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Progress in improving the protection of species and habitats in Australia

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ABSTRACT

Historically, protected areas were often designated using criteria other than biodiversity conservation as the primary objective. With the emergence of the science of systematic conservation planning, the designation of new protected areas is increasingly made with explicit conservation objectives in mind. However, assessments of the performance of protected area systems typically include all protected areas, regardless of when they were designated, potentially obscuring recent improvements in conservation planning decisions. Thus, it is often unclear to what extent systematic conservation planning principles have influenced the placement of new protected areas. Here, we compare recently designated protected areas in Australia with the protected area system that existed prior to the introduction of systematic conservation planning guidelines in 2000. We ask whether there is a difference between past and recent protection in terms of (i) the size and spatial distribution of protected areas, (ii) the characteristics of broad regions in which protection is concentrated, and (iii) the extent to which protected areas represent ecosystems and threatened species in comparison with selecting protected areas at random. We find that the protected area system was historically biased toward areas with steep slopes and low human populations. In contrast, recent protection is more likely to be allocated to regions with high human population and high numbers of threatened species; we show that this effect is not simply a result of biases in the places now available for conservation. Despite this successful realignment of practice, we find that the increase in protected area coverage in poorly protected regions has occurred more slowly than expected if protected area selections were fully guided by systematic conservation planning principles. Our results demonstrate rapid progress in improving Australia's protected area system in the last decade, and highlight the importance of separating recent from historical additions to the protected area system when measuring the performance of conservation decision-making.

1. Introduction

Protected areas are one of the most important tools for mitigating the decline of biodiversity (Bruner et al., 2001; Mulongoy and Chape, 2004; Watson et al., 2014). However, the placement of many protected areas has historically been biased toward areas not required for anthropogenic land uses such as logging, agriculture and human infrastructure (Pressey, 1994; Sellars, 1997), resulting in underprotection for many ecosystems (Fuller et al., 2010; Hoekstra et al., 2005; Pressey et al., 2002) and species (Brooks et al., 2004; Rodrigues et al., 2004).

Increasing the representation of all under-protected species and habitats is an important objective in protected area designation (Moilanen et al., 2009; Possingham et al., 2006; Watson et al., 2011). This is illustrated by its incorporation into many international strategies for reducing biodiversity loss (Mulongoy and Chape, 2004; Secretariat of the Convention on Biological Diversity, 2006), and its enshrinement in law in some countries such as Australia (Commonwealth of Australia, 1992). Systematic conservation planning is formulated to assist decision making for protecting biodiversity based on quantitative data such as distribution of species, conservation costs and landscape characteristics (Pressey and Bottrill, 2008). Consequently, one might expect recent additions to the protected area system to be less biased with respect to human land use requirements than protected areas designated before biodiversity protection was ensconced in policy. Despite this, previous evaluations of the performance of protected area systems and analyses of the biases inherent in their location tended not to distinguish historical designations from recent additions (*e.g.* Brooks et al., 2004; Coad et al., 2008; Jenkins and Joppa, 2009). Therefore it is unclear what progress has been made in translating the principles of systematic conservation planning into practice because any evaluation of protected area coverage is overwhelmingly influenced by historical decisions.

Australia is an ideal place to examine the impact of systematic conservation planning in practice. Early protected area designations in

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Australia were concentrated in areas of high esthetic value or low primary resource value (Mendel and Kirkpatrick, 2002). For example, protected area designation in 1950s and 1960s New South Wales was only given strong consideration if no other form of land use had been identified for an area (Pressey and Tully, 1994). Despite the protection of some globally important sites, such as the Great Barrier Reef and Kakadu National Park by the 1980s, the reserve system nationally was not protecting a representative sample of Australia's biodiversity (Pressey and Taffs, 2001; Watson et al., 2010). In response to this, in 2000 the Australian Government adopted a series of systematic conservation planning principles to guide further expansion of its National Reserve System (NRS). The key changes were to require that potential new protected areas are evaluated to assess the extent to which they would (i) increase comprehensiveness at a continental scale, (ii) add to the reservation of the full range of ecosystems, (iii) enable better representation of ecosystems across their geographic or environmental range, and (iv) increase the security of one or more ecosystems and associated species (Commonwealth of Australia, 1999). Over time the objectives of the NRS evolved to prioritise increasing protection in bioregions (large geographically distinct areas of land with common ecological characteristics) that have less than 10% protection (Commonwealth of Australia, 2009a; Department of Environment and Heritage, 2005) and specifically to protect threatened species (Department of Environment Water Heritage and the Arts, 2009). As such, we might expect the locations of recently designated protected areas to reflect these objectives. Here, we test whether this transfer of science into policy has delivered an improved terrestrial protected area system in Australia.

