

LETTER

Smart Protected Area Placement Decelerates Biodiversity Loss: A Representation-extinction Feedback Leads Rare Species to Extinction

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Aichi Target 11 and 12; biodiversity conservation; national parks; protected area effectiveness; Red-List species; systematic conservation planning; threatened plants.

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Abstract

Protected areas (PAs) spearhead global conservation efforts, but it has been repeatedly demonstrated that narrowly distributed species are more likely to be unrepresented in PAs. This means that where local extinctions are more likely outside PAs, a positive feedback loop could render PAs largely ineffective in decelerating extinctions, even where PAs effectively abate threats. Here we empirically test the elements of this feedback loop using distribution data for 1,572 threatened plants in Japan. Narrowly distributed species were indeed less likely to overlap PAs than widespread species, and local extinction rates for unprotected populations over 15 years were 1.5 times higher than those inside PAs. A simulation model showed that new PAs will substantially reduce extinction risk for widespread species, but not for narrowly distributed species, unless they are placed very precisely in the landscape. Our results suggest that a representation-extinction feedback will limit the effectiveness of PAs in preventing extinctions unless PA placement is carefully targeted.

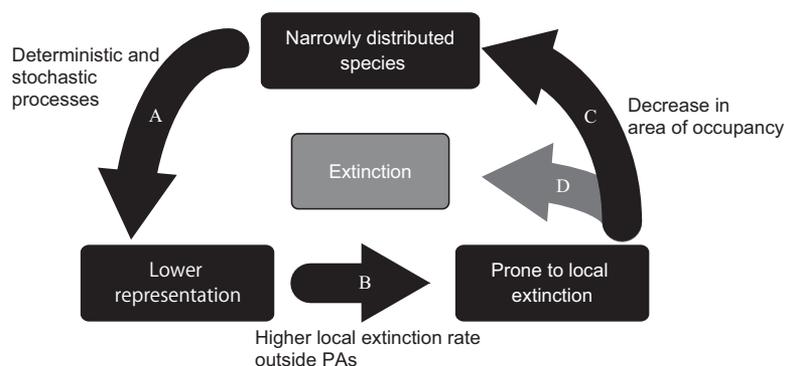
Introduction

Protected areas (PAs) spearhead global efforts to limit the impacts of human activity on biodiversity (Gaston *et al.* 2008; Watson *et al.* 2011; Jenkins *et al.* 2015). More than 200,000 marine and terrestrial PAs exist globally, covering more than 30 million km² (Deguignet *et al.* 2014). Analysis has repeatedly demonstrated that on the whole, PAs are effective in halting, or at least reducing, habitat loss and population decline (Bruner *et al.* 2001; Geldmann *et al.* 2013; Coetzee *et al.* 2014). Despite the clear overall success of PAs as a strategy to stem biodiversity decline, there is clear evidence of variation in the effectiveness of PAs themselves (Craigie *et al.* 2010; Leverington *et al.* 2010; Laurance *et al.* 2012), and poor placement of PAs means they often underrepresent

biodiversity (Pressey *et al.* 2002; Fuller *et al.* 2010; Venter *et al.* 2014), typically as a result of PA establishment being more likely in areas not suited to human land uses (e.g., areas of steep terrain or low fertility: Pressey *et al.* 2002; Joppa & Pfaff 2009).

Even where PAs are strategically placed in areas with high overall species richness, narrowly distributed species can be chronically underrepresented (Gove *et al.* 2008; Gruber *et al.* 2012). For example, Australian threatened species with a geographic range size below 10 km² are 11 times more likely to be completely unprotected than those with a range size above 1000 km² (Watson *et al.* 2011). As well as the obvious sampling effect (widespread species are highly likely to overlap PAs by chance), there is a pervasive issue that areas with high overall species richness do not correspond to areas of range size rarity

Figure 1 A representation-extinction feedback loop in which (A) narrowly distributed species are underrepresented in PA systems through nonstrategic PA location choices and stochastic effects, (B) underrepresented species suffer high rates of local extinction because of the low protection, and (C) the local extinctions further reduce the geographic range size of already narrowly distributed species, (D) eventually to extinction.



(Orme *et al.* 2005; Jenkins *et al.* 2013). On top of these deterministic processes, stochastic processes such as the mid-domain effect (Colwell *et al.* 2004) could cause narrowly distributed species to be underrepresented in PAs by chance alone. For example, where PAs are placed in a region randomly, the probability of an area within a region being covered by a PA is higher at the center than at the edge. In such a situation, species with wider distributions are more likely to overlap with the PA than narrowly distributed species because they too have a higher probability of occupying the central area.

