

# Are species listed in the Annex II of the Habitats Directive better represented in Natura 2000 network than the remaining species? A test using Spanish bats

Fulgencio Lisón<sup>1</sup> · David Sánchez-Fernández<sup>2</sup> · José F. Calvo<sup>1</sup>

Received: 16 February 2015 / Revised: 23 April 2015 / Accepted: 21 May 2015 /  
Published online: 27 May 2015  
© Springer Science+Business Media Dordrecht 2015

**Abstract** One of the main aims of protected areas is to be effective in the conservation of target species, i.e. those of the highest conservation concern. The Natura 2000 network (N2000) of protected areas is the main pillar of European action to halt biodiversity loss. Within N2000, special areas of conservation (SACs) are designated to protect habitats and species of the highest conservation interest, i.e. habitats from Annex I and species (other than birds) listed in Annex II of the Habitat Directive. Thus, a critical and urgent task is to assess the effectiveness of N2000 in the protection of these species. Here, we used distribution data for Spanish bats to test whether the species included in Annex II are better represented in N2000 than the remaining bats found in Spain, since SAC sites were specifically designated to protect the former species. In general, we found significantly high overlapping values between species distribution and N2000 sites (both groups of species are in general over-represented in N2000). However, contrary to our expectations, N2000 (even when only SACs were considered) did not offer higher representation values for the species listed in Annex II than for other species. We found that N2000 performed well even for non-target species, and that species from Annex II could have acted as effective umbrella species for the remaining bat species. Finally, the usefulness of including a species in Annex II is discussed, and guidelines to improve the efficiency of the N2000 for bat conservation are offered.

---

Communicated by Danna J. Leaman.

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10531-015-0937-1](https://doi.org/10.1007/s10531-015-0937-1)) contains supplementary material, which is available to authorized users.

---

✉ Fulgencio Lisón  
lison@um.es

<sup>1</sup> Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain

<sup>2</sup> Institut de Biologia Evolutiva (UPF-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

**Keywords** Chiroptera · Protected areas · Management police · Special areas of conservation · Special protection areas · Umbrella species

## Introduction

Despite the fact that protected areas now cover 12 % of the world's surface (McDonald and Boucher 2010), 20 years after the United Nations Convention on Biological Diversity, global biodiversity continues to decline (Butchart et al. 2010). The most common approach followed to prevent this loss of biodiversity has been the establishment of protected area networks, which have traditionally been designed to protect a target species or group of target organisms, i.e. those of the highest conservation concern. In Europe, the Natura 2000 network of protected areas (N2000) has become the mainstay of current conservation policies (Gaston et al. 2008). N2000 is based on two European Directives: (i) the Birds Directive (79/409/EEC), which provides a list of birds for which the member states are required to designate Special Protection Areas for birds (SPAs); and (ii) the Habitat Directive (92/42/EEC), which aims to protect specific animals (other than birds), plants and habitats for which each member state is required to designate special areas of conservation (SACs). Together, SPAs and SACs form the N2000 network. In the case of the SAC sites, the presence of a species in a determined annex of the Habitat Directive could be used as a proxy of conservation interest. Therefore, the species of highest conservation interest will be those appearing in Annex II of the Habitat Directive, as they are defined as “animal or plant species of community interest whose conservation requires the designation of SAC sites”. On the other hand, the species included in Annex IV are defined as “animal or plant species of community interest in need of strict protection”.

A number of studies have evaluated the effectiveness of the N2000 network to represent given taxonomic groups, e.g. vegetation (Rosati et al. 2008), invertebrates (Abellán et al. 2007; Bosso et al. 2012; D'Amen et al. 2013; Sánchez-Fernández et al. 2008, 2013), amphibians and reptiles (Abellán and Sánchez-Fernández 2015), birds (Pellissier et al. 2013) other mammals (Maiorano et al. 2011) or even subsets of species of different taxonomic groups; e.g. species included in Annex II of the Habitat Directive (Gruber et al. 2012) or threatened species (Trochet and Schmeller 2013). However, there have been no studies focused on a comparison of the effectiveness of N2000 in representing the species for which these protected areas were designated and the remaining species of the same taxonomic group.

Bats are a model group to explore these questions because all European species are included in the annexes of Habitat Directive. A total of 14 bat species appear in Annex II and the remaining European species appear in Annex IV. Bats form a homogenous group of mammals having in general similar ecological requirements (Dietz et al. 2009; Jones et al. 2009). Bats are also a diversified and threatened group (Jones et al. 2009) whose populations, in most cases, have experienced a clear decline in recent decades (Dietz et al. 2009). In some European countries, however, an increase in the range and size of the populations has been observed due to the application of specific management measures (Haysom et al. 2013). Because of their position in food webs, they are very important species for the maintenance of ecosystem functions (Jones et al. 2009; Kunz et al. 2011; Civantos et al. 2012) and provide numerous benefits for humans (Boyles et al. 2011). Nevertheless, only two studies specifically looked at the relation between the bat

distribution and the N2000 network (Lisón et al. 2013; Zehetmair et al. 2014). It should be noted that the Iberian Peninsula has great bat biodiversity with a total of 31 species, approximately 80 % of European species (Palomo et al. 2007; Dietz et al. 2009).

