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LETTER



Costs are not necessarily correlated with threats in conservation landscapes

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Abstract

The priority of an area for conservation is determined by three primary factors: its biodiversity value, the level of threat it is facing, and its cost. Although much attention has been paid to the spatial relationship between biodiversity value and threats, and between biodiversity value and costs, little is known about how costs and threats are spatially correlated. The orthodox assumption in conservation science is that costs and threats are positively correlated. Here, we adapt a classic economic theory of land use to explain how conservation scientists came to expect a positive correlation between costs and threats. We then use high-resolution, ground-truthed datasets of land sales and habitat clearance to show that this assumption is false in the state of Queensland, Australia. Our results provide an empirical counterargument to a widespread assumption in conservation science, and illustrate why spatial prioritization needs to include independent measures of costs and threats.

KEYWORDS

Acquisition, conservation costs, conservation prioritization, conservation threats, habitat loss, land economics, land use change, protected areas, systematic conservation planning

1 | INTRODUCTION

In systematic conservation planning, three primary factors combine to determine the relative priority of a particular location: its biodiversity value, the degree of threats to biodiversity, and the costs of conservation action. To date, much of the conservation literature has focused on understanding the spatial relationship between biodiversity value and conservation costs (Armsworth, 2014; Bode et al. 2008; Naidoo et al., 2006). With increased understanding of this relationship has come a large body of conservation research that seeks maximize biodiversity benefits using limited conservation funds by securing areas that offer the greatest return on investment (Bode et al., 2008; Carwardine et al. 2008; Murdoch et al. 2007; Naidoo & Iwamura, 2007; Strange, Rahbek, Jepsen, & Lund, 2006). Similarly, the spatial relationship between biodiversity value and threats has received considerable empirical attention (the irreplaceabilityvulnerability framework; Margules & Pressey, 2000; Pressey & Taffs, 2001). However, relatively little attention has been paid to how threats might be spatially co-distributed with conservation costs, and how this might affect spatial conservation priorities.

It is frequently assumed that conservation costs are positively correlated with threats (Table S1). This assumption is often explicitly stated (e.g., Boyd, Epanchin-Niell, & Siikamäki, 2015; Butsic, Lewis, & Radeloff, 2013; Costello & Polasky, 2004; Devillers et al. 2015; Merenlender, Newburn, Reed, & Rissman, 2009; Moore, Balmford, Allnutt, & Burgess, 2004; Newburn, Reed, Berck, & Merenlender, 2005;

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Visconti, Pressey, Segan, & Wintle, 2010) based on the argument that anthropogenic habitat transformation is most rapid and intense in economically profitable areas, such as those containing valuable natural resources (Costello & Polasky, 2004; Newburn et al., 2005; Visconti et al., 2010). Based on this assumption, many conservation planning exercises use metrics of threat as surrogates for conservation costs, thereby assuming that costs and threats have the same spatial distribution (Klein et al. 2008; Murdoch, Ranganathan, Polasky, & Regetz, 2010; Sala et al. 2002; Venegas-Li, Levin, Possingham, & Kark, 2018). The assumption that costs are positively correlated with threats also influences important debates in conservation theory. For example, it is often claimed that attempts to minimize conservation costs will lead to "residual reserves" (Arponen, Cabeza, & Eklund, Kujala & Lehtomäki, 2010; Boyd et al., 2015; Devillers et al., 2015), because the cheapest locations are also the least threatened.

The intuition that conservation costs and threats are positively correlated relies on the assumption that the economic value of land and threats to biodiversity are driven by the same underlying processes. However, the profitability of a given economic activity at a particular location is likely to be affected by a range of factors that might be unrelated to threats, such as agricultural labor costs, political regulations and incentives (e.g., subsidies), and noneconomic land use decisions (e.g., tradition or social perception; Vanclay & Lawrence, 1994). These same factors might have minimal influence on the degree of habitat modification required to utilize land for a given economic activity. Instead, threats to biodiversity posed by habitat modification at each respective location might depend on a range of independent factors, such as the degree of modification required to utilize land, and technological advancements in the modification of particular habitats. Furthermore, each of these factors are likely to form complex interactions through space and time, and across spatial scales (Cattarino, McAlpine, & Rhodes, 2014; Seabrook, McAlpine, & Fensham, 2006). If these potentially separate drivers of costs and threats are sufficiently influential, then it is expected that the spatial co-distribution of cost and threats might exhibit a more complex relationship than is widely assumed in the conservation literature.

