

Species richness representation within protected areas is associated with multiple interacting spatial features

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ABSTRACT

Aim To assess the relative effects of the spatial features of protected areas (PAs), and their interactions, on species richness representation.

Location Continental America and associated islands.

Methods We used a novel dataset comprising species richness estimates for amphibians, birds and mammals for more than 400 PAs in the Western Hemisphere. Using spatial tools and remote sensing imagery, we calculated four spatial features for each PA: size, shape index, fragmentation level and proximity to the closest PA. The relative effect size of both PA spatial features and environmental covariates on levels of species richness, and how they interact, were assessed using generalized mixed effect models.

Results Spatial features and environmental covariates explained about 61% of the variation in species richness within PAs, with the magnitude of the effect remaining similar among spatial features and taxonomic groups. While area had a positive effect on species richness, shape index and fragmentation had negative effects. Proximity had a significant positive effect only for mammals and a negative effect for all the taxa combined. PA spatial features showed significant interactions between them and with environmental covariates.

Main conclusions We provide the first empirical evidence for the combined and interactive effects of terrestrial PA spatial features on predicting species richness. Our results suggest that the spatial features of PAs have an important effect on species richness and while the magnitude of this effect varies across taxonomic groups, its direction is consistent. Additionally, we show that the effect of one spatial design feature can be amplified or attenuated by that of another. These findings contribute towards a better understanding of the effect of spatial features on the performance of PAs and therefore how best to enhance the spatial configuration of existing and future PAs.

Keywords

biological conservation, protected areas, spatial features, species richness.

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INTRODUCTION

The ecological effectiveness of terrestrial protected areas (PAs) – the ability to represent and maintain biodiversity elements – can be significantly influenced by their spatial features (Williams *et al.*, 2005; Lasky & Keitt, 2013). PA size, shape, fragmentation level and proximity to other PAs are spatial features that influence biophysical conditions that can promote both (1) greater environmental turnover, hence

increasing biodiversity representation; and (2) appropriate amounts of habitat and resources, thereby maintaining the persistence of biodiversity. Since the 1970s, various ecological theories concerned with the relations between levels of biodiversity and the geographical and spatial distribution of species, such as island biogeography and metapopulation dynamics (Diamond, 1975; Margules *et al.*, 1982), have provided useful insights for developing practical conservation guidelines including the best configuration of PA spatial

features. Several of these recommendations have attracted policy attention and were, for example, incorporated into the World Conservation Strategy (IUCN, 1980). Such recommendations have, however, often been based on studies evaluating the effect of specific spatial features in isolation, while multiple spatial features are likely to interact and influence PA effectiveness simultaneously (Lemes *et al.*, 2014). Some spatial design features may influence biodiversity more strongly than others, and two or more features may interact in synergistic or antagonistic ways. For instance, the size of a PA may have a strong effect on biodiversity representation and persistence, a beneficial effect that could be attenuated by high levels of habitat fragmentation within the PA. Understanding the relative effects of different spatial features, and how they interact, can provide new insights into how best to design PAs to deliver their conservation goals, and also to ensure that conservation efforts are optimally deployed.

The size of a PA is a key feature influencing the quantity of biodiversity represented (Margules *et al.*, 1982; Williams *et al.*, 2005). Larger-sized PAs typically capture a greater range of environmental variation, and hence a larger number of species. In addition, larger PAs are more likely to support viable populations (i.e. the minimum number of individuals needed to guarantee the survival of a population in the long term; Reed *et al.*, 2003).

The shape of a PA – whether it is compact (e.g. perfect circle) or non-compact (e.g. ‘starfish’) – can influence the level of biodiversity to be represented in opposing ways. Less compact PAs (i.e. shapes that depart from circularity) increase representation because, for a given area, they sample more environmental variation (the linear distance between the two closest points within a geometric shape is always larger for less compact ones (Yamaura *et al.*, 2008); however, they negatively influence species survival by increasing the edge-to-area ratios, known to increase the extent of the area exposed to anthropogenic pressures (known as edge effects; Kunin, 1997; Hansen & DeFries, 2007). In the long term, this will reduce the level of biodiversity represented within the boundaries of a PA, and therefore, PAs are generally recommended to have compact shapes (Kunin, 1997).