Since the current process for admitting new sites to Australia's NRS explicitly seeks to achieve ecosystem and threatened species representation, we reason that variables influencing the selection of new protected areas will differ from those operating before the guidelines were introduced. For example, protected areas designated since 2000 (when the NRS guidelines were introduced) might favor bioregions with little protection and areas with high numbers of threatened species, because these are explicit objectives of the new planning process. On the other hand, bioregions in which historical protection is concentrated (before 2000) might show traditional historic biases such as high elevations and steep slopes (Pressey et al., 2000; Scott et al., 2001; Joppa and Pfaff, 2009), be cheaper and less populated (Pressey, 1994), and less affected by clearing (Hoekstra et al., 2005; Pressey and Taffs, 2001).

Here, we compare recently designated protected areas in Australia with the protected area system existing prior to the introduction of systematic conservation planning principles into national legislation. We ask whether there is a difference between past and current protection in terms of (i) the size and spatial distribution of protected areas, (ii) the characteristics of bioregions in which protection is concentrated, and (iii) the extent to which protected areas represent ecosystems and threatened species in comparison with selecting reserves at random.

2. Methods

2.1. Protected area data

All officially designated protected areas are considered part of the National Reserve System (Department of Environment and Heritage, 2005). Priority areas for new protected areas are identified by the Australian government, which follow the systematic conservation principles outlined in the National Reserve System guidelines (Commonwealth of Australia, 1999). The acquisition of protected areas within these priority areas is implemented by the six states and two territories of Australia.

To compare the growth in protected areas under systematic conservation planning guidelines we compared the protected area system as it stood in 2000 with the new additions between 2000 and 2008. These years were chosen because the National Reserve System guidelines were introduced in 2000, and the following decade was a period of rapid expansion of the protected area system. Both protected area systems were obtained from the Collaborative Australia Protected Area Database, in which the source resolution is 1:250,000 and the minimum mapped area is 6.25 ha (CAPAD, 2000, 2008). From this we calculated the total area of the national protected area system in 2000 and 2008 as well as the total number and average size of protected areas in these years.

We compared protected area coverage across (i) major vegetation types and (ii) bioregions. We used the 23 major vegetation groups identified in the National Vegetation Information System (NVIS), based on structure, growth form and floristic composition of the dominant stratum of each vegetation type, with the scale of source maps typically 1:250,000, rasterized to a 100 m raster; (Department of Environment and Water Resources, 2007). For the regional analysis we used bioregions identified in Australia by the Interim Biogeographic Regionalisation (IBRA version 6.1). There are 85 bioregions in Australia, each comprising large contiguous areas of land that share pattern and composition with respect to climate, substrate, landform, vegetation and fauna. This is a vector dataset, derived from source maps typically produced at a scale of 1:250,000 (Commonwealth of Australia, 2009a). Major vegetation types and bioregions were overlaid with protected area coverage in 2000 and 2008 and the increase in protection was assessed for each in relation to their coverage in 2000.

2.2. Assessing bias in the location of protected areas

We used the 85 IBRA bioregions (version 6.1) as the spatial units for assessing environmental biases in past and recent protected area designations. Bioregions were chosen because in Australia these are used for decisions about protected area priorities and to report the status of ecosystems and their protection (Commonwealth of Australia, 2009a; Department of Environment Water Heritage and the Arts, 2009).

We chose five predictor variables within each bioregion to reflect some of the well-known historical biases in protected area placement: human population size, land cost, topographic heterogeneity (standard deviation of elevation), slope and proportion of habitat cleared. Human population size for each bioregion was obtained from the 2006 Australian census (Australian Bureau of Statistics, 2006). Land cost was the price per km^2 of acquiring all remnant vegetation in the bioregion. This was based on unimproved land value in 2006 sourced from state land valuation offices in Australia (see Carwardine et al., 2008 for further information). Topographic heterogeneity and slope data were obtained from the Global Map Elevation project (Australia), with source maps typically at a scale 1:250,000, rasterized to a 9 s (~250 m) raster (Geosciences Australia, 2006). All the regional data layers were combined into a single raster dataset by using mosaic function of ArcGIS 10, after appropriately eliminating the sea surface. Topographic heterogeneity was calculated by using the standard deviation of elevation among all pixels occurring within each bioregion. The degree of slope (0–90) was calculated using the function slope in ArcGIS 10. The average slope (0–90°) of a bioregion was used as the measure of slope steepness. The proportion of natural vegetation cleared since 1750 within each bioregion was obtained from the NVIS database (NVIS, 2001).

We derived three variables reflecting the stated objectives of the NRS within each bioregion, (i) initial protection, which was the percentage of each bioregion that was protected in 2000, (ii) whether the 10% protection target was achieved, which was whether 10% or more of the bioregion's area was protected in 2000, and (iii) threatened species richness, which was how many threatened species had a distribution that overlapped each bioregion. Maps of the geographic distributions of threatened species listed under the Environmental Protection and Biodiversity Conservation Act were obtained from the Species of National Environmental Significance database in polygon format (Commonwealth of Australia, 2008). A wide range of methods including direct plotting of records, habitat-based surrogates, digitising existing maps, and statistical modeling was used to produce the species distribution maps, and generally these maps represent area of occupancy rather than extent of occurrence (*sensu* Gaston and Fuller, 2009). We considered only polygons that were identified as having known or likely species occurrences and removed from the analysis polygons where species "may occur." At the time of this study 1700 species were listed on the database. We excluded 270 species that inhabit marine or freshwater environments and species for which range estimates were uncertain (see Watson et al., 2010 for further details), and counted how many of the remaining 1320 species had distributions that intersected each bioregion.