Here, we explore the spatial co-distribution of costs and threats in conservation landscapes. To do so, we first use a classic economic model to examine the expected relationship. We then use data on historical land acquisition costs and rates of vegetation clearing in the state of Queensland, Australia, to offer empirical insights into this same relationship. In doing so, we hope to highlight the importance of verifying the theoretical assumptions we make in conservation prioritization.

2 | METHODS

2.1 | Definitions of cost and threat

In our analysis, we focused particularly on the costs incurred by conservation organizations when acquiring land for the establishment of protected areas, and the threats to biodiversity caused by habitat clearance. We chose to focus on the acquisition costs of purchasing land for protection because it is one of the most widespread methods of conservation action, and because it is typically the focus of spatial conservation prioritization. We note, however, that (1) acquisition costs are not the sole cost incurred when establishing protected areas, which also involve management costs, and opportunity costs to stakeholders (Naidoo et al., 2006); and (2) biodiversity is threatened by processes other than habitat clearance, such as climate change, invasive species, and pollution (Allek et al. 2018).

2.2 | Theoretical analysis

To explore the theoretical relationship between acquisition costs and rates of habitat loss, we adapted von Thünen's (1826) classic "isolated state" model, which describes how different economic activities arrange themselves in space, and how these patterns affect the cost of land. In the von Thünen model, land quality is homogeneous, distributed radially around a central marketplace. Each location is amenable to the same economic activities (in the original model, these were types of agriculture). Each activity i generates commodities that can be sold at constant price p_i net their production $\cos c_i$. Commodities have different transport $\cos \tau_i$, which accrue at a constant rate with distance. The profit generated by an activity at a distance r from the market is therefore a declining linear function of distance:

$$\pi_i(r) = p_i - c_i - \tau_i r. \tag{1}$$

To maximize their net profits, all parties compete to secure the land that is closest to the market, as this minimizes transportation costs. The rent P(r) generated by an area of land is defined by the most profitable land use at that distance:

$$P(r) = \max_{i} \left[p_i - c_i - \tau_i r \right]. \tag{2}$$

These rents can be considered proportional to acquisition costs. Note that all economic activity—and in our model, all threat—will cease at distances $r > (p_i - c_i) / \tau_i$ (for all values of i). Beyond this distance high transport costs make all activities unprofitable.

We incorporated threats to biodiversity into von Thünen's model using a simple model of habitat degradation. We assumed that each activity *i* threatens a particular proportion

 λ_i of the habitat at that location with degradation or loss. The most profitable land use in each location therefore determines both the local acquisition cost and the magnitude of the threat to biodiversity.

We analyzed both a deterministic and a stochastic version of the extended von Thünen model to explore the relationship between acquisition costs and threats. For the deterministic model, we chose values for τ_i , λ_i , p_i and c_i at random from uniform distributions U(0,1) for four different land use types, and assumed these parameters were constant in space. For the stochastic model, we included economic heterogeneity by adding normally distributed random noise to production costs at each discrete radial distance from the market. We added ecological heterogeneity by adding similar noise to the degradation caused by each activity. Specifically, we defined c_i $(r_x) = \overline{c_i} + \epsilon_x$, and λ_i $(r_x) = \overline{\lambda_i} + \delta_x$, where ϵ_x , $\delta_x \sim N(0,\sigma)$ and $\overline{c_i}$ and $\overline{\lambda_i}$ are the mean values for each activity.

2.3 | Empirical analysis

For our empirical analysis, we examined the spatial codistribution of surrogates for conservation acquisition costs, and rates of habitat loss, on land parcels in Queensland, Australia (Figure 1). Queensland is a large state, covering 185 million hectares and containing a broad range of ecosystems, ranging from tropical and subtropical ecosystems along the east coast, to arid assemblages west of the Great Dividing Range. Queensland is divided into private and state land parcels, each of which represents a legal property. Because these parcels are the resolution at which most conservation action takes place, they were used as replicates in our analysis.

