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Changes in potential mammal diversity in national parks and their implications for conservation

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Abstract

Observed species richness (OSR) is a widely used and well-studied biodiversity metric. However, non-observed species in favorable ecosystems are also relevant. Two metrics that include observed and potential species were recently defined: potential biodiversity (hereafter potential species richness—PSR) and geometric mean of favorabilities (GMF). We used these metrics to evaluate the national park network of mainland Spain at two time periods (2002 and 2015), using terrestrial mammals on a UTM 100-km^2 grid. PSR and GMF are based on the favorability function, a species distribution model that assesses how favorable an area is for the presence of a species, over and above its prevalence in the study area. For each park and for the whole network, we calculated the mean and sum of OSR, PSR, and GMF in each time period, as well as changes between periods. OSR and PSR were higher inside than outside the park network in both time periods. Thus, although the network covers a very small proportion of the country, it performs well for the representation of mammal species and their favorable areas. However, mean PSR was lower in 2015 than in 2002 inside the national park network, whereas the opposite was the case outside the network. Mountainous Parks generally not only concentrated highly favorable areas for mammals, but they also showed less favorable areas in 2015 compared to 2002, although the reduction was moderate to low. This is a result to consider for future analyses because if the tendency increases, it may have consequences for the conservation of mammals and for the adequacy of the national park network.

Key words: conservation planning, dark diversity, environmental favorability, potential biodiversity, protected areas.

There are several different forms of biodiversity metrics, which are essential tools in conservation ecology (Whittaker 1972; Purvis and Hector 2000). These metrics are needed, among other reasons, to gauge the state of an ecosystem, population trends if they are applied at different time points (Harrison et al. 2014), and the adequacy of protected areas (Estrada et al. 2008). Although the term "biodiversity" encompasses all biotic variation, from genes to ecosystems (Purvis and Hector 2000), more simplistic metrics that are focused on a particular aspect of biodiversity are generally applied. Observed species richness is a very common and well-studied metric, which is widely applied from local to global scales (Griffiths 1999; Orme et al. 2005). However, some authors have pointed out that the set of non-observed species in a favorable ecosystem is as valuable as the set of known species (Pärtel et al. 2011a). From this perspective, they defined the concept of "dark diversity" as being composed of those species that theoretically can inhabit a particular site, but that are absent from it for some reason. Mokany and Paini (2011) offered a probabilistic approach to

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quantifying dark diversity that incorporates the continuous nature of species distributions, and that can be calculated, for instance, from occurrence probability values given by species distribution models (SDMs).

With this background, Real et al. (2017) proposed the term "potential biodiversity". In this approach, instead of separating observed diversity and dark diversity, all species can be understood in terms of the probability that they will be found in each region, whether or not they have been observed there. Thus, a species would not be assumed to be inside a region or otherwise; rather, it would be treated as having some relative likelihood of occurring within the region. An important point is that presence probability values are not directly comparable between species differing in prevalence (see below); thus, to estimate potential biodiversity, favorability (a function of probability and prevalence, also taking values between 0 and 1) should be used instead (Real et al. 2006). The summed favorability values may then be considered the potential biodiversity of the region (Real et al. 2017).

Presence probability values are not comparable between species because the probability of a species occurrence in a particular location is affected by both the overall prevalence of the species, and the degree to which the environmental conditions at that location make the occurrence of the species more or less likely than its general prevalence (see Cramer 1999; Hosmer and Lemeshow 2000; Real et al. 2006). Favorability is precisely the latter, i.e., it reflects only the response of the species to the environment, regardless of its prevalence across the study region. Therefore, favorability values are directly comparable between species, even if these have different numbers of presences in the study area (Acevedo and Real 2012). Thus, it is the interaction between favorabilities that enables the combination of SDMs when several species are involved (Estrada et al. 2011). Favorability can also be directly treated with fuzzy logic (Real et al. 2006), which is in line with the views of Pärtel et al. (2011b) who considered species pools as fuzzy sets.

Another biodiversity metric recently defined is the geometric mean of favorabilities (Real et al. 2017), which is inspired by the geometric mean of species abundances (Buckland et al. 2011), and gives more weight to favorability values closer to one. The geometric mean of species abundances has proved to be an efficient measure compared with other biodiversity metrics (Buckland et al. 2005). However, it cannot be used when abundance is 0, and it is too sensitive to species with marked spatial changes in abundance. These limitations are overcome by the geometric mean of favorabilities (Buckland et al. 2011; Real et al. 2017). Moreover, Real et al. (2017) defined the increment in the geometric mean of favorabilities as a measure for assessing changes of this quantity in two periods of time.