Using data on bat species from mainland Spain and the Balearic Islands, we aim to check for differences in the effectiveness of N2000 sites for representing species according to the annex in which they are included and the type of protected area (SACs, SPAs or the whole N2000 network). Our hypothesis is that species of Annex II are better represented (at least in SAC sites) than the remaining species, because SACs were designated specifically to protect these species. We discuss the usefulness for a species to be included in Annex II, and provide guidelines for improving the efficiency of N2000 for bat conservation.

## Materials and methods

### Bat distribution data

The biological dataset on bat distribution in mainland Spain and the Balearic Islands was elaborated from distribution maps published in the Atlas and Red Book of Spanish terrestrial mammals (Palomo et al. 2007) with a resolution of  $10 \times 10$  km UTM cells. This dataset was updated with new records at the same resolution from our own field sampling and a comprehensive compilation of the recent bibliography (see Supporting Information).

We used data from 29 of the 31 species present in the study area. We did not include *Myotis nattereri/escalerai*, because these species have only recently been separated and their distributions are not yet known well (Ibáñez et al. 2006; Palomo et al. 2007). For the sibling species *Eptesicus serotinus* and *E. isabellinus*, we considered the distribution of the latter to be confined to South-Southeast Iberia (Andalusia and Murcia) (Ibáñez et al. 2006; Juste et al. 2013; Lisón et al. 2010, 2011, 2014), while the former is distributed throughout the rest of the Iberian Peninsula. Although there may be a contact zone (Santos et al. 2014), molecular data reinforces this allopatric distribution in Spain (Juste et al. 2013). Eleven out of the 29 species considered are present in Annex II of Habitat Directive and 18 in Annex IV (Table 1).

### Evaluation of effectiveness of protected areas

We calculated the percentage of area of each cell (UTM  $10 \times 10$  km) of the study area overlapped by SACs, SPAs and the whole N2000 network using ArcGis 9.3 (ESRI, Redlands, CA, USA). Then, the level of representation of each species was calculated as the mean percentage overlap (MPO) between species distribution (grid cells in which the species occurs) and the protected area system considered. The level of representation of a given species was compared with what would be expected by chance given its distribution range (number of grid cells occupied). To do this, we compared the MPO of each species with the values expected from 10,000 random distributions with an equal number of grid cells (i.e. equivalent range size) selected from the entire study area, following the approach proposed by Sánchez-Fernández and Abellán (2015). A two-tailed test was used to estimate the probability that the observed value was significantly ( $\alpha = 0.05$ ) greater or smaller than the null distribution. This allowed us to obtain a significance value and so, identify those species significantly under and over- represented by each protected area networks.

**Table 1** Mean percentage overlap (MPO; mean  $\pm$  95 % CI) by each bat species in the different systems of protected areas analysed (SAC, SPA and N2000)

