.

Margules, C.R., Nicholls, A.O., Pressey, R.L., 1988. Selecting networks of reserves to maximise biological diversity. Biol. Conserv. 43, 63–76.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

McKinney, M.L., 2002. Effects of national conservation spending and amount of protected area on species threat rates. Conserv. Biol. 16, 539–543.

Mendel, L.C., Kirkpatrick, J.B., 2002. Historical progress of biodiversity conservation in the protected area system of Tasmania, Australia. Conserv. Biol. 16, 1520–1529.

Merenlender, A.M., Newburn, D., Reed, S.E., Rissman, A.R., 2009. The importance of incorporating threat for efficient targeting and evaluation of conservation investments. Conserv. Lett. 2, 240–241.

Miller, D.C., Agrawal, A., Roberts, J.T., 2013. Biodiversity, governance, and the allocation of international aid for conservation. Conserv. Lett. 6, 12-20.

Moilanen, A., Wilson, K.A., Possingham, H.P., 2009. Spatial Conservation Prioritization: Quantitative Methods and Computational Tools. Oxford University Press, New York.

Myers, N., Russell, A., Mittermeier, Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends Ecol. Evol. 21, 681–687.

NatureServe, 2006. NatureServe Explorer: An Online Encyclopaedia of Life [web application]. Version 4.7. NatureServe, Arlington, Virginia. <http://www.natureserve.org/explorer> (accessed March 2006).

Nilsson, C., Gotmark, F., 1992. Protected areas in Sweden: is natural variety adequately represented? Conserv. Biol. 6, 232–242.

O'Connor, C., Marvier, M., Kareiva, P., 2003. Biological vs. social, economic and political priority-setting in conservation. Ecol. Lett. 6, 706–711.

Olson, D.M., Dinerstein, E., 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conserv. Biol. 12, 502–515.

Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol. Conserv. 141, 1505–1524.

Prendergast, J.R., Quinn, R.M., Lawong, J.H., 1999. The gaps between theory and practice in selecting nature reserves. Conserv. Biol. 13, 484–492.

Pressey, R.L., 1994. Ad Hoc reservations: forward or backward steps in developing representative reserve systems. Conserv. Biol. 8, 662–668.

Pressey, R.L., 2002. The first reserve selection algorithm – a retrospective on Jamie Kirkpatrick's 1983 paper. Prog. Phys. Geogr. 26, 434–441.

Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L., Weinman, K.M., 1996. How well protected are forests of north-eastern new South Wales? – Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. Forest Ecol. Manage. 85, 311–333.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I., Williams, P.H., 1993. Beyond opportunism: key principles for systematic reserve selection. Trends Ecol. Evol. 8, 124–128.

Pressey, R.L., Whish, G.L., Barrett, T.W., Watts, M.E., 2002. Effectiveness off protected areas in north-eastern New South Wales: recent trends in six measures. Biol. Conserv. 106, 57–69.

Pressey, R.L., Bottrill, M.C., 2008. Opportunism, threats, and the evolution of systematic conservation planning. Conserv. Biol. 22, 1340–1345.

Rodrigues, A.S.L., Tratt, R., Wheeler, B.D., Gaston, K.J., 1999. The performance of existing networks of conservation areas in representing biodiversity. Proc. Roy. Soc. Lond. B Biol. Sci. 266, 1453–1460.

Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonesca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.K., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.

Runte, A., 1983. Reply to sellars. J. Forest Hist. 27, 135–141.

Scott, M.J., Davis, F.W., McGhie, G., Wright, G., Groves, C., Estes, J., 2001. Nature reserves do they capture the full range of America's biological diversity? Ecol. Appl. 11, 999–1007.

Simberloff, D., 1988. The contribution of population and community biology to conservation science. Annu. Rev. Ecol. Syst. 19, 473–511.

Simberloff, D.S., Abele, L.G., 1982. Refuge design and island biogeographic theory: effects of fragmentation. Am. Nat. 120, 41–50.

Tuvi, E.L., Vellak, A., Reier, U., Szava-Kovats, R., Partel, M., 2011. Establishment of protected areas in different ecoregions, ecosystems, and diversity hotspots under successive political systems. Biol. Conserv. 144, 1726–1732.

Underwood, E.C., Klausmeyer, K.R., Morrison, S.A., Bode, M., Shaw, M.R., 2008. Evaluating conservation spending for species return: a retrospective analysis in California. Conservation Lett. 2, 130–137.

U.S. Census Bureau, 2010. Resident Population and Housing Data. <http://2010.census.gov/2010census/data/> (accessed March 2011).

U.S. Department of Agriculture (USDA), 2009. 2007 Census of Agriculture. USDA National Agriculture Statistics Service, Washington, DC.

Visconti, P., Pressey, R.L., Segan, D.B., Wintle, B.A., 2010. Conservation planning with dynamic threats: the role of spatial design and priority setting for species' persistence. Biol. Conserv. 143, 756–767.

Wilson, K.A., Carwardine, J., Possingham, H.P., 2009. Setting conservation priorities. Ann. N.Y. Acad. Sci. 1162, 237–264.

Wilson, K.A., McBride, M.F., Bode, M., Possingham, H.P., 2006. Prioritizing global conservation efforts. Nature 440, 337–340.

Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., Possingham, H.P., 2007. Conserving biodiversity efficiently: what to do, where, and when. PloS Biol. 5, e223.

Withey, J.C., Lawler, J.J., Polasky, S., Plantinga, A.J., Nelson, E.J., Kareiva, P., Wilsey, C.B., Schloss, C.A., Nogeire, T.M., Ruesch, A., Ramos Jr., J., Reid, W., 2012. Maximising return on conservation investment in the conterminous USA. Ecol. Lett. 15, 1249–1256.

Yuan-Farrell, C., Marvier, M., Press, D., Kareiva, P., 2005. Conservation easements as a conservation strategy: is there a sense to the spatial distribution of easements? Nat. Areas J. 25, 282–289.