Potential biodiversity and the geometric mean of favorabilities are novel metrics that can be used together with more traditional metrics to assess the adequacy of protected area networks, such as Spanish National Parks. Previous studies have evaluated the adequacy of Spanish protected areas in conserving different forms of biodiversity. These comprise a variety of taxonomic groups, including different groups of vertebrates (e.g. Rey Benayas and de la Montaña 2003; López-López et al. 2011; Lisón et al. 2015), invertebrates (Romo et al. 2007; Sánchez-Fernández et al. 2013), plants (Castro et al. 1996; Araújo et al. 2007, 2011), and lichens (Martínez et al. 2006); and a variety of conservation criteria, such as species richness (Araújo et al. 2007; Romo et al. 2007), rarity (Castro et al. 1996; Rey Benayas and de la Montaña 2003), vulnerability (Rey Benayas and de la Montaña 2003; Traba et al. 2007), and endemicity (López-López et al. 2011). As a result, some studies have found that protected areas effectively include the most relevant areas for biodiversity (Martínez et al. 2006; Lisón et al. 2015), whereas others have found that the current configuration of protected area networks is insufficient to cover important areas for biodiversity or hotspots (Rey Benayas and de la Montaña 2003; Traba et al. 2007; López-López et al. 2011). In these previous works, National Parks were generally included as part of the protected reserves (Castro et al. 1996; Rey Benayas and de la Montaña 2003; Romo et al. 2007; Sánchez-Fernández et al. 2013) and were not evaluated independently. However, we consider it necessary to perform a separate evaluation of the National Park network, because conservation policy in Spain is carried out by the Environmental Ministry in the case of National Parks, and by the autonomous regions in the case of protected natural areas (Estrada et al. 2008). Additionally, the National Park network in Spain was established a century ago (in 1916), and thus it is an optimal time to evaluate the contribution of these Parks to the conservation of biodiversity.

Our specific aims in this study are to assess: 1) the contribution of each National Park in mainland Spain to the overall capacity of the National Park network to cover observed species richness (OSR), potential biodiversity (hereafter potential species richness—PSR), and the geometric mean of favorabilities (GMF) of terrestrial mammals, and 2) the current spatio-temporal trends in this capacity.

Materials and Methods

Biodiversity metrics

Our study species were 63 terrestrial non-flying mammals inhabiting mainland Spain. Real et al. (2017) analyzsed their distributions on a grid of $10\,\text{km} \times 10\,\text{km}$ UTM (Universal Transverse Mercator) cells ($n = 5,\ 167$) at two time periods (2002 and 2015). Data from 2002 came from the mammal atlas of Spain at that time (Palomo and Gisbert 2002), whereas data from 2015 came from the database of the Spanish Ministry of Agriculture, Food and the Environment (downloaded 26 July 2015 from http://www.mapama.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/bdn-ieet-default.aspx). Biodiversity values in each UTM cell of mainland Spain were calculated by Real et al. (2017), who performed species distribution modelling for each species at the two time periods with methods and variables described previously (Barbosa et al. 2009; Real et al. 2009; Barbosa and Real 2010). Environmental favorability for each species was obtained after applying the favorability function (Real et al. 2006). Analyses were performed with package *fuzzySim* (Barbosa 2015), in the R statistical environment (R Core Team 2014).

From favorability values, potential species richness was obtained in each UTM cell of mainland Spain as the sum of raw favorabilities (i.e., without binary transformations), considering favorable areas for all species, whether or not they have been observed in each region. The analysis was performed separately for the two time periods. The geometric mean of favorabilities was also calculated at both time periods, as well as its increment from 2002 to 2015. These analyses were performed using the R functions provided in Real et al. (2017). For comparison, observed species richness was also calculated at the two time periods, as well as its change from 2002 to 2015. Note that the change in GMF is calculated through the increment (an exponential equation with values always above zero, and higher than one if the increment is positive) (Real et al. 2017), which is not simply a subtraction of the values at two periods of time (as occurs with the change in OSR and PSR).

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Maps with values of the different biodiversity metrics across mainland Spain can be seen in Real et al. (2017). In summary, the highest values for observed and potential species richness, although not equally distributed, were located in northern and central-western Spain. The GMF was highest in north-eastern Spain. Overall patterns were essentially similar for 2002 and 2015. The changes in OSR and PSR from 2002 to 2015 were mainly concentrated in the Spanish region of Extremadura (central-western Spain), while the increase in the GMF was more spread throughout the southern half of Spain.

Contribution of each national park

The National Park network of Spain was established a century ago (in 1916) and is currently formed by 15 National Parks, 9 of which are located in mainland Spain. National Parks are the areas with the highest level of protection in Spain. They are defined as "natural areas with high ecological and cultural value, little transformed by exploitation or human activity which, due to the beauty of their landscapes, the representativeness of their ecosystems or the singularity of their flora, fauna, geology or geomorphological formations, possess outstanding ecological, aesthetic, cultural, educational and scientific values whose conservation deserves a preferential attention and are declared of general interest of the State" (BOE 2014). We downloaded a map of the National Parks from the webpage of the Spanish Ministry of the Environment (http://www.mapama.gob.es/es/red-parques-nacionales/sig/; Figure 1) and intersected it with the UTM grid of mainland Spain at a resolution of 10 km × 10 km.