For our primary analysis, we used a dataset of property sales that occurred between 2000 and 2008 (Adams, Segan, & Pressey, 2011b). Because these record real market transactions, they are likely to accurately reflect acquisition costs. However, we note that actual acquisition costs for conservation might vary from standard land transactions, because of differing objectives and negotiation dynamics (Armsworth, 2014). All sale prices were adjusted to 2008 Australian dollars (AUD) based on annual inflation rates (Australian Bureau of Statistics 2017). Our primary analyses assumed that it would be necessary for a conservation organization to purchase entire parcels. Thus, the mean cost per hectare of vegetation on each parcel was calculated as the total price of the parcel divided by the number of hectares of vegetation on the parcel. In the Supporting Information, we also provide analyses assuming that vegetated subsections of each parcel can be purchased, which might affect the relative cost-effectiveness of purchases depending on what proportion of each parcel is vegetated (Adams et al., 2011b).

To estimate threats to biodiversity, we measured the amount of anthropogenic vegetation clearing that occurred on each parcel between 2009 and 2018. This measure of threat,

therefore, reflects the amount of vegetation clearing that could have been prevented by purchasing and protecting vegetation in 2008. We chose to measure clearing between 2009 and 2018 because (1) measuring clearing after the land was sold avoids the possibility that clearing affected the sale price; (2) cost data were available immediately before this period; (3) threat data were available up until the year 2018; and (4) this period spans different phases of land clearing policy (discussed in Section 2.4). For each parcel, we divided the area of vegetation cleared by the area of remnant vegetation in 2008 to give the mean proportion of remnant vegetation that was cleared. In the Supporting Information, we also provide results when vegetation clearing was standardized by total parcel size.

Land clearing was estimated from the Statewide Landcover and Trees Study (SLATS; Queensland Department of Science, Information Technology and Innovation 2017), which uses Landsat satellite imagery to measure woody vegetation clearing in Queensland, and is verified by extensive field surveys. All clearing is classified according to the economic or natural process responsible (e.g., mining, pasture, and natural disaster). We included only direct, anthropogenic clearing in our analysis. We excluded all parcels within 1 km of presentday protected areas to avoid the possibility that clearance rates were affected by protection. We also restricted our analyses to rural land parcels with remnant vegetation in 2008 under the assumption that urban areas and parcels without vegetation are unlikely candidates for conservation acquisition. Finally, because the SLATS dataset detects only woody vegetation clearing, we removed parcels that contained any non-woody vegetation types. The amount of remnant vegetation on each parcel at the time of purchase was calculated by combining the SLATS dataset with data from the National Vegetation Information System (NVIS Technical Working Group 2017).

To explore how the relationship between our estimates of conservation acquisition cost and threat might vary according to ecological and economic variation, we intersected parcels with layers of bioregions and land use types (see Supporting Information for further details). For all analyses, we used Kendall's rank correlation coefficient to measure associations between cost and threat. Kendall's coefficient is useful when datasets contain many zero values, such as parcels that experienced no vegetation clearing.

2.4 | Supporting analyses

We performed several supporting analyses to test the robustness of our results. We repeated our analyses using two alternative surrogates for conservation acquisition costs. The first was unimproved land values as estimated by the Queensland Valuer-General between 2002 and 2006 (Carwardine et al. 2010), converted to 2006 AUD (Australian Bureau of Statistics 2017). For the analysis using land valuations, we