High levels of fragmentation of a PA can strongly undermine the number of species found within its boundaries (Lasky & Keitt, 2013). Fragmentation leads to a reduction in biodiversity representation as only more tolerant species can persist in a modified and degraded habitat, thus leading to a reduction of local biological diversity (Fahrig, 2003). Also, it reduces species survival by increasing patch isolation, exposure to edge effects and the likelihood of stochastic extinction (Fahrig, 2003). Hence, low levels of habitat fragmentation within PAs are encouraged.

Short distances between PAs promote species dispersal and recolonization of areas in which species have become locally extinct, which increases species representation and survival within individual PAs (Kitzes & Merenlender, 2013). Therefore, a distance between PAs that fosters the interaction

between spatially separated populations has been recommended (Williams *et al.*, 2005).

A high proportion of the studies evaluating the effects of spatial features on how well individual PAs represent biodiversity are based on theoretical approaches (e.g. mathematical optimization models (Possingham *et al.*, 2000; McDonnell *et al.*, 2002; Williams, 2008; Jafari & Hearne, 2013). Those based on empirical research are restricted to either small geographical scales, small numbers of PAs or limited taxonomic groups. While these studies have made significant contributions to this topic, there is still a lack of research using empirical data that encompass a broader geographical extent, a more representative number of PAs, and a wider variety of biodiversity. Such studies will facilitate a more comprehensive understanding of the actual role of spatial features in the performance of existing PAs, therefore expanding those traditional guidelines concerning PA spatial configuration.

Progress in testing the effect of spatial features on PA effectiveness has been hampered by a lack of appropriate field data on actual levels of species representation within PAs. This has meant that many studies have had to be based on the distribution ranges of species (Brooks *et al.*, 2004; Rodrigues *et al.*, 2004; Araújo *et al.*, 2007; Cantú-Salazar & Gaston, 2010). Although distribution range datasets are the most appropriate available to date, they tend to overestimate species presence in PAs and can introduce significant biases into analyses (Hurlbert & Jetz, 2007). The consequences of such overestimation have recently been explored by Cantú-Salazar & Gaston (2013) in a comparison of richness estimates for PAs obtained from species range maps and from species inventories (i.e. number of observed species). As a result, a new dataset has been published, which compiles species sampling inventories within hundreds of PAs across the whole Western Hemisphere for amphibians, birds and mammals (Cantú-Salazar & Gaston, 2013). Although not without their own problems (likely suffering more from omission than commission errors), these data provide an excellent novel opportunity to test the effect of the spatial features of PAs on their species richness.

Using Cantú-Salazar & Gaston’s (2013) dataset, this study analyses for the first time to what extent the combined and interactive effects of terrestrial PA spatial features predict variation in levels of species richness. Using more than 400 PAs from the Western Hemisphere, we test how the features size, shape, fragmentation level and proximity to other PAs affect the richness of amphibian, bird and mammal species within PAs. Given the nature of the data, this study focuses on only one component of PA effectiveness, representation, using species richness as a proxy for biodiversity. Finally, we discuss the implications of (1) using species richness data derived from species inventories vs. range maps in analyses such as this, and (2) the findings for extending current guidelines on PA spatial features.

METHODS

Data

A species richness dataset for amphibians, birds and mammals of more than 400 PAs in the Western Hemisphere was obtained from Cantú-Salazar & Gaston (2013). Their study compiled species numbers reported for PAs based on inventories (i.e. observed species richness), which are openly available from Internet sources. Searches were focused on management plans from national agencies, technical reports, environmental assessments, official PA websites, biodiversity databases and conservation agencies. The compiled inventory species checklist (> 115,600 records) was standardized with nomenclature according to the IUCN and Nature Serve databases, and only native species were retained (see Cantú-Salazar & Gaston (2013) for details).

Data on the spatial structure of the PAs were obtained from the World Database on Protected Areas (WDPA, 2012; <http://www.wdpa.org>). The final dataset included PA polygons of which 335 had associated amphibian species richness data, 454 had data for birds, 377 had data for mammals, and 405 had data for all three taxa (hereafter 'all taxa'). 'All taxa' data were made up only by those PAs with species richness records for all three taxa. Data for five biophysical variables – latitude, altitude, annual temperature, annual precipitation and terrestrial ecoregion – were extracted for each PA. Latitude was extracted based on each PA centroid. Altitude, annual temperature and precipitation were obtained from the WORLDCLIM dataset (Hijmans *et al.*, 2005) at 1 km² resolution in raster format. The terrestrial ecoregion (i.e. a biogeographic regionalization of the Earth's terrestrial biodiversity) with which each PA overlapped was assigned from The Nature Conservancy global vector map (see details Appendix S1).