For each National Park and for the whole Park network in each time period, we calculated, in the protected cells, the mean and sum of each of the three biodiversity metrics calculated by Real et al. (2017), i.e., OSR, PSR, and GMF, as well as the change in these indices from 2002 to 2015. We performed these analyses in two ways: considering all UTM cells overlapping with a particular Park as equally protected, and considering the degree of protection of each cell according to the proportion of the cell included in the Park. We also estimated mean values of the biodiversity metrics outside the network, i.e., in non-protected cells across mainland Spain. We used the functions *group_by* and *summarise* available in the R package *dplyr* (Wickham and Francois 2016) to calculate these statistics. We tested for significant differences in mean values inside and outside the National Park network with the Mann–Whitney U-test. Significant differences in mean values among National Parks were tested with the Tukey honest significant difference method (Tukey HSD).

Figure 1. National Park network of mainland Spain. A: Aigüestortes i Estany de Sant Maurici, C: Cabañeros, D: Doñana, G: Sierra de Guadarrama, M: Monfragüe, O: Ordesa y Monte Perdido, P: Picos de Europa, S: Sierra Nevada, T: Tablas de Daimiel.

Results

The values of the different biodiversity metrics in the cells covered by National Parks can be seen in Figure 2. Highest values for observed and potential species richness were concentrated in northern Parks. The GMF was highest in north-eastern Parks. The changes in OSR and PSR from 2002 to 2015 were concentrated in Monfragüe and Cabañeros National Parks (see location in Figure 1), while the increase in the GMF was highest in the Parks located in the southern half of Spain.

Mean values of the biodiversity metrics were higher within than outside the National Park network for all metrics except the change of PSR and the increment of the GMF (Table 1). However, the differences in GMF between the National Parks and the remaining territory were not significant at any period of time (Table 1).

The National Park with the highest mean and sum values for most indices was Picos de Europa (see location in Figure 1), both when considering all overlapping cells as protected (Figure 3, Table 3) and when values were corrected for the proportion of each cell covered by a National Park (Tables 2 and 4, Figure 4). The Park with the lowest mean values was Tablas de Daimiel (central-southern Spain), although Doñana (SW Spain) also had relatively low values of the mammal biodiversity metrics, and sometimes there were no significant differences between these two Parks (Figure 3). On the other hand, the changes in OSR and PSR between the two time periods were sharpest in Monfragüe (W Spain), whereas the increment in the GMF was largest in Doñana and Sierra Nevada (S Spain; Figures 3, 4, Tables 2–4). We represent in Figure 4 the mean values of the biodiversity metrics in 2015 corrected for the protected proportion of each UTM cell (Table 2). Although sum values could theoretically be affected by the area of the National Park, the Park with the highest values was not the largest (Tables 3 and 4).

There was a strong positive correlation between OSR and PSR in National Parks (values corrected for the protected proportion) (Table 5). However, the correlation of both biodiversity metrics with the geometric mean of favorabilities, although significant, was weaker. None of the biodiversity metrics correlated significantly with the change in OSR from 2002 to 2015. The correlation of OSR, PSR, and GMF with the change in PSR was negative, but weak. Intermediate correlation values appeared between the increment in the GMF and both OSR and PSR (Table 5).

Discussion

In this work, we evaluated the spatial trends in observed and potential mammal diversity in Spanish National Parks at two periods of time. We considered two metrics of potential diversity: potential species richness and geometric mean of favorabilities. The inclusion of these metrics to assess the contribution of each National Park gives importance not only to observed species but also to dark diversity, i.e., to absent species for which the area is favorable (Pärtel et al. 2011a). Different reasons may arise for the absence of these species in favorable areas, with dispersal limitation, habitat specialization, and type of reproduction being recently identified as