Because the upper bound of the degree of protection within a bioregion is constrained by the area of native vegetation remaining, we included the area available for protection (km^2) present within the bioregion as a covariate. The distribution of this remnant vegetation was obtained from the National Vegetation Information System database (NVIS, 2001).

2.3. Data analysis

We used multivariate regression to investigate predictors of protected area coverage in 2000 ("past protection"), 2008 ("current protection") and protected areas dedicated between the years of 2000 and 2008 ("protection increase"). Protection increase was log $(x + 1)$ transformed while current and past protection were $x^{1/4}$ transformed to normalise the response variables. Transformation of past protection did not remove three statistical outliers. However Cook's distance was $D_i < 1$ and removal of the outliers did not change the results of our analysis so they were left in given that they represented real data. All continuous predictor variables were transformed to normalise them as follows: Mean land cost, area available for reservation, human population size and threatened species richness were log transformed, while proportion of habitat cleared was log $(x + 1)$ transformed. Initial protection, topographic heterogeneity and mean slope were $x^{1/4}$ transformed. The type of transformation was chosen in each case based on the type of data and the best resulting fit with a normal distribution.

Collinearity between continuous variables may cause unstable estimates for the parameters in a regression model (Mac Nally, 2000). Three predictor variables—the human population size in a bioregion (POP), threatened species richness within a bioregion (TS) and the mean land cost within a bioregion (CO)—were strongly correlated with each other (TS and POP; $r = 0.78$, TS and CO; $r = 0.77$, POP and CO; $r = 0.83$). The proportion of cleared habitat within a bioregion was positively correlated with the threatened species richness within a bioregion ($r = 0.66$) and human population size in a bioregion ($r = 0.59$). The average slope within a bioregion (degrees) and the topographic heterogeneity within a bioregion were also strongly positively correlated ($r = 0.80$). Despite these high correlations, all variables were left in the model and hierarchical partitioning alongside the model selection procedure was used to identify which variable had the most influence on the different response variables (Chevan and Sutherland, 1991; Mac Nally, 1996). Interpretations of results were based largely on the hierarchical partitioning component and then backed up by the regression models where there was no correlation. Both the model selection and hierarchical partitioning procedures were carried out using a Gaussian error distribution with the transformed data.

All predictor variables were chosen because of their suspected influence on the distribution of protected areas, determined either from other studies on historic biases in protected area placement or from systematic principles guiding the acquisition of protected areas in Australia. We therefore had no *a priori* reason to select some combinations of predictors over others. We thus constructed models for past protection, current protection and protection increase based on all possible combinations of the main effects of the predictor variables, and ranked them according to Akaike's Information Criterion (AIC; Akaike, 1979; Bozdogan, 1987; Johnson and Omland, 2004). Table 1 lists the predictor variables included in models for past and current levels of protection, and the degree of change between the two.

We evaluated models based on AIC using stepwise selection in R version 2.7.1. For each of the possible models for all protection types we also calculated the model likelihood value (AIC weight; wAIC) to rank the models in order from best fit to worst fit. We then used hierarchical partitioning to quantify the independent contribution of each predictor variable to the response variable (Quinn and Keough, 2002) and thus identify the most important effects within the models (Mac Nally, 2002). We used the package hier.part (Walsh and Mac Nally, 2008) in R version 2.7.1, employing r^2 as the goodness-of-fit measure.

2.4. Comparison with unbiased growth in protected area system

We constructed a null model to simulate random expansion of the protected area system between 2000 and 2008 as a baseline against which to compare the recent expansion in protected areas. We overlaid a grid of 10×10 km cells onto bioregions and remnant vegetation to create a set of planning units. We then overlaid these planning units onto protected area coverage in 2000 and removed any planning units that overlapped with protection in 2000. This left us with 83,906 planning units with an average size of 78.98 km^2 available for selection. Selectable planning units equal to the amount of area protected between the years 2000 and 2008 were then randomly drawn 50 times to create a benchmark randomization with which to compare the real protected area increase. We compared three performance measures for the randomised and observed increase in protection.

2.4.1. Performance measure 1: protection of underrepresented bioregions

A commonly used target for the protection of a bioregion in Australia is 10% coverage by protected areas, so we used this same threshold as a means to identify under-represented bioregions. To first compare the effect of real protection increases we calculated the number of bioregions that were protected at or above 10% in 2000 and then between the years of 2000 and 2008. We then overlaid the randomly created protected area systems across bioregions and calculated the number

Table 1
Predictor variables included in each model for explaining patterns in protected area coverage. Past protection is the total area protected (km^2) within each bioregion in 2000, prior to the introduction of the National Reserve System guidelines. Current protection is the total area protected (km^2) per bioregion in 2008, which includes past protection and protection increases between 2000 and 2008. Protection increase is the area newly protected between 2000 and 2008.