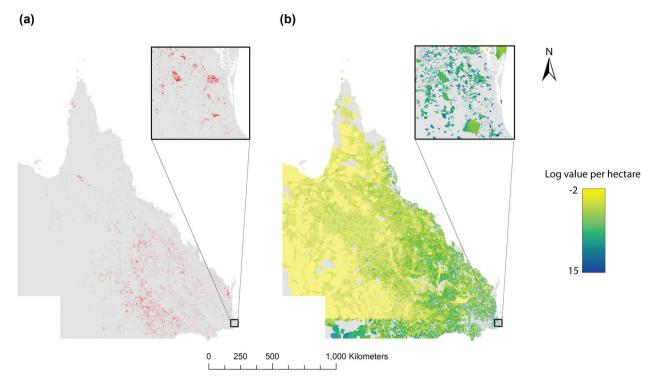


FIGURE 1 The spatial distribution of land valuation and threats from land clearing in Queensland, Australia. Panel (a) shows anthropogenic land clearing (red) that has occurred in Queensland from mid-2007 to mid-2018 derived from the Statewide Landcover and Trees Study (SLATS). Panels (b) shows unimproved land valuation in log 2006 AUD per hectare of vegetation derived from valuations collected by the Queensland Valuer-General. Gray areas represent parcels where land valuations were not performed (e.g., on public land), or parcels where no remnant vegetation was present in the year 2006. Only land valuations, and not sales prices, were used for production of the above map due the low number of property sales in the dataset

measured land clearing between 2007 and 2018. Our second surrogate was the agricultural profitability of land in 2006, modeled by Marinoni et al. (2012). Agricultural profitability is a useful alternative measure because it might better reflect the opportunity costs of conservation (forgone economic profits) as well as acquisition costs.

We repeated our correlation test for two separate phases of land clearing policy in Queensland to test whether our results varied across regulatory regimes. We also stratified our analyses across each of Queensland's 13 bioregions, to see if our results were sensitive to changes in geographic location, extent, or government jurisdiction. Finally, because land prices can exhibit efficiencies of scale, with larger parcels having lower per-hectare costs, we stratified our analysis according to parcel size (0-1 ha, 1–10 ha, 10–100 ha, and over 100 ha). Outputs from these analyses are available in the Supporting Information.

3 | RESULTS

3.1 | Theoretical analysis

If only a single economic activity occurs in a region, the von Thünen model predicts that land cost will decline linearly with distance to market, as net profitability is reduced by transport costs (Figure 2a). Land cost declines to zero at distances $r > (p_1 - c_1)/\tau_1$, once the single activity becomes unprofitable. This simple, single-activity case supports the intuition that cost and threat are correlated (Figure 2b): with low cost (unprofitable) land experiencing low degradation (wilderness), and high cost (profitable) land experiencing greater degradation (λ_1).

With multiple economic activities, a positive correlation between costs and threats can no longer be assumed. Land cost still declines with distance to market, although following a piecewise linear relationship as a sequence of different economic activities maximize net profits (Figure 2c). Habitat degradation remains lowest in land with the lowest cost (wilderness), but is otherwise unrelated to net profitability (Figure 2d). Unless the most profitable activities are also the most ecologically degrading, high-cost land will not face the greatest threats. The result is an uncertain correlation between land costs and threats.

Figure 2e shows how the optimal land use changes through space as a consequence of varying production costs, and Figure 2f shows the consequences for the relationship between costs and threats when ecological heterogeneity adds further noise. The resulting relationship is complex, and unlikely