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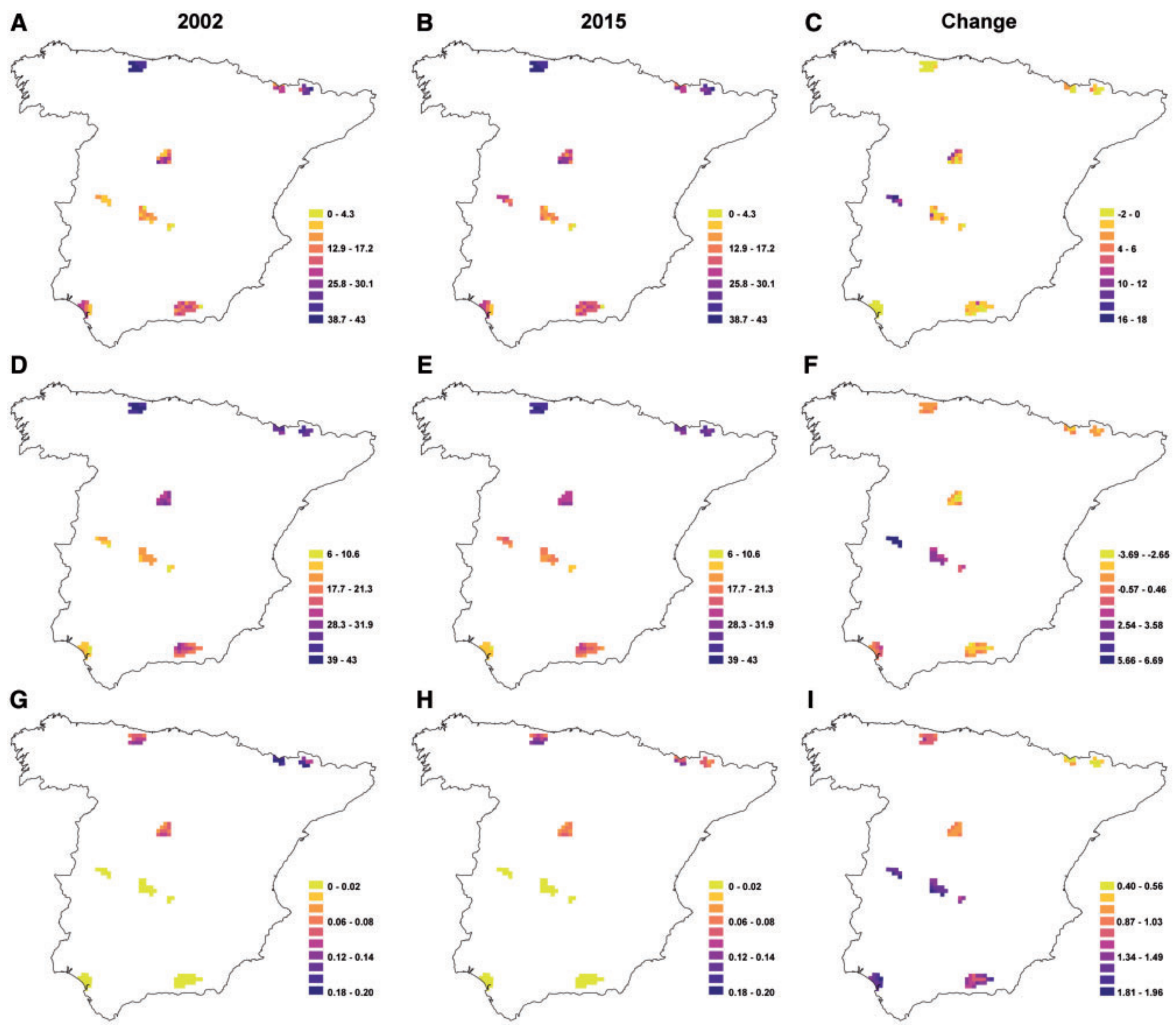

Figure 2. Observed species richness (A, B, C), potential species richness (D, E, F), and geometric mean of favorabilities (G, H, I), for Spanish terrestrial mammals in 2002, 2015 and the change from 2002 to 2015 in the grid cells intersecting National Parks in mainland Spain. North is up, and grid squares measure 100 km^2.

primary causes related to species life-history traits (Estrada et al. 2015, 2017; Riibak et al. 2017). Additionally, artifactual or anthropic reasons are also possible, such as insufficient sampling effort (Real et al. 2017) or excessive human pressure (Nores 2007; Lucas et al. 2016).

The evaluation of the whole National Park network of mainland Spain showed that mean values of OSR and PSR were higher inside the network than outside it, at both analyzed periods of time (Table 1). Thus, although the network covers a very small proportion of the country, it performs well for the representation of mammal species and their favorable areas. This result is partially in agreement with previous studies that evaluated the level of congruence between Spanish protected areas and hotspots for mammals. For instance, Araújo et al. (2007) found that Iberian protected areas represented more mammal species than expected by chance, and thus protected areas provided effective samples of species among mammals, a result that was not generalizable to other vertebrate or plant groups. On the other hand, Rey Benayas and de la Montaña (2003) found a positive relationship between protected areas and rare mammals, although the relationship was not significant for other conservation criteria, such as richness or vulnerability. This is in accordance with López-López et al. (2011), who found that protected areas were not particularly concentrated in areas of high mammal species richness.

Our results also showed that the change in PSR from 2002 to 2015 was smaller (and negative) inside the network than outside it (Table 1). This means that mean potential species richness was lower in 2015 than in 2002 inside the National Park network, whereas the opposite was the case outside the network. This could indicate that while National Parks have highly favorable areas for mammals, for some reason favorable areas decreased slightly in the studied time period. Hence, some changes occurred outside the network from 2002 to 2015 that implied distributional changes of mammals and their favorable areas in a positive way. This is a result to consider for future analyses. It will be important to assess whether the tendency is reversed or increased, in which case this could have consequences for the conservation of mammals and for the adequacy of the National Park network.