Response variable	Predictor (units)	Influence
Past protection	Area available for protection (km^2)	Covariate
Area protected in 2000 per bioregion	Proportion of habitat cleared (%)	Historic bias
	Mean land cost ($/km)	
	Human population size (count)	
	Topographic heterogeneity (SD of elevation)	
	Mean slope (degrees)	
	Threatened species richness (count)	Systematic conservation planning influence
Current protection	In addition to above:	Systematic conservation planning influence
Area protected in 2008 per bioregion	10% reservation target met? (binary)	
Protection increase	In addition to above:	Systematic conservation planning influence
Increase in area protected from 2000 to 2008 per bioregion	Initial protection (% of bioregion protected in 2000)	

of bioregions that would be protected at or above 10% if planning unit selection had occurred randomly.

2.4.2. Performance measure 2: protection of broad vegetation types

We compared real increases in protection of broad vegetation types with our random null model by overlaying the randomly created protected area system onto the 23 NVIS major vegetation types.

2.4.3. Performance measure 3: protection of threatened species

The number of threatened species protected by the NRS was calculated by overlaying protected area coverage for 2000 and 2008 across the ranges of the 1320 threatened species. Following Rodrigues et al. (2004) gap species were identified as those species occurring entirely outside protected areas (none of their range overlapped with a protected area). The percentage of all gap species and gap taxa were calculated nationally for both years. Randomised protection increase was overlaid with the distribution of gap species not covered by any protected areas in 2000. Gap species from 2000, which also had no part of their range covered by the randomised protection increases were considered gap species for the randomised solutions.

3. Results

Between 2000 and 2008, protected areas increased rapidly in number, but the new sites were much smaller in area than those comprising the system in 2000. A total of 4212 protected areas was added, representing an increase in the area of Australia under protection of more than 50% from 617,386 km^2 to 984,871 km^2 (Table 2). The number of protected areas almost doubled in this period, and the average size of sites decreased from 119 km^2 to 105 km^2. The median size of protected areas decreased from 0.92 km^2 to 0.88 km^2 (Table 2). While several large protected areas were designated in central Australia, the majority of new protected areas were small (Fig. 1).

Of the 23 major vegetation types, the three most extensively covered by protected areas in 2000 were heathlands, eucalypt low open forests, and rainforests and vine thickets, and the largest protected area increases occurred for the latter two of these (Fig. 2). However, new protection occurred across 15 of the 23 major vegetation types, with no obvious tendency for greater proportional increases in initially poorly protected types (Fig. 2). Similarly, new protected areas were not preferentially allocated to bioregions with low levels of protection in 2000, although the highest percentage of protection was in a bioregion with less than 5% protection in 2000 (Appendix A). Many bioregions with less than 10% protection received small increases in protection between 2000 and 2008 (Appendix A).

3.1. Changing biases in protected area placement

In 2000, protection was greater in bioregions characterised by high mean slopes, low human population size, greater threatened species richness and less area available for protection (Table 3a). The top three models had a combined weight of 0.62, and the 95% model set contained nine models (Table 3). Hierarchical partitioning showed that area available for protection, mean slope, human population size, threatened species richness and topographic heterogeneity all contributed over 10% of the variation explained by the full model (Fig. 3a). These variables, other than topographic heterogeneity, were also included in the best fitting model (Table 3a). Mean slope explained almost 35% of the variance in the full model, followed by area available for protection, which explained close to 25% (Fig. 3a).

Like protection in 2000, coverage of bioregions as the protected area system stood in 2008 was greater in bioregions with high mean slopes, low human population size, higher threatened species richness and a smaller area available for protection (Table 3b). The top three models again had a combined weight of 0.62 and the 95% model set contained nine models (Table 3b). Area available for protection and human population size were present in all nine of these models. Hierarchical partitioning showed that the area available for protection explained over 55% of the variation explained by the full model (Fig. 3b). Threatened species richness, proportion of habitat cleared, human population size and mean slope all contributed almost 10% to the variance (Fig. 3b), and these variables appeared in the best fitting model (Table 3b). Whether the target of 10% protection was met, which was selected as part of the second and third models for best fit, contributed the least to the variance explained by the full model (Fig. 3b).

The predictors of protection increase within a bioregion differed from those for past and current protection. Threatened species richness and human population size were both strong positive predictors of protection increases (Table 3c), which for the latter variable was in contrast to its negative relationship with overall protection in 2000 and 2008. Hierarchical partitioning revealed that threatened species richness, area available for protection and human population size contributed the most to the variation explained by the full model (Fig. 3c). Of these, threatened species richness explained over 35% of the variation while human population size and area available for protection both contributed over 20% of the variation. The model containing these three variables had the second highest Akaike weight (Table 3c). Initial protection, mean land cost and whether the target of 10% protection was met, contributed the least to the variation explained by the full model. The bias in protection associated with high mean slope had all but disappeared (Fig. 3c).