Spatial features

Using geographic information system (GIS) tools and remote sensing images for each PA polygon, we measured four spatial design features: size, shape, fragmentation level and proximity to the closest other PA. (1) The size of each PA was measured in ArcGIS 10 (ESRI, 2004; www.esri.com) using the default function 'calculate geometry' from the attribute table. (2) Shape was derived as the ratio of a PA's perimeter to the perimeter of a circle of the same area, also known as the circularity index (R_c) (Bogaert *et al.*, 2000). R_c indicates the extent of a shape's departure from a perfect circle, which is the most compact shape. While a perfect circle has an R_c equal to one, the R_c of a shape that departs markedly from circularity approaches zero. (3) Among many methods, fragmentation can be assessed in terms of habitat degradation, habitat isolation, landscape connectivity and the size of patches. To estimate fragmentation levels, we focused on land-cover type heterogeneity using variation in plant productivity. This was calculated using the coefficient of

variation (CV) ($CV = \sigma/\mu$; σ , standard deviation; μ , average) of the Normalized Difference Vegetation Index (NDVI) pixel values extracted for each PA. NDVI is a widely used estimator of plant productivity as they are linearly related (Monteith, 1981). The annual NDVI for the 2008–2013 period was obtained from the MODIS (TERRA) (Moderate Resolution Imaging Spectroradiometer – LPDAAC, NASA) dataset. (4) Proximity was measured as the shortest linear distance between two PAs. Given we are using a subset of PAs, we measured proximity of the PAs used in this study with respect to all existing PA polygons. Proximity was calculated in the R v2.14.2 statistical language (R Core Team, 2012) using the 'gDistance' function from the 'rgeos' (Bivand & Rundel, 2012). Finally, all maps were projected to Behrmann equal area for calculations, thus balancing the distortion between area, shape and distance within the region where the highest proportion of assessed PAs occurs.

Statistical analysis

To assess the relative effect size of PA spatial features on species richness and how they interact, we used generalized linear mixed effect models with a Poisson error structure using the package 'lme4' (Bates *et al.*, 2008) in the R statistical language. Analyses were carried out for amphibians, birds and mammals separately and for the combination of all three (all taxa). Species richness was used as the dependant variable in all models, with size, shape index, fragmentation level and proximity being incorporated as fixed factors. To account for environmental variables influencing species richness, latitude, altitude, annual temperature and precipitation were included as covariates. In all models, we assessed the interactions between combinations of spatial features and between spatial features and the covariates. Interactions between spatial features were as follows: area*fragmentation, area*shape and fragmentation*shape (Table S1). Interactions between spatial feature and covariates were as follows: altitude*area, altitude*fragmentation, altitude*shape and fragmentation*latitude (Table S1). 'Country' was incorporated as a random (intercept) factor to control for potential bias associated with each nation (e.g. sampling effort and number of records). Also, 'ecoregion' was included as a second random factor to account for the habitat effect on species richness within PAs. To set the fixed effects on a common scale and make them comparable, we standardized all using the 'arm' package (Gelman *et al.*, 2008).

We used a multimodel inference approach to model selection and simplification. All subsets of models were produced based on the global model and ranked according to their AIC_c values (package 'MuMIn'; Bartoń, 2011). Following Richards (2008), we retained all models where ΔAIC_c was < 6 to choose with 95% confidence the set of most parsimonious models. Using the function 'model.avg' from the MuMIn package, we averaged the sets of best-supported models, producing the average parameter estimates and the relative importance of each parameter. Conditional R^2 (variance

Table 1 Four different sets of top models investigating spatial features and environmental variables that predict variation of protected area representation of amphibians, birds, mammals and all taxa species richness together, ranked by AIC_c.