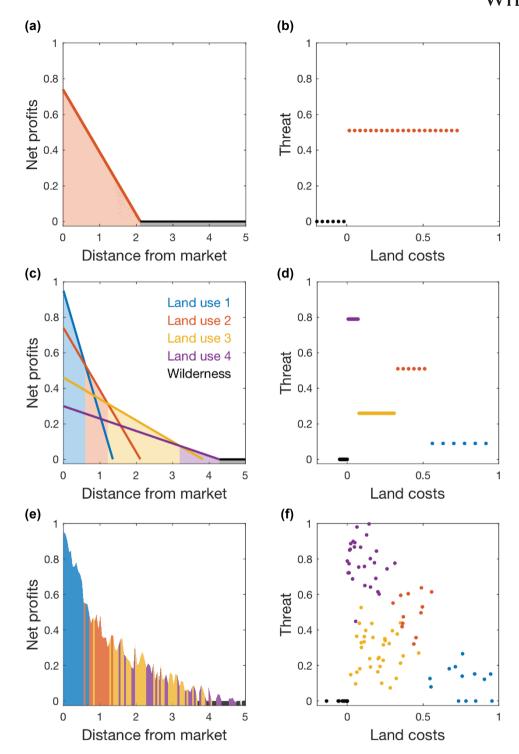


FIGURE 2 The relationship between land costs (net profits) and threat from of land clearing as predicted by the von Thünen model. Panels (a), (c), and (e) show the relationship between distance from market, optimal economic activity, and net profits on land. Different colors denote different economic activities, with black denoting wilderness areas where no economic activity is profitable. Each activity produces commodities that can be sold at market for a net profit indicated by the y-intercept. As distance to market increases, transport costs make each activity less profitable at a rate described by the slope of each line. Panels (b), (d), and (f) show scatter plots of the relationship between cost and threat according to the same model. Each point represents a discrete distance from the market. Panels (a) and (b) show a positive correlation between cost and threat according to the predictions of a deterministic, single-sector version of the model. Panels (c) and (d) show that the presence of multiple economic sectors can invalidate this assumption. Panels (e) and (f) show that the presence of ecological and economic variation further complicates the relationship. See the Supporting Information for further details of parameter values

to produce a simple positive correlation between costs and threats.

3.2 | Empirical analysis

We observed no apparent structure in the co-distribution of acquisition costs and land clearance rates in Queensland (Figure 3). Both sales price and land valuation were weakly negatively correlated with clearance rates (sales price, Figure 3a, Kendall's rank correlation $\tau = -0.14$, p = < .01, n = 7.620; land valuation; Figure 1b, $\tau = -0.02$. p = < .01, n = 104,273). There was also no correlation between agricultural profitability and the rate of land clearing (Figure S1, $\tau = \sim 0.00$, p = .16, n = 62,402). These results were consistent regardless of whether it was necessary to purchase entire parcels or if vegetated subsections could be purchased, and whether clearance rates were standardized by vegetation area or parcel area (Table S2). The relationship was unaffected by changes in land clearing policy (Figure S2, Table S2). These results were also generally consistent across all of Queensland's bioregions, with the exception of the Mulga Lands ($\tau = 0.20$, $p = \langle .01, n = 2,142 \rangle$ and South East Queensland ($\tau = 0.04$, p = < .01, n = 46,181), which were weakly positively correlated. Among parcels of similar size, the relationship became slightly positive (up to $\tau = 0.18$; Table S2). However, the relationship was still weak and highly variable (Figure S3).

Some portion of the observed variation appears to be driven by economic and ecological variation among parcels (Figure 3c and d). For example, we found that particular bioregions cluster at different locations along the cost axis (Figure 3c). As a consequence, parcels in two different bioregions that face the same level of threat can have very different acquisition costs. There appeared to be similar clustering with economic land use (Figure 3d), but to a lesser extent.

4 | DISCUSSION

Our results offer a counterpoint to the widespread assumption that costs and threats have a simple positive relationship in conservation landscapes. Instead, the relationship appears to be complex and highly variable. Both our theoretical and empirical results show how at least some of this variation appears to occur according to economic and ecological spatial heterogeneity. It is beyond the scope of this study to empirically determine whether economic and ecological variation itself is driving some of this variation, or whether processes that underlie or co-vary with this heterogeneity are responsible. However, it is clear that in Queensland, spatial variation in acquisition costs is being driven to a large extent by factors that are at least partially independent of the factors driving spatial patterns of vegetation clearing. These observations are consistent with those from the land economics literature,

in which it is well understood that the profitability of land is typically only one of many drivers of spatial patterns in landuse change, which can form complex interactions across spatial extents and scales (Cattarino et al., 2014; Ellis, Baerenklau, Marcos-Martínez, & Chávez, 2010). In Queensland, for example, farmers' decisions to clear vegetation are motivated not only by potential profits, but also a variety of other factors, such as the perceived attractiveness of native vegetation types (Seabrook, McAlpine, & Fensham, 2008).