3.2. Comparison with unbiased growth in protected area system

The number of bioregions exceeding the stated national target of 10% protection increased from 36 to 48 (of 85 bioregions) between 2000 and 2008 (Appendix A). This outperformed the null expectation if protected areas were placed at random (increase from 36 to 45), indicating that new protection was targeting some bioregions that had not yet met the reservation target, and that the placement of new protected areas was not simply being driven by the locations of intact habitat available for reservation.

Observed protection increases were biased toward a small number of broad vegetation types such that for the majority of vegetation types, observed protection was lower than that achieved by random allocation (Fig. 2). Tussock grass, which was the least protected in 2000, doubled with random increases from 2.74% to 5.85% (Fig. 2). This was in comparison to real protection, which only increased protection of tussock grass to 3.07% (Fig. 2).

Protection increases between the years of 2000 and 2008 reduced the number of gap species by 52, an effect driven almost entirely by the protection of plant species not previously in the reserve system

Table 2
Changing protected areas in Australia. The area, number and median and average size of protected areas is shown for (i) the year 2000 prior to the introduction of the National Reserve System guidelines, (ii) the entire protected area system as it stood in 2008, and (iii) new protected areas added between 2000 and 2008.

	Protected area system in 2000	Protected area system in 2008	New protected areas
Total area (km^2)	614,386	984,871	370,485
Number of sites	5128	9340	4212
Median size (km^2)	0.92	0.88	0.87
Average size (km^2)	119	105	87

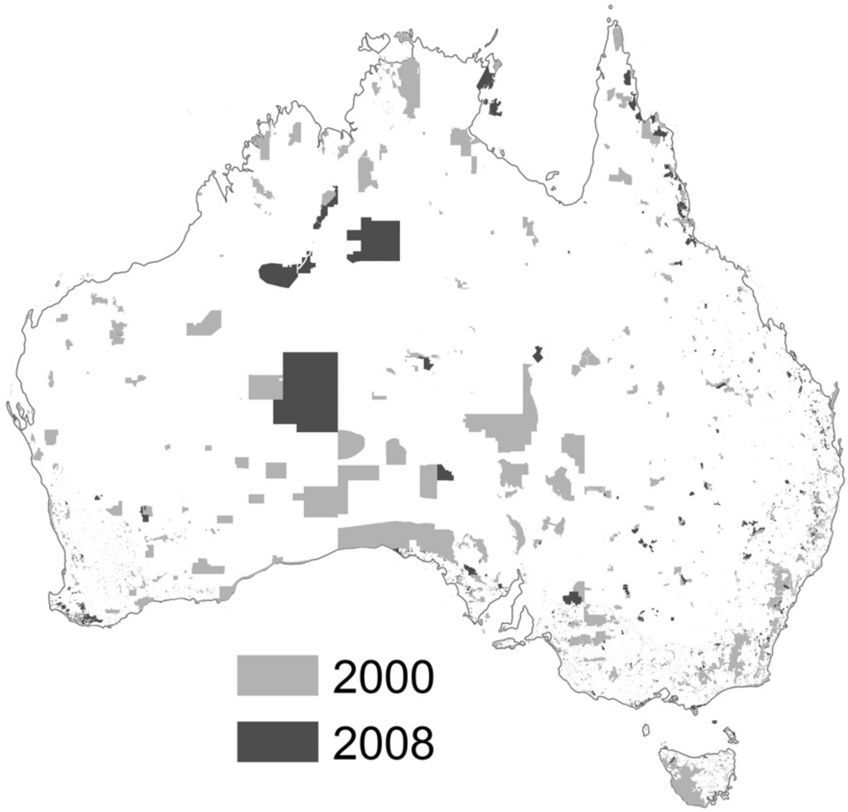

Fig. 1. Coverage by all gazetted IUCN I-VI protected areas in Australia in 2000 and 2008. Light gray depicts protected areas in 2000 and dark gray depicts protected areas gazetted between the years of 2000 and 2008.

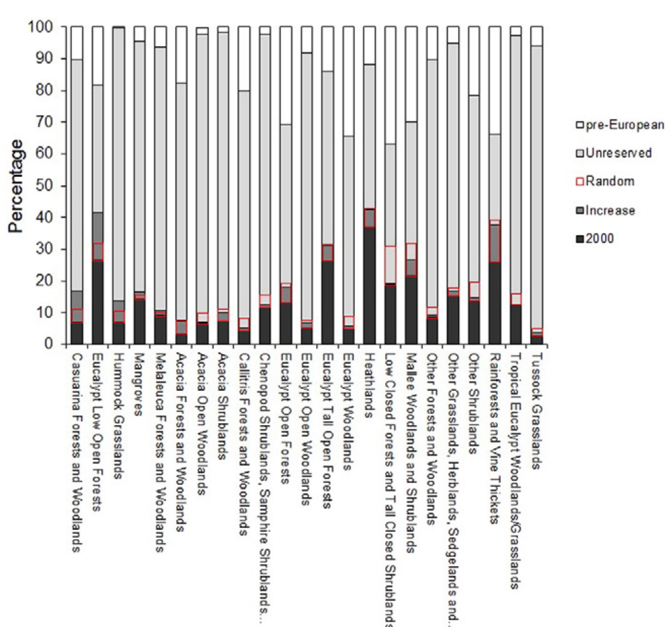

Fig. 2. Protection of remaining vegetation for 23 major vegetation types in Australia. The black shading indicates protection in 2000, the dark gray shading indicates increases in protection between the years 2000 and 2008, while the red outline indicates the mean value for 50 randomised protection increases. Light gray indicates the area not within a protected area at 2008, and white shading indicates the portion of the vegetation type that has been cleared since European settlement, and is therefore not available for reservation (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

(Table 4). In contrast, random allocation of new protection reduced the number of gap species by only 38, substantially lower than the actual achievement (Table 4).