	Int.	A	Sh	Prox	Fr	Lat	Alt	Temp	Ppt	A*Fr	A*Sh	Fr*Sh	Alt*A	Alt*Fr	Alt*Sh	Fr*Lat	ΔAIC _c	Weight
Amphibian	2.42	0.081	-0.08		-0.52	-0.06	0.238	0.885	0.59	-0.374	0.79	0.585	0.292	-0.222	-0.243	0.259	0.0	0.340
	2.44	0.084	-0.07		-0.51		0.244	0.907	0.62	-0.337	0.85	0.588	0.293	-0.187	-0.253		2.13	0.117
	2.42	0.081	-0.08	0.006	-0.52	-0.06	0.238	0.884	0.59	-0.376	0.79	0.585	0.293	-0.221	-0.242	0.259	2.21	0.113
	2.40	0.065	-0.10		-0.55	-0.07	0.257	0.914	0.58	-0.490	0.86	0.510	0.328		-0.234	0.214	2.38	0.103
2.41	0.090	-0.07		-0.51	-0.09	0.245	0.894	0.61	-0.355	0.84	0.586	0.303	-0.180	-0.250		2.98	0.076	
2.43	0.070	-0.09		-0.53		0.259	0.933	0.61	-0.437	0.90	0.521	0.322		-0.245		3.31	0.065	
2.40	0.077	-0.09		-0.53	-0.10	0.260	0.918	0.60	-0.452	0.89	0.522	0.333		-0.242		3.92	0.048	
2.44	0.084	-0.07	-0.004		-0.51		0.244	0.908	0.62	-0.337	0.85	0.588	0.292	-0.187	-0.253		4.33	0.039
2.40	0.065	-0.10	0.010		-0.55	-0.08	0.257	0.911	0.58	-0.491	0.85	0.509	0.330	-0.233	-0.233	0.215	4.51	0.036
2.41	0.090	-0.07	0.005		-0.51	-0.09	0.245	0.892	0.61	-0.356	0.84	0.585	0.304	-0.179	-0.250		5.18	0.025
2.43	0.070	-0.09	-0.001		-0.53		0.259	0.933	0.61	-0.437	0.90	0.521	0.322		-0.245		5.50	0.022
Bird	5.08	0.290	-0.23	0.007	-0.12	-0.12	0.163	0.367	0.27	-0.221	0.30	0.236	0.067	-0.195	-0.159	0.329	0	0.66
	5.08	0.290	-0.23	0.007	-0.12	-0.12	0.164	0.367	0.27	-0.220	0.30	0.235	0.067	-0.195	-0.160	0.327	1.33	0.34
Mammal	3.60	0.391	-0.02	0.127	-0.295	-0.26	0.455	0.545	0.18	-0.531	0.52	0.161	0.057	0.071	-0.192	0.653	0.000	0.346
	3.59	0.398	-0.02	0.126	-0.292	-0.26	0.459	0.546	0.19	-0.482	0.52	0.161	0.055	0.069	-0.195	0.645	0.300	0.297
3.60	0.389	-0.02	0.125	-0.285	-0.285	-0.25	0.458	0.536	0.19	-0.504	0.51	0.183	0.055	-0.198	0.656	1.270	0.184	
3.60	0.396	-0.02	0.124	-0.281	-0.281	-0.25	0.461	0.536	0.19	-0.458	0.51	0.183		-0.201	0.648	1.440	0.169	
All taxa	5.5	0.109	-0.26	-0.109	-0.185	-0.23	0.189	0.312	0.325	-0.320	-0.11	0.111	0.129		-0.215	0.322	0.00	0.637
	5.5	0.108	-0.26	-0.109	-0.186	-0.23	0.188	0.315	0.324	-0.325	-0.11	0.106	0.131	0.0155	-0.213	0.321	1.13	0.363

Int, intercept; [spatial features] – A, area; Sh, shape index; Prox, proximity; Fr, fragmentation; [environmental covariates] – Lat, latitude; Alt, altitude; Temp, annual temperature; Ppt, annual precipitation; [spatial feature*spatial feature interactions] – A*Fr, area*fragmentation; A*Sh, area*shape; Fr*Sh, fragmentation*shape; [spatial feature*environmental covariate interactions] – Alt*A, altitude*area; Alt*Fr, altitude*fragmentation; Alt*Sh, altitude*shape; Fr*Lat, fragmentation*latitude; Weight, Akaike weight.

explained by fixed + random effects) and marginal R^2 (variance explained only by the fixed effect) were calculated for the top model (i.e. $\Delta AIC = 0$) using the methods described in Nakagawa & Schielzeth (2013).