In the light of these deterministic and stochastic processes that can bias PAs away from narrowly distributed species, we propose and empirically test a representation-extinction feedback loop in which narrowly distributed species are unrepresented in the PA system, become even narrower in distribution because of the poor protection, are consequently less likely to receive future protection, and suffer from spiraling extinction risk (Figure 1). This representation-extinction feedback could mean disproportionately grave extinction risk for narrowly distributed species without careful placement of PAs, even where those PAs are well managed.

Here we empirically test the elements of this feedback loop using comprehensive distribution data for 1,572 threatened plant species in Japan at two points in time. We determine whether (i) narrowly distributed species are underrepresented in PAs, (ii) local extinctions are more likely outside PAs than inside them, and (iii) random placement of new PAs will limit their benefit for narrowly distributed species.

Methods

Data

Distribution and persistence of threatened species

We focused on plant taxa (species, subspecies, and distinct varieties, hereafter species for ease of use) meeting the following criteria. First, we required that a species was

listed in the second edition of the Red List of Japan (Biodiversity Center of Japan; <http://www.biodic.go.jp/rdb/rdb.f.html>), which was based on extensive survey of more than 500 experts organized by the Japanese Society for Plant Systematics, and represents a wide consensus on the status of plants in 1994–1995 (Yahara *et al.* 1998). The second edition of the Red List provides a gridded database of species' distributions. Second, we selected all species categorized as Critically Endangered, Endangered or Vulnerable. Information on which to assess species as Near Threatened was only partially available, and the remaining species were Data Deficient. Finally, we required that the distribution of each species was confirmed and mapped in the spatial database accompanying the Red List. Species distributions were collected at the second order standard mesh system of Japan with a resolution of 5' in latitude and 7' 30" in longitude (approximately 10 km × 10 km in Japan), so we set the spatial unit of all subsequent analysis to these grid cells (hereafter 10-km grid cells). We regarded a distribution record of a species in a grid cell as representing a population. The final dataset comprised of 1,572 species distributed across 3,392 grid cells (21,619 populations in total). By comparing distribution maps for each species in the second edition of the Red List to those in the fourth edition (census conducted in 2010–2011; Ministry of Environment 2015a, 2015b), we identified all local extinctions from 10-km grid cells between 1994–1995 and 2010–2011 for each species.

Distribution of PAs

We compiled a spatial database of all PAs that strictly regulate land modification and/or collection of plants (The Nature Conservation Society of Japan 2013; see Appendix 1 for details of PA types). We mapped PAs using polygon boundary data from 2014, and because only a limited number of PAs were newly designated between 1994–1995 and 2010–2011, and historical boundary data for 1994–1995 were unavailable, we assumed the PA

system to be unchanged between the time periods. We dissolved all PA polygons to remove overlaps, and in the absence of a defensible threshold, conservatively treated all grid cells that partially or completely overlapped PAs as protected, and the remainder as unprotected (Rodrigues *et al.* 2004).

Data analyses

To determine whether narrowly distributed species are underrepresented in PAs, we modeled the relationship between the number of protected grid cells (response variable) and the number of occupied grid cells, hereafter area of occupancy (AOO) (explanatory variable), using segmented Poisson regression (Muggeo 2003). Where the slope of the relationship is steeper after the break point detected by the segmented regression, species with a larger AOO than the break point are better represented than the more narrowly distributed species. We employed a single break point because models with further break points did not converge. We also used linear Poisson regression, comparing Akaike information criteria (AIC) values (Burnham & Anderson 2002) among the segmented model, linear model, and a null model employing only the intercept.

To discover whether PA coverage is associated with a reduced extinction risk, we modeled local extinctions for each species in each grid cell between 1994–1995 and 2010–2011 using protection status of the grid cell (Prot), the AOO of a species in 1994–1995 (AOO), and their interaction using a generalized linear mixed model (GLMM). We used a logit link function and a binomial error distribution, and to account for the effect of species identity and of the environmental conditions in grid cells, we entered species ID (SID) and grid cell ID (GID) as random effects. The full model was thus:

$$\text{Logit}(\text{EX}_{ij}) = \beta_0 \text{AOO}_i + \beta_1 \text{Prot}_j + \beta_2 \text{AOO}_i \text{Prot}_j + \text{SID}_i + \text{GID}_j + \varepsilon_{ij}$$

where EX_{ij} indicates whether population of species i observed in 1994–1995 at grid cell j is extinct (1) in 2010–2011 or not (0); AOO_i is AOO of species i in 1994–1995; Prot_j is Prot of the grid j [i.e., unprotected (1) or protected (0)]; $\text{AOO}_i \text{Prot}_j$ is the interaction between AOO_i and Prot_j ; ε_{ij} is the error term; β_m is the coefficient of variable m . Starting with the full model, we built models in all cases using the best subset procedure (a total of five models), and based model selection on AIC (Burnham & Anderson 2002).