There are several caveats to our analyses that require consideration. First, in some cases, the relationship became weakly positive among parcels of similar size (Table S2). One possible explanation for this is that parcels of similar size are likely to have similar land use types and ecological characteristics. For example, in Queensland, very large parcels are likely to be used predominantly for cattle grazing in semiarid regions. Nonetheless, even among parcels of similar size, the relationship was weak (up to $\tau = 0.18$) and highly variable (Figure S3). Furthermore, there is no reason to suspect that conservation organizations would be restricted to purchasing parcels of similar size. Second, Queensland is only a single case study; empirical findings might differ for other conservation regions. However, our empirical observations are consistent with our theoretical analysis, indicating that that these patterns are likely to apply to any conservation landscape containing economic and ecological variability. These results are of particular relevance to conservation planning, because the spatial extent of planning regions are often deliberately chosen to encompass ecologically diverse areas, both because the goal is to represent a comprehensive range of ecological features (Kukkala & Moilanen, 2013; Margules & Pressey, 2000), and because larger planning regions offer efficiencies of scale (McDonald, 2009). Third, we considered only one aspect of threats to biodiversity, that is, habitat clearance. Queensland's biodiversity is also threatened by a variety of other processes, such as pollution, climate change, and invasive species (Allek et al., 2018). However, these other measures of threat are less likely to be linked to land costs than land clearing. Finally, our analyses do not consider all types of conservation costs. Management costs, in particular, can dominate conservation expenditures in other contexts, such as in marine conservation, where acquisition costs are less relevant (Adams, Mills, Jupiter, & Pressey, 2011a; Hunt, 2013).

Our findings have several important implications for conservation prioritization and practice. The belief that costs and threats are strongly and positively correlated in conservation landscapes is still broadly held and stated in conservation science (Table S1). However, our results show that threats cannot be assumed to be a good proxy for conservation acquisition costs. Rather than simply using threats as a proxy for costs (e.g., Klein et al., 2008; Murdoch et al., 2010; Sala et al., 2002; Venegas-Li et al., 2018), future conservation planning exercises should measure costs independently, or

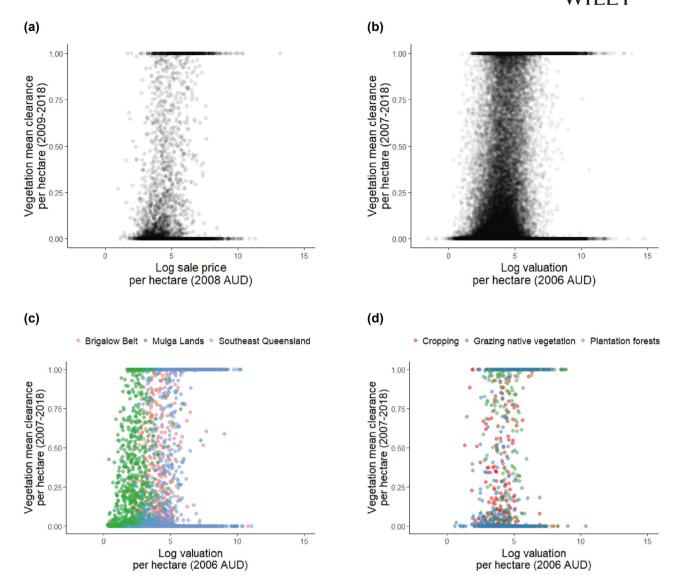


FIGURE 3 Scatter plots of the relationship between land sales and valuations, and rates of land clearing in Queensland. Panel (a) shows the log sale price of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2009 and mid-2018 on each parcel. Panel (b) shows the log unimproved land value of parcels per hectare of vegetation in relation to the mean proportion of each hectare of vegetation that was cleared between mid-2007 and mid-2018 on each parcel. Panel (c) shows log unimproved land values of parcels and rates of land clearing in three different bioregions: the Brigalow Belt (red), Mulga Lands (green), and Southeast Queensland (blue) bioregions. For this panel, a random subset of parcels within each bioregion was taken for visual clarity. Panel (d) shows log unimproved land values of parcels and rates of land clearing on land used predominantly for three different economic activities: cropping (red), grazing on native vegetation (blue), and plantation forests (green)

devise more sophisticated statistical models that explain the factors driving the spatial distribution of both costs and threats. Our results also show that most parcels experienced relatively low rates of land clearing, regardless of acquisition cost (Figure S4). As a result, any conservation plan that does not explicitly consider threat levels when prioritizing locations could be inadvertently biased toward low-threat, residual protected areas (Devillers et al., 2015; Joppa & Pfaff, 2009). Finally, our results show that landscapes are likely to contain a substantial number of highly cost-effective conservation opportunities. In Queensland in 2008, there was a large

amount of vegetation that faced large, imminent threats, but which could have been acquired at relatively low cost. Thus, conservation prioritizations that consider the actual relationship between threats and costs are likely to find a landscape full of relative bargains: locations facing serious threat from relatively unprofitable activities.