3.3. Discussion

Our data show that newly protected areas in Australia are being increasingly placed in human dominated landscapes, and that appraisals of the overall performance of the current reserve system will not pick up this recent change in how protection is allocated. In the past, regions with protected areas were characterised by steep slopes, high topographic heterogeneity and low human population size — biases known to influence historic area selection in Australia and globally (Pressey and Tully, 1994; Joppa and Pfaff, 2009; Watson et al., 2009). In contrast, these variables were not important predictors for bioregions where recent protection increases have occurred. Rather, new acquisitions were concentrated in bioregions with large numbers of threatened species, one of the key objectives of the NRS (Department of Environment Water Heritage and the Arts, 2009). The biases associated with slope and topographic heterogeneity are almost absent in new protected area designations, and the pattern of new protected area designation is markedly different from random allocation, suggesting that it does not arise simply because of a constraint on where reserves could be placed. Because the recent additions are a relatively small change to a large existing reserve system, current protected area coverage, when viewed in its entirety, was much more closely aligned with past protection than it was with the recent protection increases. This highlights how a focus on measuring the performance of protected area systems against explicit criteria can be potentially misleading if analyses are conducted over long time frames that include historic protected areas.

Systematic conservation planning often aims to achieve ecosystem representation as well as threatened species protection, yet the trade-

Table 3
Predictors of protected area coverage by bioregion for (a) all protected areas designated by 2000, (b) all protected areas designated by 2008 and (c) new protected areas designated between 2000 and 2008. Within each time period all models comprising the 95% set with a cumulative Akaike weight > 0.95 are listed. Parameter estimates are listed under each predictor that was included within that model, with standard error included in brackets.

Time period	Area available for protection	Threatened species richness	Human population size	Mean slope	Proportion of habitat cleared	Topographic heterogeneity	Mean land cost	10% target met?	AIC	wAIC
(a) 2000	−1.367 (0.657)	2.097 (1.261)	−1.580 (0.457)	18.793 (5.744)				N/A	154.1	0.333
	−1.641 (0.722)	2.520 (1.037)	−1.525 (0.461)	18.219 (5.784)	−0.370 (0.402)			N/A	155.2	0.164
	−1.058 (0.857)		−1.608 (0.461)	24.570 (11.757)		0.679 (1.204)		N/A	155.76	0.124
	−2.633 (0.562)	3.151 (0.932)	−1.490 (0.482)					N/A	156.58	0.110
	−1.277 (0.883)	3.037 (1.021)	−1.554 (0.464)	25.611 (11.799)	−0.417 (0.409)	0.877 (1.219)		N/A	156.64	0.066
		2.820 (1.017)	−1.588 (0.467)	38.086 (8.103)	−0.273 (0.399)	1.886 (1.007)		N/A	156.89	0.070
	−1.648 (0.743)	2.929 (1.014)	−1.523 (0.465)	18.190 (5.859)	−0.370 (0.405)		0.010 (0.235)	N/A	157.2	0.040
	−1.068 (0.867)	2.559 (0.914)		24.626 (11.843)		0.694 (1.22)	0.025 (0.237)	N/A	157.75	0.038
(b) 2008	−3.987 (0.681)	1.901 (0.935)	−1.1738 (0.474)	12.650 (5.958)					158.34	0.386
	−4.451 (0.711)	1.879 (0.919)	−1.130 (0.467)	14.209 (5.912)				1.101 (0.567)	160.3	0.124
	−4.623 (0.720)		−0.426 (0.319)	16.791 (5.888)				1.118 (0.578)	160.71	0.118
	−3.624 (0.746)	2.446 (1.041)	−1.100 (0.476)	11.891 (5.978)	−0.489 (0.416)				160.83	0.095
	−4.044 (0.816)	2.362 (1.032)	−1.056 (0.474)	13.216 (6.052)	−0.442 (0.413)		0.068 (0.246)	1.023(0.588)	161.02	0.057
	−4.846 (0.918)	1.933 (0.930)	−1.162 (0.473)	22.905 (12.047)		−1.063 (1.242)	0.090 (0.249)	1.036 (0.590)	161.47	0.046
	−4.179 (0.909)	2.608 (1.052)	−1.145 (0.478)	23.166 (12.148)	−0.561 (0.421)	−1.338 (1.255)			161.6	0.053
	−4.548 (0.947)	2.521 (1.043)	−1.096 (0.475)	24.168 (12.051)	−0.515 (0.418)	−1.319 (1.255)	0.103 (0.248)	0.979 (0.590)	161.79	0.039
	−3.287 (0.660)	2.503 (1.057)	−1.004 (0.477)		−0.438 (0.422)	−0.900 (0.626)		0.998 (0.579)	162.29	0.038
(c) New areas	0.757 (0.260)	1.316 (0.275)							32.016	0.270
	0.794 (0.261)	0.917 (0.433)	0.267 (0.224)						32.538	0.188
	0.831 (0.274)	1.338 (0.277)						0.234 (0.272)	33.244	0.132
	0.876 (0.275)	0.923 (0.433)	0.279 (0.224)					0.252 (0.271)	33.622	0.096
	0.915 (0.324)	0.857 (0.445)	0.259 (0.225)	1.794 (2.836)					34.114	0.075
	1.003 (0.344)	1.244 (0.300)		2.372 (2.865)				0.265 (0.275)	34.519	0.061
	1.033 (0.344)	0.850 (0.445)	0.270 (0.225)	2.192 (2.861)				0.281 (0.274)	34.993	0.057
	1.189 (0.421)	0.894 (0.446)	0.233 (0.226)	6.943 (5.778)		−0.605 (0.591)			34.996	0.041
	0.790 (0.266)		0.634 (0.145)						35.114	0.041