RESULTS

Protected areas included in the analysis were widely distributed within the Western Hemisphere, with a higher proportion in the United States, Canada, Mexico, Brazil, Argentina and Peru (Table S2). PAs with higher numbers of species were, however, concentrated in the north-west of South America along the Andes range (Fig. 1). The taxonomic group with the highest number of species within PAs was birds, followed by mammals and amphibians (Fig. 1).

The conditional R^2 (variance explained by the whole model) of top models for amphibians, birds, mammals and all taxa was 0.74, 0.69, 0.58 and 0.81, respectively. The marginal R^2 (variance explained by the fixed effects) of global models for amphibians, birds, mammals and all taxa was 0.63, 0.48, 0.51 and 0.61, respectively. After considering only those models within $\Delta 6 AIC_c$ units, there were eleven models for amphibians, two for birds, four for mammals, and two for all taxa (Table 1). The direction of the spatial feature

effects was the same across all of the taxonomic groups, except for proximity, which had a significant negative effect in all taxa combined and a significant positive effect in mammals only (Fig. 2a). The direction of the covariate effects latitude, altitude, annual temperature and precipitation did not differ among taxonomic groups (Fig. 2b).

Protected area size showed a positive effect on species richness (Fig. 2a). However, this effect was not significant for amphibians. For mammal richness, proximity was positive. In contrast, shape and fragmentation level showed general negative effects (Fig. 2a). This indicates that less compact shapes with low fragmentation levels benefit species richness representation. However, the effect of shape was not significant for mammal richness (Fig. 2a). There were negative effects of latitude on species richness and positive effects of altitude, annual temperature and precipitation (Fig. 2b). This indicates that species richness was higher within PAs located in lower latitude, at higher altitudes, with higher annual temperature and precipitation. All the interactions between spatial features that were tested were significant across all groups (Fig. 2a). For the three different taxonomic groups, area showed a negative interaction with fragmentation (Fig. 2a), but a positive interaction with shape (the bigger the area, the greater the effect of compact shapes in decreasing species richness). This last interaction, unlike for the other three groups, was negative for all taxa combined (the larger the PA, the lesser the negative effect of shape on richness; Fig. 2a). Fragmentation and shape had a positive interaction indicating that the higher the levels of fragmentation, the greater the negative effect of shape (Fig. 2a).

Several of the interactions between the environmental covariates and the spatial features of PAs were significant (Fig. 2b), suggesting that the overall effects of spatial features on the level of species richness was affected by environmental conditions. Altitude had a significant positive interaction with PA size, except for mammals. Altitude also interacted negatively with fragmentation for birds, while a negative interaction with shape was found for all of the groups (Fig. 2a).

This suggests that at higher altitudes, the positive effect of area is bigger and the negative effect of both fragmentation and shape are smaller.

The relative strength of predictor effects did not differ substantially across taxa (Fig. 2). The relative importance of predictors (i.e. proportion of time it appears in the top model) and 95% confidence interval of estimates are provided in Table S3.

DISCUSSION

Understanding how the spatial features of PAs affect their representation of biodiversity is a complex challenge. PAs aim to protect a wide range of biodiversity components, which are not only affected by spatial features, but also by other ecological and environmental factors whose effects are not trivial to untangle. By assessing hundreds of PAs across a