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Picos de Europa had the highest values of the biodiversity metrics for mammals. This Park represents the ecosystems linked to the Atlantic forest and is a mountainous system characterized by the presence of several different species of mammals and birds. National Parks with the lowest biodiversity metrics were Tablas de Daimiel and Doñana. This was not an unexpected result, as those National Parks were not characterized by or declared because of the presence of mammals. Tablas de Daimiel is a unique European wetland. It is an exceptional habitat for all fauna linked to the aquatic environment, especially birds and particularly waterfowl. The most important ecosystem in Doñana is the marsh, which is of extraordinary importance as a place of passage, breeding and wintering of thousands of European and African birds (http://www.mapama.gob.es/es/red-parques-nacionales/). Although we evaluated the network at two periods of time (2002 and 2015), it is worth noting that not all the National Parks had been declared before these periods: Monfragüe and Sierra de Guadarrama were declared in 2007 and 2013, respectively. Thus, although natural values are not strictly dependent on the declaration of the Park, a higher level of protection is expected for the oldest National Parks.

Table 1. Mean values for the three biodiversity metrics in the national park network (NP1) and outside the network (NP0) in 2002 and 2015, and changes from 2002 to 2015

Period	Metric	NP0	NP1	U	Sig
2002	OSR	12.55	19.09	173,627	***
	PSR	19.30	24.03	196,485	***
	GMF	0.0252	0.0503	240,162.5	n.s.
2015	OSR	14.63	21.63	154,550	***
	PSR	19.72	23.98	182,713	***
	GMF	0.0256	0.0383	246,214	n.s.
Change from 2002 to 2015	OSR	2.08	2.55	267,696	n.s.
	PSR	0.422	−0.0458	329,171	***
	GMF	1.31	1.21	284,730	n.s.

OSR: observed species richness, PSR: potential species richness, GMF: geometric mean of favorabilities. The statistic (U) and significance (sig) of the Mann–Whitney tests are also shown., ***: $P < 0.001$, ns: $P > 0.05$.

Other studies also found that hotspots for mammals were located in northern Spain (Rey Benayas and de la Montaña 2003; Araújo et al. 2007; Levinsky et al. 2007; López-López et al. 2011). This reinforces the relevance of the northern National Parks (Picos de Europa, Ordesa y Monte Perdido, and Aigüestortes i Estany de Sant Maurici) regarding their contribution to preserving mammal species (see Figures 2–4, Tables 2–4). The abovementioned studies also highlighted hotspots for mammals around Sierra de Guadarrama (Rey Benayas and de la Montaña 2003; Araújo et al. 2007; Levinsky et al. 2007; López-López et al. 2011), although, as stated previously, the declaration of this National Park was not made until 2013. All of these previous results are in agreement with ours, and reinforce the importance of mountainous systems as favorable areas for several mammal species (Levinsky et al. 2007).

Regarding changes in the biodiversity metrics between 2002 and 2015, observed species richness increased in all National Parks except for Picos de Europa (Figures 3–4, Tables 2–4). Thus, it is