off between the two objectives can make it difficult to achieve both simultaneously (Venter et al., 2014). Indeed, we have shown that while threatened species coverage has improved since 2000, bioregional representation has been slower to expand. Perhaps surprisingly, the level of protection in a bioregion in the year 2000 had little influence on the degree of protected area increases over the subsequent eight years. We expected that bioregions with low initial protection, or at least those with protection below 10%, would be targeted for new protection. However, we found no clear relationship between the amount of initial protection within a bioregion and the protection increase for that bioregion. Nor did we find that bioregions with initial protection below 10% received more protection after 2000. Protection increases between 2000 and 2008 occurred in only three more bioregions to a level above 10% than a randomised protection increase. Likewise, new protection since 2000 did not favor those broad vegetation types that were least well protected in 2000 and instead has been concentrated in two of the most well protected vegetation types; eucalypt low open forests and rainforests. Tussock grasslands, like many other grasslands throughout the world (Hoekstra et al., 2005), continue to have the lowest level of protection of all Australia's ecosystems. This is despite many tussock grass species being listed as nationally threatened in Australia (Commonwealth of Australia, 2009b). Poor representation of bioregions is not limited to terrestrial conservation in Australia, with a recent analysis of marine protected areas in Australia showing poor representation of marine bioregions (Barr and Possingham, 2013).

Biases in past protected area designations may mean that achieving protection targets such as increasing representation of underrepresented bioregions is now much more difficult. Past biases in the location of protected areas away from flat, productive landscapes (Pressey and Tully, 1994; Scott et al., 2001; Joppa and Pfaff, 2009) left many of the

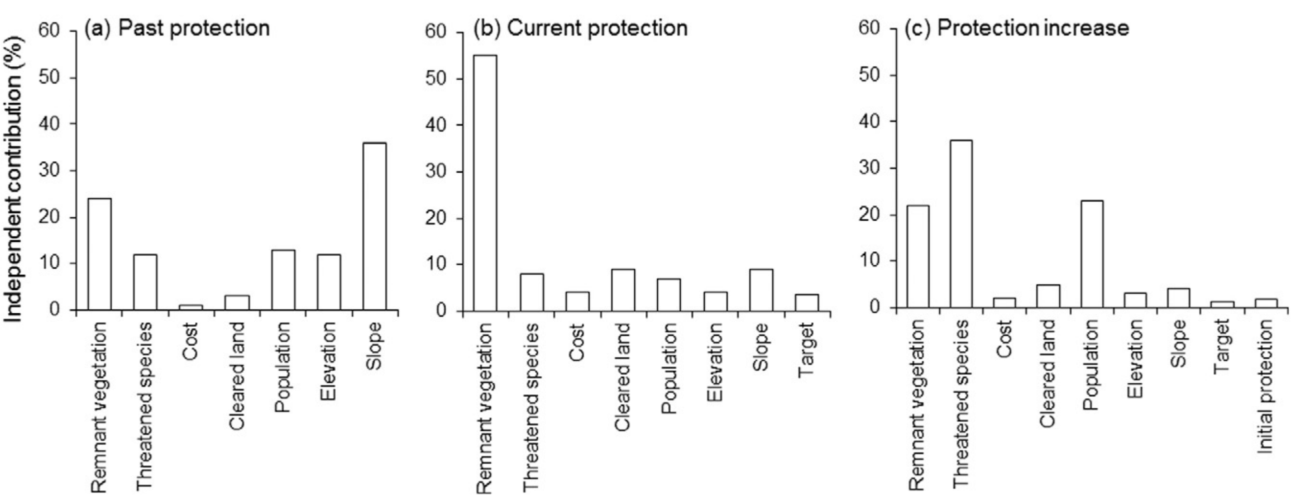

Fig. 3. Independent contribution of each variable to model fit for protected area coverage across bioregions in a) past protection, b) current protection and c) protection increase, as determined by hierarchical partitioning.