To determine whether the lower representation of narrowly distributed species was associated with a greater risk of local extinction, we modeled the relationship between number of extinct populations between 1994–

1995 and 2010–2011 (response variable) and the AOO in 1994–1995 (explanatory variable). We adopted the segmented and linear Poisson regression models described above.

Finally, we constructed a simulation based on the empirical data to examine whether the whole feedback process described in Figure 1 could limit the benefit of new PAs for narrowly distributed species when PAs are placed randomly. We simulated sequential random placement of PAs to a landscape of 68×68 grid cells, approximating the total number of grid cells in Japan, with no pre-existing PAs, and estimated the change in representation rate and expected time to species extinction for three virtual species, with AOO of $9 (= 3 \times 3)$, $81 (= 9 \times 9)$, and $529 (23 \times 23)$ grid cells, respectively. In the simulation, we placed an approximately equal area of PAs onto the landscape for 10 time steps in patches that matched the empirical Japanese data described above to the nearest square. Patches of PAs to be placed in each time step were generated by splitting the pool of PAs into 10 approximately equal area subsets randomly. Each time step in the model corresponded to 15 years, and we used the empirically estimated local extinction rate of 4.9% inside and 8.7% outside PAs in our model (see Results section for the local extinction rates). Although the real-world distributions of species and PAs have complex spatial structure (e.g., spatial autocorrelation), we did not account for this in our simulation because (i) its purpose is to generalize the consequence of any stochastic effect (i.e., mid-domain effect and/or sampling effect), and of the representation-extinction feedback beyond geographically and taxonomically dependent spatial patterns, and (ii) many narrowly distributed Japanese plants occur on islands disrupting a spatially structured simulation model. The procedure of the simulation is provided in Appendix 2.

In addition to the above simulation model sequentially placing PAs, we ran models without placing PAs to obtain a baseline to assess the benefit of PA placement, comparing median expected time to extinction with and without PA placement.

Results

Of the 1,572 threatened Japanese plants, 250 were not represented in any PAs. A mean of $52.3 \pm 36.9\%$ of the AOO of species in 1994–1995 was protected, although it must be borne in mind our definition of conserved grid cells was highly conservative, requiring only nonzero overlap between a PA and an occupied grid cell. Plant species with small AOO were systematically underrepresented in the PA system (Figure 2A). The most parsimonious model of the relationship between AOO

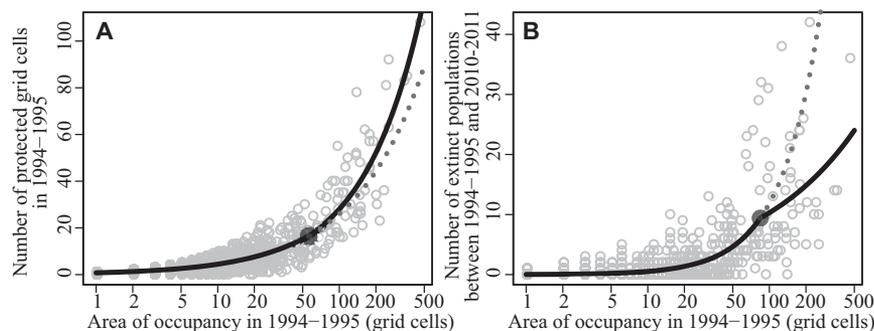


Figure 2 Change in the interspecific relationship between AOO in 1994–1995 and (A) coverage by PAs and (B) the number of local extinctions between 1994–1995 and 2010–2011. Solid lines indicate the relationships modeled by segmented regression and gray filled circles indicate the position of the breakpoint identified by the models. Dashed lines show the continuation of the relationship prior to the breakpoint.