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REFERENCES

- Adams, V. M., Mills, M., Jupiter, S. D., & Pressey, R. L. (2011a). Improving social acceptability of marine protected area networks: A method for estimating opportunity costs to multiple gear types in both fished and currently unfished areas. *Biological Conservation*, 144, 350–361.
- Adams, V. M., Segan, D. B., & Pressey, R. L. (2011b). How much does it cost to expand a protected area system? Some critical determining factors and ranges of costs for Queensland. *PLoS One*, 6, e25447.
- Allek, A., Assis, A. S., Eiras, N., Amaral, T. P., Williams, B., Butt, N., ... Beyer, H. L. (2018). The threats endangering Australia's at-risk fauna. *Biological Conservation*, 222, 172–179.
- Armsworth, P. R. (2014). Inclusion of costs in conservation planning depends on limited datasets and hopeful assumptions. *Annals of the New York Academy of Sciences*, 1322, 61–76.
- Arponen, A., Cabeza, M., Eklund, J., Kujala H., & Lehtomäki, J. (2010). Costs of integrating economics and conservation planning. *Conservation Biology*, 24, 1198–1204.
- Australian Bureau of Statistics. (2017). Consumer price index: Concepts, sources and methods. Australian Bureau of Statistics, Canberra, Australia.
- Bode, M., Wilson, K. A., Brooks, T. M., Turner, W. R., Mittermeier, R. A., & McBride, M. F., ... Possingham, H. P. (2008). Cost-effective global conservation spending is robust to taxonomic group. Proceedings of the National Academy of Sciences of the United States of America, 105, 6498–6501.
- Boyd, J., Epanchin-Niell, R., & Siikamäki, J. (2015). Conservation planning: A review of return on investment analysis. *Review of Environmental Economics and Policy*, *9*, 23–42.
- Butsic, V., Lewis, D. J., & Radeloff, V. C. (2013). Reserve selection with land market feedbacks. *Journal of Environmental Management*, 114, 276–284.
- Carwardine, J., Wilson, K. A., Ceballos, G., Ehrlich, P. R., Naidoo, R., Iwamura, T., ... Possingham, H. P. (2008). Cost-effective priorities for global mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11446– 11450.
- Carwardine, J., Wilson, K. A., Hajkowicz, S. A., Smith, R. J., Klein, C. J., Watts, M., & Possingham, H. P. (2010). Conservation planning when costs are uncertain. *Conservation Biology*, 24, 1529–1537.
- Cattarino, L., McAlpine, C. A., & Rhodes, J. R. (2014). Land-use drivers of forest fragmentation vary with spatial scale: Scale-dependent drivers of fragmentation. Global Ecology and Biogeography, 23, 1215–1224.
- Costello, C., & Polasky, S. (2004). Dynamic reserve site selection. Resource and Energy Economics, 26, 157–174.