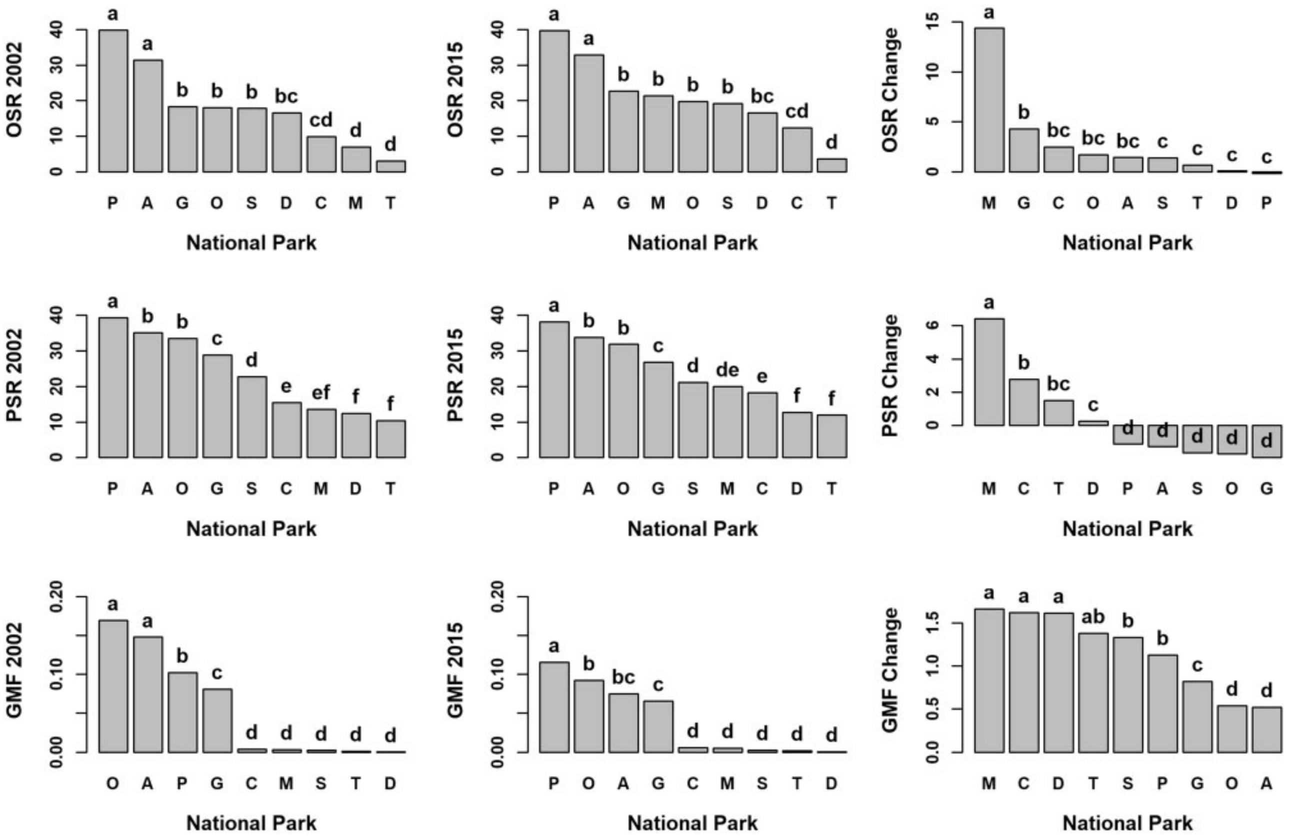

Figure 3. Mean values in each National Park for observed species richness (OSR), potential species richness (PSR) and geometric mean of favorabilities (GMF) in 2002, 2015, and the change from 2002 to 2015. National Park names as in Figure 1. Parks without significant differences according to the TukeyHSD test share the same lower-case letter.

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Table 2. Mean values in each national park (NP) for the three biodiversity metrics in 2002 and 2015, and changes from 2002 to 2015

NP	2002			2015			Change from 2002 to 2015		
	OSR	PSR	GMF	OSR	PSR	GMF	OSR	PSR	GMF
A	6.24	6.89	0.0258	6.44	6.57	0.0134	0.192	−0.322	0.104
C	2.95	4.54	0.000993	3.45	5.34	0.00157	0.492	0.804	0.468
D	8.42	6.52	0.0000627	8.49	6.49	0.0000987	0.0714	−0.0352	**0.794**
G	5.52	7.83	0.0247	6.09	7.31	0.0193	0.565	−0.526	0.205
M	2.13	4.03	0.000952	6.17	5.81	0.00152	**4.04**	**1.78**	0.448
O	5.87	11.94	**0.0591**	6.59	11.06	0.0289	0.721	−0.879	0.169
P	**19.50**	**19.53**	0.0527	**19.44**	**18.99**	**0.0604**	−0.0539	−0.538	0.564
S	7.02	9.65	0.00108	7.52	8.85	0.00129	0.500	−0.796	0.487
T	0.472	1.07	0.000135	0.535	1.22	0.000184	0.0629	0.152	0.137

Values are corrected for the proportion of the grid cell covered by a national park. OSR: observed species richness, PSR: potential species richness, GMF: geometric mean of favorabilities. Maximum and minimum values are grey shaded, with maximum values in bold. National park names as in Figure 1.

Table 3. Sum values for the three biodiversity metrics in each national park (NP) in 2002 and 2015, and changes from 2002 to 2015

NP	Area (ha)	2002			2015			Change from 2002 to 2015		
		OSR	PSR	GMF	OSR	PSR	GMF	OSR	PSR	GMF
A	13,927	220	246.03	1.03	230	236.96	0.523	10	−9.07	3.64
C	40,907	138	216.36	0.0497	173	255.09	0.0778	35	38.73	22.67
D	53,416	232	173.74	0.00172	233	177.24	0.00273	1	3.50	22.59
G	33,960	239	374.59	1.05	295	349.29	0.851	56	−25.31	10.67
M	18,010	56	108.73	0.0248	171	159.99	0.0407	**115**	**51.26**	13.29
O	15,692	181	335.78	**1.69**	198	318.41	0.922	17	−17.36	5.38
P	63,601	**518**	**511.10**	1.33	**516**	**496.28**	**1.50**	−2	−14.82	14.65
S	85,883	392	501.16	0.0445	423	464.98	0.0556	31	-36.18	**29.29**
T	3011	9	31.22	0.00365	11	35.71	0.00504	2	4.48	4.15

OSR: observed species richness, PSR: potential species richness, GMF: geometric mean of favorabilities. Maximum and minimum values are grey shaded, with maximum values in bold. National park names as in Figure 1.