Table 1 Parameter estimates and SE for segmented and linear Poisson regressions, explaining (A) the number of protected grid cells of each species by their AOO and (B) the number of extinct grid cells between 1994–1995 and 2010–2011 of each species by their AOO in 1994–1995. Models were ranked and arranged in order of increasing AIC

Parameters	Estimate	SE	z	P
(A) The number of protected grid cells (AIC of the null model = 17031.72)				
Segmented Poisson regression: AIC = 6574.67				
Intercept	−0.271	0.035	−7.699	0.000
AOO (before the breakpoint)	0.766	0.014	56.616	0.000
AOO (change in the estimate after the breakpoint)	0.129	0.039	3.284	NA
Linear Poisson regression: AIC = 6585.03				
Intercept	−0.345	0.028	−12.460	0.000
AOO	0.801	0.008	103.470	0.000
(B) Number of grid cells extinct in 2000–2012 (AIC of the null model = 7539.87)				
Segmented Poisson regression: AIC = 3173.54				
Intercept	−3.739	0.115	−32.570	0.000
AOO (before the breakpoint)	1.349	0.034	39.660	0.000
AOO (change in the estimate after the breakpoint)	−0.824	0.102	−8.070	NA
Linear Poisson regression: AIC = 3260.88				
Intercept	−3.150	0.078	−40.590	0.000
AOO	1.142	0.019	61.350	0.000

and the number of grid cells protected was the segmented model (Table 1), in which the slope was significantly steeper after a breakpoint at 56.1 grid cells (95% CI = 27.6–114.0; Figure 2A). This confirms that narrowly distributed species are underrepresented in the PA system as hypothesized in our feedback loop (process A in Figure 1).

Between 1994–1995 and 2010–2011, local extinctions occurred among 1,590 populations of 378 species, from a total pool of 21,619 populations of 1,572 species. These 1,590 local extinctions were distributed across 821 grid cells (225 protected, 596 unprotected), and 321 grid cells (76 protected, 243 unprotected) experienced local extinction of more than two species (mean \pm SD of the number of locally extinct species per grid cell; 1.66 ± 1.34 in protected cells, 2.04 ± 1.99 in unprotected cells). Species

with small AOO were disproportionately subject to local extinctions; the most parsimonious model relating the number of local extinctions to AOO was segmented (Table 1), with a significantly shallower slope after the breakpoint at 84.2 grid cells (95% CI = 68.1–104.2; Figure 2B).

Protection status and AOO in 1994–1995 were significant predictors of extinction from a grid cell between 1994–1995 and 2010–2011 (Table 2), consistent with step B in our hypothesized feedback loop that species with lower representation are more prone to local extinction (Figure 1). The overall probability of extinction from a grid cell was higher in unprotected grid cells (8.7%) than in protected grid cells (4.9%), and PAs thus decreased the chance of local extinctions of threatened species by approximately two-thirds (Table 2).

Table 2 Parameter estimates and SE for a GLMM explaining probability of local extinction of a species in a grid cell between 1994–1995 and 2010–2011 (1 = extinct, 0 = persisted) by protection status of the grid cell [Prot: unprotected (1) or protected (0) grid], AOO, and their interaction. Species and grid cell ID were included as random effects. Models were ranked and arranged in order of increasing AIC, and Δ is the difference in AIC from that of the best model. Estimates and SE of all models with $\Delta < 10$ are shown

Parameters	Estimate	SE	z	P
Prot + AOO; AIC = 9724.73 ($\Delta = 0.00$)				
Intercept	-4.615	0.197	-23.420	0.000
Prot	0.409	0.108	3.781	0.000
AOO	0.130	0.053	2.434	0.015
Prot + AOO + Prot \times AOO; AIC = 9726.72 ($\Delta = 1.98$)				
Intercept	-4.632	0.239	-19.353	0.000
Prot	0.437	0.253	1.728	0.084
AOO	0.135	0.066	2.056	0.040
Prot \times AOO	-0.008	0.062	-0.125	0.901
Prot; AIC = 9728.95 ($\Delta = 4.21$)				
Intercept	-4.264	0.128	-33.335	0.000
Prot	0.433	0.108	3.995	0.000

Simulation model results based on the relationship between the AOO and extinction probability revealed that the benefit of PAs was highly skewed toward species with the largest AOO. Median representation of virtual species with large (529 grid cells) and intermediate (81 grid cells) AOO increased over time when protected areas were randomly placed. Contrastingly, median representation of the virtual species with small AOO (nine grid cells) remained zero over the time steps, although the upper 95% CI overlapped 1 after time step 4 (Figure 3A). These differences in representation translated into a widening difference in time to extinction between narrowly and broadly distributed species (Figure 3B). Expected time to extinction increased over time for the species with large AOO but decreased for the species with small AOO species (Figure 3B). Likewise, PAs improved median of expected time to extinction by more than 1.5-fold and 1.3-fold from the baseline (i.e., expected time to extinction under no PA placement) at time step 10 for the species with large and intermediate AOO, respectively (Figure 3C). However, the benefit of placing PAs was limited to less than 1.1-fold for the species with small AOO, suggesting that the representation-extinction feedback loop is a real possibility unless PA placement is specifically targeted toward narrowly distributed species.