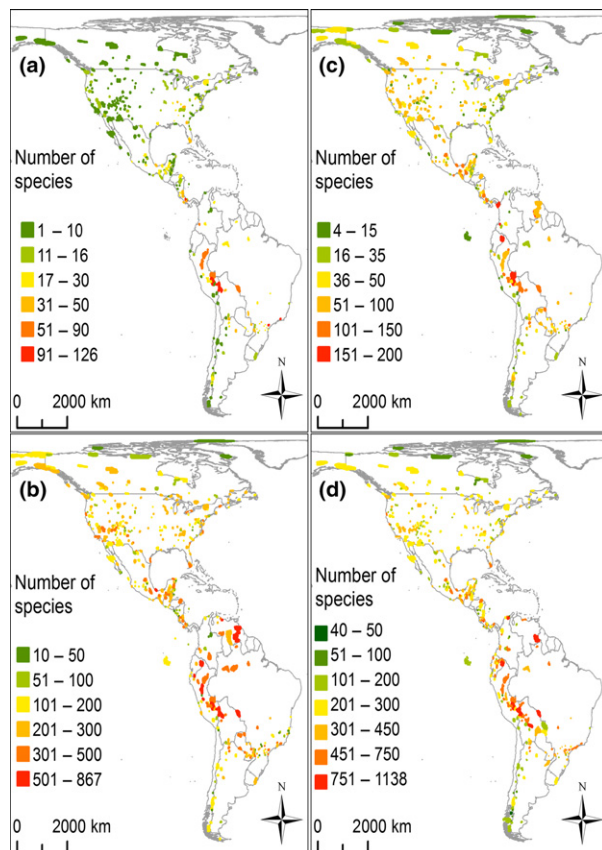


Figure 1 Maps of species richness in analysed protected areas of the Western Hemisphere. (a) Amphibians; (b) birds; (c) mammals; and (d) all taxa.