Table 4
Gap species falling outside the protected area system. Number of threatened gap species in 2000 and 2008 in comparison with the expectation if protection was spread randomly among bioregions.

Taxa	Total species	Number of gap species		
		2000	2008	Random
All	1320	213	161	175
Amphibians	24	1	0	0
Birds	55	4	4	2
Mammals	55	4	4	3
Reptiles	23	4	4	3
Vascular plants	1163	200	149	167

most productive lands open to intense human use (Hansen and Rotella, 2002; Pressey et al., 2000; Seabloom et al., 2002). This now makes it more difficult to acquire protected areas in those regions. For example, five of Australia's 85 bioregions cannot reach 10% protection without extensive revegetation because the natural vegetation has been so extensively cleared (Commonwealth of Australia, 2009a). Although this could be part of the reason why protected areas did not increase in some poorly conserved bioregions, this is not often the case, since the randomised protection increase for all but five broad vegetation types was higher than the observed increase, indicating that there is habitat still available for protection in these areas. However while the remnant vegetation may still be present, it may not be available for acquisition or inclusion into the National Reserve System because it occurs only on private land (Natural Resource Management Ministerial Council, 2004). As we did not include availability for purchase or land tenure into our analysis we were unable to assess if this is the case, but it would be an interesting avenue for further research. Indeed, many areas of high importance now occur on private land (*e.g.*, the majority of grasslands (Zimmer et al., 2010)), although these might often expensive to purchase, or not available for acquisition or covenanting (Commonwealth of Australia, 2009a). Additionally some habitats may not be in sufficiently good condition for inclusion within the NRS. For example, tussock grasslands have largely been modified by grazing, weed invasion and land management practices associated with grazing domestic stock (Department of Environment and Water Resources, 2007), and in large part now only exist in small patches (Tulloch et al., in press). This makes it difficult to find good quality examples of this habitat type that are also available for purchase at a reasonable cost, and small patch sizes of remaining habitat could also explain why recently designated protected areas are much smaller than those already in the system prior to 2000.

Although the number of protected areas established between 2000 and 2008 was almost equal to the number designated before 2000, the average size of protected areas decreased by around 25% and was biased toward bioregions with high human populations, which could mean that biodiversity within these protected areas could be especially vulnerable to threats. Protected areas that are smaller need to be more connected to other habitats to ensure the persistence of species (Fuller et al., 2006; Gaston et al., 2008; Onal and Briers, 2006), yet Australia's smaller protected areas are poorly connected to other natural areas (Mackey et al., 2008). This means that many critical habitats for species may not be connected to protected areas, reducing the viability of species within the protected areas (Hansen and Rotella, 2002; Hansen and DeFries, 2007). To buffer these impacts, protected areas should generally be larger (Gaston et al., 2008), yet if additional habitat patches are not available for protection then increasing the overall extent of protection may not be an option. In these cases extensive management outside of the protected area will be needed, which focuses on restoring connections between critical habitats and buffering the impact of human presence (DeFries et al., 2007; Hansen and DeFries, 2007). The emergence of major connectivity conservation initiatives around Australia such as the Great Eastern Ranges Corridor, the Northern Australia Tropical Savannah Lands Corridor, Gondwana Link, the Trans-Australia Ecolink Corridor, Habitat 141 and Biolinks present an opportunity to improve connectivity among protected areas in some human-dominated around Australia (Worboys and Pulsford, 2011).

We chose bioregions as our units of measurement for protected area increase because we wanted to chart the progress of the NRS at the geographic level at which new protected area designation is assessed. However, because of the coarse scale of bioregions (85 across the entire continent), the effects of some variables could have been obscured. The size of a bioregion could have masked the influence of clearing within our model due to the heterogeneity of clearing within a bioregion. For example, the Brigalow Belt South bioregion in Queensland has been subjected to substantial clearing, yet retains large tracts of vegetation where the landscape is less fertile and more rugged because it is less suitable for clearing (Maron et al., 2011). The size of a bioregion could also have masked the influence of cost. Our cost value was the land value of the remnant vegetation in the bioregion divided by the area of the bioregion. However, there is potential for significant price variations within a bioregion such that only places that can be cheaply purchased within a bioregion may have been protected.

By separating Australia's protected coverage into past and recent additions we have shown that the characteristics of bioregions where protected areas have been established since 2000 have changed radically from historically designated sites. Systematic conservation planning is manifestly beginning to have a positive impact on Australia's protected area system with the protection of threatened species improving rapidly. On the other hand, some threatened habitats continue to remain severely under-represented within the NRS. Many of the impediments to achieving full representation are likely associated with the availability of habitat for purchase. However, even randomised protection outperformed the observed increases in protection for many poorly protected vegetation types, suggesting that there is substantial scope for improving the way Australia expands its protected area system.

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