Discussion

Narrowly distributed species have long been targeted for conservation action because they are known to be

susceptible to extinction through stochastic events (Fontaine *et al.* 2007; Davidson *et al.* 2009, 2012). Indeed, the tendency for lower representation in narrowly distributed species has prompted gap analyses that have recommended increasing their coverage (Gove *et al.* 2008; Watson *et al.* 2011; Gruber *et al.* 2012). Here we have shown that nonstrategic location of PAs can lead to a representation-extinction feedback loop in which narrowly distributed species are underrepresented in the PA system, suffer local extinctions as a result, and become even more narrowly distributed compounding the effect (Figure 1).

We have shown that narrowly distributed threatened plants in Japan are underrepresented in the national PA system (Figure 2A). Further, local extinctions arising from this underrepresentation of narrowly distributed species can further limit the benefit of new PA placement and lead to a representation-extinction feedback in which narrowly distributed species slide to extinction despite increasing the overall protection of a landscape. This suggests that narrowly distributed species could be underrepresented whenever PA designation does not explicitly target them, leading to a representation-extinction feedback loop. We highlight an urgent need to ensure narrowly distributed species are explicitly represented when PA systems are expanded.

The tendency of narrowly distributed Japanese threatened plant species to be underrepresented in the PA system aligns with previous evaluations conducted in western Australia (Gove *et al.* 2008), continental Australia (Watson *et al.* 2011), and Europe (Gruber *et al.* 2012). In addition, a global gap analysis showed that threatened species, which often have smaller distributions than nonthreatened species, are more likely to be unprotected (Rodrigues *et al.* 2004). The pattern could arise from rapid extinctions of populations outside PAs and/or by biased or poorly targeted placement of PAs (Gaston *et al.* 2008). Indeed, our results suggest that both could operate concurrently. Although ad-hoc PA placement has been widely studied (Gove *et al.* 2008; Jackson *et al.* 2009; Watson *et al.* 2011), we have further demonstrated that a simple mid-domain effect can also generate this effect by chance.

The local extinction rate of populations in protected grid cells was about two-thirds (odds ratio = 1.50) of that in nonprotected grids (Table 2). This difference presumably arises from a combination of direct effectiveness of PA designation, and the bias in PA placement toward areas that are less threatened by land use (Pressey *et al.* 2002; Joppa & Pfaff 2009). However, the former seems likely to be the stronger effect in our case because (i) we used grid cell ID as a random effect to account for unmeasured influences arising from the conditions within each