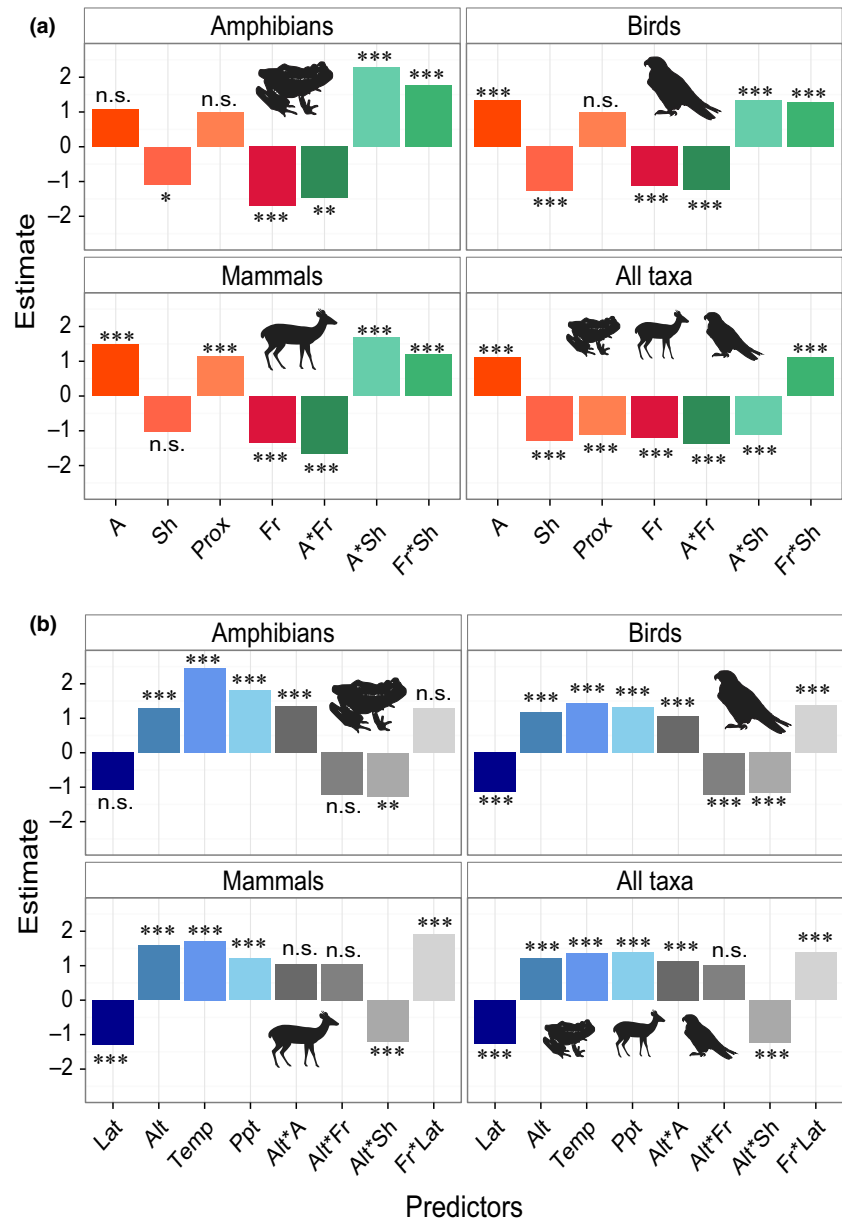


Figure 2 Estimates of averaged models for amphibians, birds, mammals and all taxa together. Size of the bar indicates relative strength of each predictor on species richness representation, and sign (above or below zero line) indicates direction of the effect. A positive effect (above zero line) indicates that species richness representation is favoured with high values of the predictor, while a negative effect (below zero line) indicates that low predictor values lead to higher species richness representation. Predictor effects are illustrated in two groups: (a) spatial features (red) and interactions between spatial features (green); (b) environmental covariates (blue) and interactions between spatial features and environmental covariates (grey). A, area; Sh, shape index; Prox, proximity; Fr, fragmentation; Lat, latitude; A*Fr, area*fragmentation interaction; A*Sh, area*shape interaction; Fr*Sh, fragmentation*shape interaction; Fr*Lat, fragmentation*latitude interaction. Significance of the effect, *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns, not significant. Given that Poisson coefficients come out on a log-scale, estimate values have been exponentiated in order to represent graphically the real magnitude of the effects.

continental scale, this study provides the first evidence of the combined and interactive effects of PA spatial features on species richness, a key component of biodiversity to be conserved within the PA system. While there has been considerable progress in understanding the importance of the configuration of PA spatial features and how these affect biodiversity representation, spatial features have mostly been tested independently. This has hampered a more comprehensive understanding of the actual role that PA spatial design plays in their ability to represent and maintain biodiversity elements, and subsequent achievement of conservation goals.

Our results show that the combined effects of size, shape, fragmentation, proximity and key environmental variables explain about 61% of the variance observed in the aggregated species richness of amphibians, birds and mammals within

PAs. The results empirically support findings on the direction of the effects from previous studies that assessed features independently or through mathematical models (Table S1).

In addition to the variance explained by the spatial features and environmental variables (i.e. fixed effects), a further 20% was explained by ecoregion and country, totalling 81% of the variance for the whole model (i.e. fixed + random effect). Given the empirical and large scale nature of the data used in this study, our results suggest that there are other local factors that explain the remaining 19% of the variance in species richness representation. These factors are likely related to the management within PAs (Leverington *et al.*, 2010; Lawson *et al.*, 2014) (the internal threats; e.g. poaching, habitat transformation), and the anthropogenic pressures from the surrounding landscape (Hansen &

DeFries, 2007). All of these influence species survival and as a consequence their representation.

Area and fragmentation were the features that better predicted species richness representation across the three taxa, with fragmentation reducing the positive effect of area (i.e. negative interaction between fragmentation and area) (Fig. 2a, Table 1). Our measurement of fragmentation was based on land-cover heterogeneity, which can be produced by both anthropogenic or natural forces (Fischer & Lindenmayer, 2007). Our results demonstrate how high levels of heterogeneity within PAs can be detrimental to species richness. This negative relation has previously been described as the 'area-heterogeneity trade-off', in which any increase in environmental heterogeneity within a fixed space leads to a reduction in the average amount of effective area available for individual species, thereby affecting species survival (Allouche *et al.*, 2012). This negative interaction provides an example of how conservation effort in addressing a specific spatial feature (e.g. making PAs bigger) may be ineffective if other features (i.e. level of environmental heterogeneity) and their potential interactions are not taken into account.

Environmental covariates also had an effect on species richness within PAs and this effect interacted with spatial features (Fig. 2b). Surprisingly, altitude had a positive effect on species richness and a positive interaction with area, indicating that at higher altitudes, the positive effect of area on species richness is greater (Fig. 2b). This likely reflects the numerous biodiversity hotspots distributed along the Andes ranges (Fig. 1), known for their high level of endemism and species richness (Myers *et al.*, 2000).

The overall effects of the spatial features of PAs also differed between taxa, suggesting that the representation of amphibians, birds and mammals is affected in different ways by PA spatial features. This might be explained by the inherent ecological attributes of each group. Mammals were the only group for which PA shape did not have a significant effect (Fig. 2a). Large-bodied mammals often have large home ranges (Jetz *et al.*, 2004; Ottaviani *et al.*, 2006), which may encompass or go beyond PA boundaries (assuming these are unfenced), thus eliminating the greater spatial turnover normally captured by non-compact shapes. Indeed the positive interaction between area and shape for mammals (Fig. 2a), suggests that non-compact shapes capture higher spatial turnover of mammal species only with large PAs. While proximity had a positive effect on the richness of some groups, it had no significant effect on others. A lack of effect could indicate that some PAs are close enough that they do not experience environmental turnover; hence, they are acting as one functional unit of protection. This adds even further complexity to the assessment of PA spatial features, as the administrative boundary used in this study likely interacts with the functional boundary determined by spatial features such as proximity.