Table 4. Sum values in each national park (NP) for the three biodiversity metrics in 2002 and 2015, and changes from 2002 to 2015

NP	Area (ha)	2002			2015			Change from 2002 to 2015		
		OSR	PSR	GMF	OSR	PSR	GMF	OSR	PSR	GMF
A	13,927	43.70	48.21	0.180	45.05	45.96	0.0938	1.34	−2.26	0.728
C	40,907	41.34	63.56	0.0139	48.23	74.82	0.0219	6.89	11.26	6.55
D	53,416	117.82	91.30	0.000877	118.82	90.80	0.00138	1	−0.492	**11.11**
G	33,960	71.76	101.81	0.321	79.11	94.97	0.251	7.35	−6.84	2.67
M	18,010	17.06	32.21	0.00762	49.36	46.45	0.0122	**32.30**	**14.25**	3.59
O	15,692	58.71	119.37	0.591	65.93	110.58	0.289	7.21	−8.79	1.69
P	63,601	**253.45**	**253.93**	**0.685**	**252.74**	**246.93**	**0.785**	−0.701	−7.00	7.33
S	85,883	154.40	212.22	0.0238	165.41	194.71	0.0284	11.01	−17.51	10.70
T	3011	1.42	3.20	0.000404	1.61	3.66	0.000551	0.189	0.457	0.410

Values are corrected for the proportion of the grid cell covered by a national park. OSR: observed species richness, PSR: potential species richness, GMF: geometric mean of favorabilities. Maximum and minimum values are grey shaded, with maximum values in bold. National park names as in Figure 1.

worth remarking that the Park with the highest OSR is the same that simultaneously decreased slightly in its mammal richness, and the reduction is a bit highest for PSR. As stated above, mountainous Parks concentrate highly favorable areas for mammals, but these Parks (Picos de Europa, Ordesa y Monte Perdido, Aigüestortes i Estany de Sant Maurici, Sierra de Guadarrama, and Sierra Nevada) also had less favorable areas based on the data from 2015 compared to 2002. In any case, these negative changes in PSR were moderate to low, and even the Park with the lowest mean value, i.e., Sierra de Guadarrama, was less favorable in 2015 for only two species (PSR Change = −1.9, see Figure 3). The pattern of changes in the geometric mean of favorabilities was less clear, and the results differ if we consider mean or sum values in the National Parks or whether or not the protected proportion was included. For this metric, a negative increment from 2002 to 2015 occurs when values are below one. Although this pattern is not maintained for all statistics, mountainous Parks were again highlighted as having a negative increment on the GMF (Figure 3). Therefore, special attention should be paid to mountainous Spanish National Parks if the intention is for them to maintain high levels of mammal diversity.

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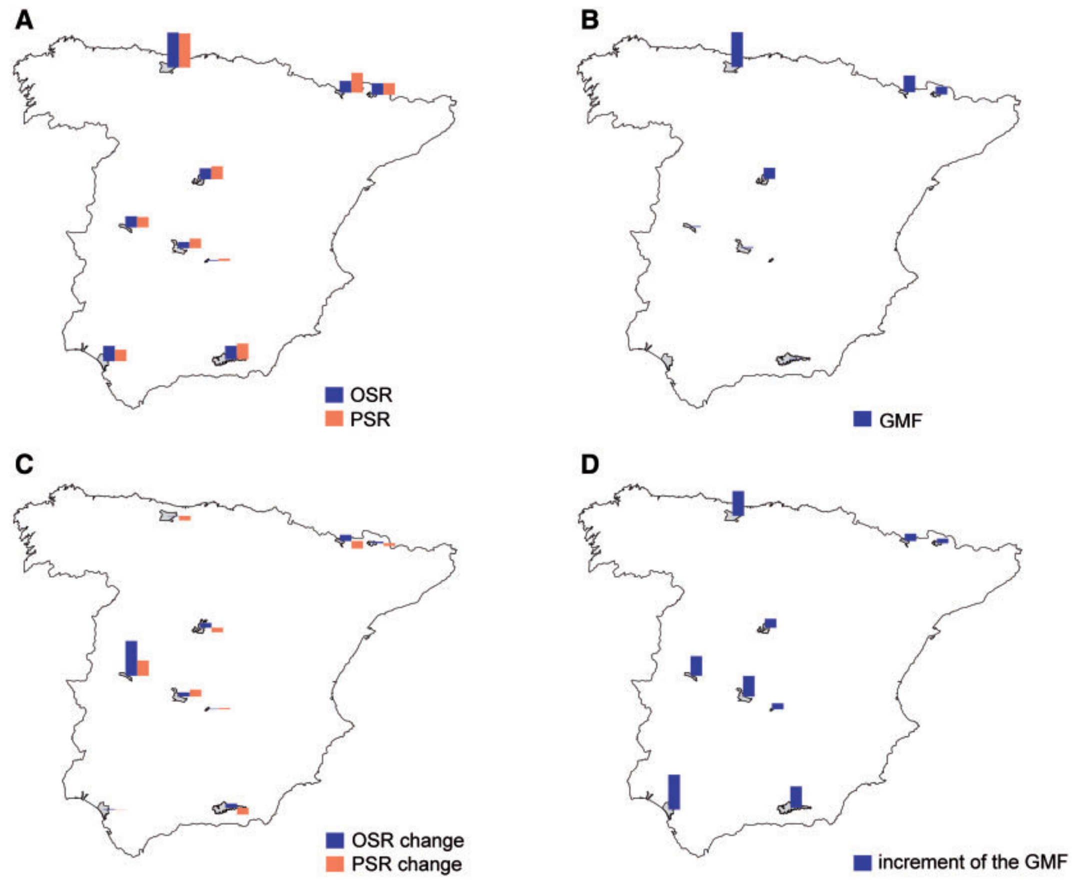