- Devillers, R., Pressey, R. L., Grech, A., Kittinger, J. N., Edgar, G. J., Ward, T., & Watson, R. (2015). Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25, 480– 504.
- Ellis, E. A., Baerenklau, K. A., Marcos-Martínez, R., & Chávez, E. (2010). Land use/land cover change dynamics and drivers in a low-grade marginal coffee growing region of Veracruz, Mexico. Agroforestry Systems, 80, 61–84.
- Hunt, C. (2013). Benefits and opportunity costs of Australia's Coral Sea marine protected area: A precautionary tale. *Marine Policy*, 39, 352– 360.
- Joppa, L. N., & Pfaff, A. (2009). High and far: Biases in the location of protected areas. PLoS One, 4, e8273.
- Klein, C. J., Chan, A., Kircher, L., Cundiff, A. J., Gardner, N., Hrovat, Y., ... Airamé, S. (2008). Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. *Conservation Biology*, 22, 691–700.
- Kukkala, A. S., & Moilanen, A. (2013). Core concepts of spatial prioritisation in systematic conservation planning. *Biological Review*, 88, 443–464.
- Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, 405, 243–253.
- Marinoni, O., Navarro Garcia, J., Marvanek, S., Prestwidge, D., Cliffordb, D., & Laredoa, L.A. (2012). Development of a system to produce maps of agricultural profit on a continental scale: An example for Australia. *Agricultural System*, 105, 33–45.
- McDonald, R. I. (2009). The promise and pitfalls of systematic conservation planning. Proceedings of the National Academy of Sciences of the United States of America, 106, 15101–15102.
- 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. *Conservation Letters*, 2, 240–241.
- Moore, J., Balmford, A., Allnutt, T., & Burgess, N. (2004). Integrating costs into conservation planning across Africa. *Biological Conserva*tion, 117, 343–350.
- Murdoch, W., Polasky, S., Wilson, K. A., Possingham, H.P., Kareiva, P., & Shaw, R. (2007). Maximizing return on investment in conservation. *Biological Conservation*, 139, 375–388.
- Murdoch, W., Ranganathan, J., Polasky, S., & Regetz, J. (2010). Using return on investment to maximize conservation effectiveness in Argentine grasslands. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 20855–20862.
- Naidoo, R., Balmford, A., Ferraro, P. J., Polasky, S., Ricketts, T. H., & Rouget, M. (2006). Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, 21, 681–687.
- Naidoo, R., & Iwamura, T. (2007). Global-scale mapping of economic benefits from agricultural lands: Implications for conservation priorities. *Biological Conservation*, 140, 40–49.
- Newburn, D., Reed, S., Berck, P., & Merenlender, A. (2005). Economics and land-use change in prioritizing private land conservation. *Con*servation Biology, 19, 1411–1420.
- NVIS Technical Working Group. (2017). *Australian vegetation attribute manual: National Vegetation Information System, Version 7.0.* Canberra, Australia: Department of the Environment and Energy.
- Pressey, R. L., & Taffs, K. H. (2001). Scheduling priority conservation action in production landscapes: Priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. *Biological Conservation*, 100, 345–376.

- Queensland Department of Science, Information Technology and Innovation. (2017). Land cover change in Queensland 2015–16: A Statewide Landcover and Trees Study report. Queensland Department of Science, Information Technology and Innovation, Brisbane.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., & Dayton, P.K. (2002). A general model for designing networks of marine reserves. *Science*, 298, 1991–1993.
- Seabrook, L., McAlpine, C., & Fensham, R. (2006). Cattle, crops and clearing: Regional drivers of landscape change in the Brigalow Belt, Queensland, Australia, 1840–2004. *Landscape and Urban Planning*, 78, 373–385.
- Seabrook, L., McAlpine, C., & Fensham, R. (2008). What influences farmers to keep trees? *Landscape and Urban Planning*, 84, 266–281.
- Strange, N., Rahbek, C., Jepsen, J. K., & Lund, M. P. (2006). Using farmland prices to evaluate cost-efficiency of national versus regional reserve selection in Denmark. *Biological Conservation*, 128, 455–466.
- Vanclay, F., & Lawrence, G. (1994). Farmer rationality and the adoption of environmentally sound practices; a critique of the assumptions of traditional agricultural extension. *European Journal of Agricultural Education and Extension*, 1, 59–90.
- Venegas-Li, R., Levin, N., Possingham, H., & Kark, S. (2018). 3D spatial conservation prioritisation: Accounting for depth in marine environments. *Methods in Ecology and Evolution*, 9, 773–784.

- 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. *Biological Conservation*, 143, 756–767.
- von Thünen, J. H. (1826). Der isolierte Staat in Beziehung auf Landwirtschaft und Nationalökonomie. Heidelberg, Germany: Jena, G. Fischer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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