Both species richness data derived from checklists (as used in this study) and from distribution range maps suffer from

sources of error and should inevitably be treated with some caution. As pointed out by Cantú-Salazar & Gaston (2013), while checklist-based species richness data have the disadvantage of containing geographical biases and point locality gaps (suffering from omission errors especially in species rich PAs), range map derived species richness estimates tend to suffer from commission errors especially in species poor PAs and overestimate species representation especially in small sites. This raises two key points regarding the assessment of the effect of PA features on species richness. First, geographical bias and point locality gaps in checklist species data tend to result in an under-representation of isolated and smaller PAs to which access is limited and, consequently, an over-representation of well-connected and larger PAs. This over-representation can to some degree be controlled for, as we do, by including as a random effect the biased geographic level in the model ('Country' in our case). Second, the potential influence of the inherent commission and omission errors of species distribution data on PA spatial features analyses could be addressed by comparing, when possible, the results from both checklist and range map types of data. We conducted this comparison (Fig. S1) and the combined effects of PA spatial features on species richness are consistent (Figs 2 & S1). The direction of PA spatial feature effects is exactly the same for all groups, excepting for proximity, which has a positive effect when using the checklist data for mammals and a negative effect when using range maps for birds (Figs 2 & S1). The negative effect might reflect the high level of commission error in range map data, as only PAs that are widely separated will differ in their levels of species richness. The interactions between spatial features are also consistent between analyses using the two data sources (Figs 2 & S1), only differing in the statistical significance of the area*shape effect, which again might be an effect of the commission error from range maps.

From the results reported here four key recommendations can be made to those concerned with the designation and spatial configuration of PAs: (1) Biodiversity representation data based on observed records is a very valuable tool to comprehensively assess the effects of PA spatial features and it is, therefore, crucial to promote such data for as many as possible existing PAs. (2) The overall effect of PA spatial features was influenced by environmental variables, thereby general guidelines on PAs design should ideally account for local conditions. (3) Untangling to what extent and how inherent ecological attributes of different taxa (e.g. home range size) are linked to PA spatial features effects is a relevant information that should be increasingly explored and considered in PA design. (4) Given that the positive effect of one spatial feature (e.g. size) can be attenuated by another (e.g. fragmentation), a preliminary assessment of the potential interactions between spatial features can help to optimize the effect of the design and avoid wastage of resource. Such an assessment can be carried out prior to PA establishment using available spatial data.

ACKNOWLEDGEMENTS

Protected area data were extracted from the 2012 World Database on Protected Areas (WDPA). The WDPA is a joint product of IUCN and UNEP prepared by UNEP-WCMC and the IUCN-WCPA working with Governments, the Secretariats of Multilateral Environmental Agreements, collaborating Non-Government Organizations and individuals. For further information go to www.wdpa.org or contact: protectedareas@unep-wcmc.org. We thank two anonymous referees for thoughtful and constructive comments on the initial manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Description of the terrestrial ecoregion dataset used as a random effect in the GLM models.

Table S1 Predictors of the global model investigating the effects of PA spatial features on species richness.

Table S2 Number of PA records per country according to biodiversity group.

Table S3 Results of GLM models for predictors of species richness within PAs.

Figure S1 Estimates of averaged models for amphibians, birds, mammals and all taxa together using species richness data derived from range maps.

BIOSKETCH

América Paz Durán is a conservation biologist with interest in understanding how to promote the protection of biodiversity and ecosystem services together with human development. She has undertaken investigations on the effectiveness of protected areas, spatial conservation prioritization and land-use trade-offs.

Author contributions: A.P.D., R.I. and K.J.G. conceived the idea; A.P.D. and R.I. designed and conducted the analysis; and all the authors contributed to the writing, which was led by A.P.D. and R.I.

Editor: Mathieu Rouget