Figure 4. Mean values of the biodiversity metrics in 2015 corrected for the proportion of each cell covered by a National Park. (A) Observed (OSR) and potential species richness (PSR), (B) geometric mean of favorabilities (GMF), (C) change in observed and potential species richness from 2002 to 2015, (D) increment of the geometric mean of favorabilities from 2002 to 2015. In each map, bars are scaled by the maximum value. Exact values can be seen in Table 2.

Table 5. Pearson's correlations between biodiversity metrics corrected for the proportion of the grid cell covered by a national park

	PSR02	GMF02	OSR15	PSR15	GMF15	OSRChg	PSRChg	GMFChg
OSR02	0.898	0.619	0.983	0.899	0.766	−0.0722 ns	−0.384	0.651
PSR02	1	0.755	0.911	0.994	0.788	0.0897 ns	−0.485	0.632
GMF02		1	0.620	0.741	0.900	0.0157 ns	−0.455	0.109 ns
OSR15			1	0.924	0.753	0.111 ns	−0.293**	0.694
PSR15				1	0.786	0.154 ns	−0.391	0.669
GMF15					1	−0.0567 ns	−0.362	0.211*
OSRChg						1	0.494	0.245*
PSRChg							1	0.0311 *ns*

Correlations were performed with only the cells intersecting national parks. OSR: observed species richness, PSR: potential species richness, GMF: geometric mean of favorabilities, 02: 2002, 15: 2015, chg: change from 2002 to 2015. All correlations have $P < 0.001$, except those marked with asterisks or *ns*., $^{**}P < 0.01$, $^{*}P < 0.05$, ns: not significant.

Methodological aspects

We performed different summary statistics. However, we consider the mean values of the metrics corrected by the protected proportion (Table 2) to more realistically reflect the contribution of each National Park. Mean values are not affected by the size of the Park, whereas sum values are. The correction for the protected proportion of the cell adjusts the values and balances their importance (Díaz-Gómez et al. 2013; Sánchez-Fernández and Abellán 2015). It is not realistic to assign, for instance, all species recorded in a 100 km^2 cell to a National Park if their overlap is small. In our case, mean OSR in Picos de Europa, for instance, was around 40 species (Figure 3) but this figure dropped to ~20 when the protected proportion of the cells was considered (Table 2). Similar patterns appeared for other biodiversity metrics and National Parks.

One way to evaluate a reserve network with small numbers of Parks and small geographical coverage, such as the Spanish National Parks, is to focus attention on the contribution of each Park, rather than on the biodiversity metric itself. In other words, the intention is not to determine if the most favorable areas for a species or the highest species richness are well covered by protected

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areas in general (Scott et al. 1993; Estrada et al. 2008), but to assess how each Park contributes to this protection. Thus, the importance of each National Park is relative to the contribution of the other Parks in the network. Another possibility is to focus attention on how well species, or any biodiversity metric, are represented in the Parks. In this case, an overall value of protection is given to each species (Díaz-Gómez et al. 2013), and a species is considered adequately protected by the National Park network when the proportion of the overall value of protection covered by the network is larger than the proportion of the country covered by the network (Estrada and Real submitted). The use of one of these evaluation methods depends on the objective of the study. In this case, our aim was to gauge the contribution of each National Park to the protection of potential mammal diversity, rather than to assess how well each species was covered by the National Park network.

Concluding remarks

Mammal diversity was higher in the Spanish National Park network than outside the network, and the Parks with highest diversity values were mountainous Parks located in northern Spain. However, these high-diversity Parks had less favorable areas in 2015 compared to 2002. Mammal diversity in the Spanish National Parks should be evaluated again in the mid-long term, when updated distribution data become available, to assess whether or not the tendency of these Parks to have less favorable areas has increased. This will have important conservation implications for mountainous Parks to maintain high levels of mammal diversity.

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