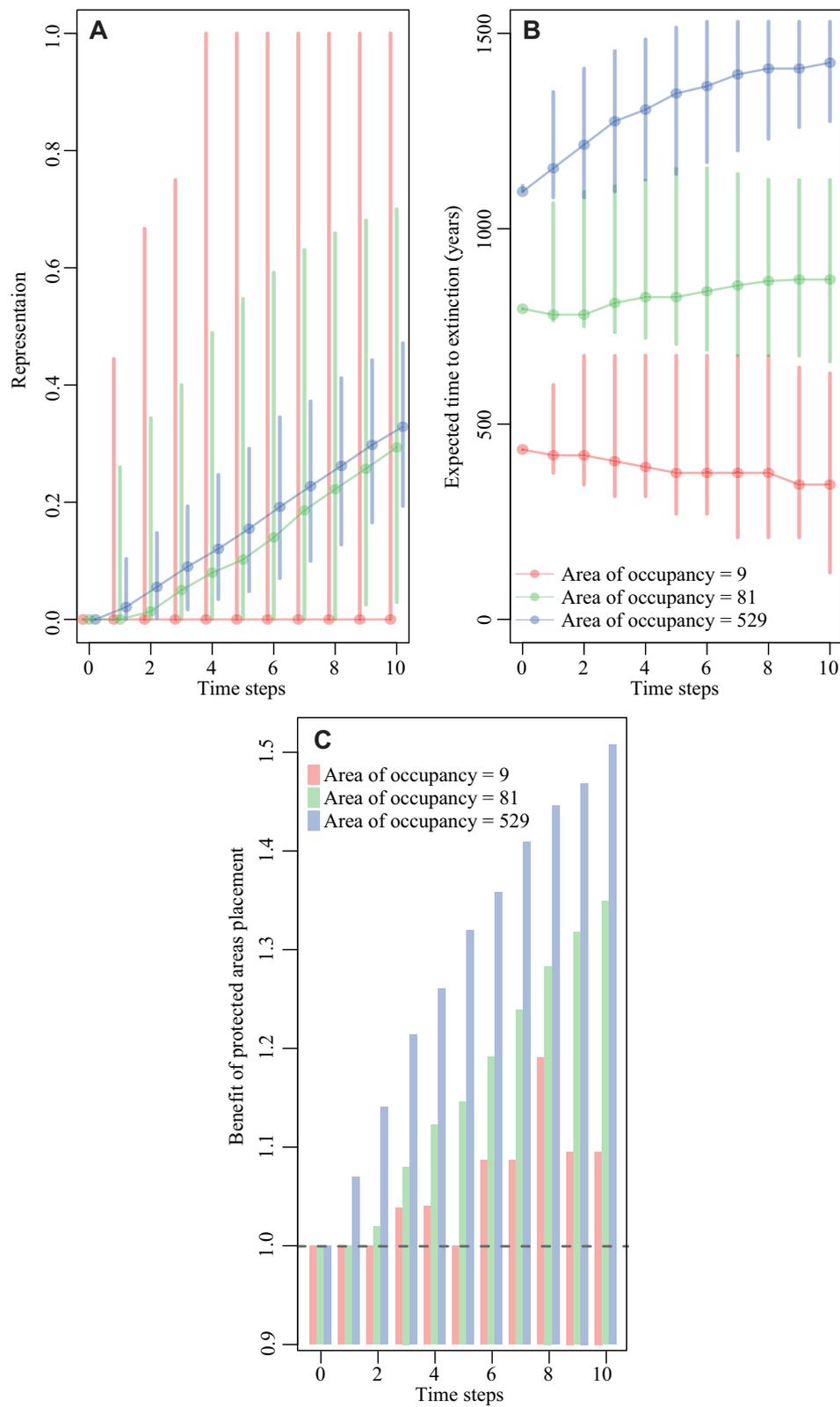


Figure 3 Change in conservation status of three virtual species over time by (A) representation in PAs, (B) expected time until extinction, and (C) benefit of PA placement. For (A) and (B), vertical bars indicate 95% CI and points indicate median of the simulation.

grid cell and (ii) the local extinction rate remained lower in protected grid cells ($5.2 \pm 0.27\%$; mean \pm SE) than in nonprotected grid cells ($8.8 \pm 0.25\%$) even if we confine the analysis to species occurring in both protected and nonprotected grid cells (884 species). It should be noted that the true effectiveness of PAs is likely to be higher than our estimate, as we conservatively regarded a grid cell only partially covered by a PA to be fully protected. This was because plant distribution data within the 10-km grid cells were unavailable. Moreover, the probability of local extinction was also positively related to the proportion of a grid cell protected (Appendix 3), suggesting PA coverage itself was an important factor.

To our knowledge, ours is the first study to measure the contribution of PAs to the persistence of plants at a national scale (but see Kadoya *et al.* 2014). However, it should be noted that local extinction rate was about 5% in 15 years even in the conserved grids, and although PAs do reduce the chance of local extinction, rapid declines are still occurring even in protected landscapes. It is possible that unmanaged threats still occur in PAs such as illegal collection, browsing by overabundant ungulates, and successional change (Gurevitch & Padilla 2004; Gove *et al.* 2008).

Perhaps surprisingly, AOO was positively related to the probability of local extinction at a population level (Table 2), although this effect was not apparent at the species level (Figure 2B). It is possible an extinction filter is operating, in which vulnerable populations of widely distributed species are currently declining, while many narrowly distributed species were already extinct prior to 1994–1995, and currently rare species are relatively stable.

We have demonstrated significant empirical support for a representation-extinction feedback in which narrowly distributed species are underrepresented in PA systems, leading to a higher risk of local extinction and further reductions in AOO. Strategic location of new PAs to explicitly account for this effect is paramount.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix 1. PA systems included in this study.

Appendix 2. Procedure for the simulation.

Appendix 3. Parameter estimates and SE for GLMM explaining probability of local extinction of a species in a grid between 1994–1995 and 2010–2011 by proportion of PAs in a grid, area of occupancy and their interaction.

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