Species	Species code	Grids number	SAC (mean $\pm$ 95 % CI)	SPA (mean $\pm$ 95 % CI)	N2000 (mean $\pm$ 95 % CI)	Annex of Habitat Directive	IUCN category in Spain
<i>Barbastella barbastellus</i>	Bbar	207	44.1 $\pm$ 4.6	31.4 $\pm$ 4.7	45.7 $\pm$ 4.7	II	NT
<i>Eptesicus isabellinus</i>	Eisa	112	30.2 $\pm$ 6.7	24.9 $\pm$ 6.2	33.2 $\pm$ 6.5	IV	–
<i>Eptesicus serotinus</i>	Eser	726	24.7 $\pm$ 2.2	18.4 $\pm$ 2.1	28.0 $\pm$ 2.3	IV	–
<i>Hypsugo savii</i>	Hsav	344	41.7 $\pm$ 3.5	31.1 $\pm$ 3.6	44.0 $\pm$ 3.6	IV	NT
<i>Myotis alcathoe</i>	Malc	16	69.0 $\pm$ 14.7	35.3 $\pm$ 23.2	69.0 $\pm$ 14.7	IV	–
<i>Myotis bechsteini</i>	Mbec	79	59.3 $\pm$ 7.9	46.2 $\pm$ 8.8	59.6 $\pm$ 7.9	II	Vu A2ab(iii)
<i>Myotis blythii</i>	Mbly	221	35.0 $\pm$ 4.5	25.3 $\pm$ 4.5	36.9 $\pm$ 4.6	II	Vu A2ac
<i>Myotis capaccinii</i>	Mcap	107	21.5 $\pm$ 4.7	17.0 $\pm$ 4.4	25.5 $\pm$ 4.9	II	EN B2ab(ii)
<i>Myotis daubentonii</i>	Mdau	635	27.3 $\pm$ 2.5	20.4 $\pm$ 2.5	29.7 $\pm$ 2.6	IV	–
<i>Myotis emarginatus</i>	Mema	296	34.8 $\pm$ 3.6	24.7 $\pm$ 3.6	37.9 $\pm$ 3.7	II	Vu A2c
<i>Myotis myotis</i>	Mmyo	654	27.7 $\pm$ 2.5	21.8 $\pm$ 2.4	30.8 $\pm$ 2.6	II	Vu A2ac
<i>Myotis mystacinus</i>	Mmys	89	49.8 $\pm$ 7.4	30.8 $\pm$ 8.0	50.2 $\pm$ 7.4	IV	NT
<i>Miniopterus schreibersii</i>	Msch	674	31.8 $\pm$ 2.5	23.7 $\pm$ 2.5	34.2 $\pm$ 2.6	II	Vu A2ac
<i>Nyctalus lasiopterus</i>	Nlas	69	64.7 $\pm$ 7.6	52.3 $\pm$ 9.2	65.1 $\pm$ 7.6	IV	Vu B1 ab(iii)D1
<i>Nyctalus leisleri</i>	Nlei	374	44.2 $\pm$ 3.6	32.2 $\pm$ 3.7	45.8 $\pm$ 3.6	IV	NT
<i>Nyctalus noctula</i>	Nnoc	20	23.3 $\pm$ 15.6	14.8 $\pm$ 12.9	24.0 $\pm$ 16.1	IV	Vu B1 ab(iii)D1
<i>Plecotus auritus</i>	Paur	233	43.1 $\pm$ 4.6	27.3 $\pm$ 4.6	44.2 $\pm$ 4.6	IV	NT
<i>Plecotus austriacus</i>	Paus	616	28.3 $\pm$ 2.5	22.4 $\pm$ 2.5	32.5 $\pm$ 2.6	IV	NT
<i>Plecotus macbullaris</i>	Pmac	4	93.9 $\pm$ 5.9	87.3 $\pm$ 23.1	93.9 $\pm$ 5.9	IV	–
<i>Pipistrellus nathusii</i>	Pnat	34	31.1 $\pm$ 9.3	19.0 $\pm$ 8.4	31.2 $\pm$ 9.3	IV	NT
<i>Pipistrellus kuhlii</i>	Pkuh	663	27.6 $\pm$ 2.3	21.2 $\pm$ 2.3	30.1 $\pm$ 2.4	IV	–
<i>Pipistrellus pipistrellus</i>	Ppip	1983	24.2 $\pm$ 1.4	22.1 $\pm$ 1.4	29.3 $\pm$ 1.4	IV	LC
<i>Pipistrellus pygmaeus</i>	Ppyg	1662	24.1 $\pm$ 1.5	23.3 $\pm$ 1.5	29.5 $\pm$ 1.6	IV	LC

**Table 1** continued

Species	Species code	Grids number	SAC (mean ± 95 % CI)	SPA (mean ± 95 % CI)	N2000 (mean ± 95 % CI)	Annex of Habitat Directive	IUCN category in Spain
<i>Rhinolophus euryale</i>	Reur	431	32.6 ± 3.2	26.5 ± 3.3	35.8 ± 3.2	II	Vu A2ac
<i>Rhinolophus ferrumequinum</i>	Rfer	1167	29.8 ± 1.9	22.5 ± 1.8	32.7 ± 1.9	II	NT
<i>Rhinolophus hipposideros</i>	Rhip	997	30.3 ± 2.0	23.0 ± 2.0	32.6 ± 2.0	II	NT
<i>Rhinolophus mehelyi</i>	Rmeh	166	32.3 ± 5.6	26.3 ± 5.5	35.2 ± 5.7	II	EN A3c
<i>Tadarida teniotis</i>	Tten	826	30.4 ± 2.3	26.4 ± 2.3	35.2 ± 2.3	IV	NT
<i>Vespertilio murinus</i>	Vmur	5	60.3 ± 48.3	51.3 ± 42.4	60.3 ± 48.3	IV	–
All grids		5436	23.7 ± 0.8	19.6 ± 0.8	27.7 ± 0.8		

Also, the Annex of Habitat Directive where the species occurs and its IUCN category in Spain (Palomo et al. 2007)

Assessments were performed separately for SACs, SPAs and N2000. This approach has certain advantages over traditional “gap analyses” (Scott et al. 1993; Araújo et al. 2007) to assess the effectiveness of protected areas, since gap analysis require the choice of arbitrary targets and thresholds which can greatly influence the obtained results, i.e. the results could be completely different, depending on (i) the threshold used to solve the mismatch between the spatial resolution of data form species and protected areas (Araújo 2004) and (ii) the different representation targets used to consider a species as represented by a protected area network (Vimal et al. 2011). The approach used here avoids these typical methodological uncertainties and is particularly useful when the aim is to explore differences in the effectiveness of protected area networks in representing species with distinct features and varying range sizes. Then, using linear mixed-effect models (LME), we tested whether bat species included in Annex II have higher MPO values than the remaining species (Annex IV). All analyses were performed with R software (R Core Team 2014).

Finally, we analysed the official technical reports of each SAC site (available at the Spanish Government website <http://www.magrama.gob.es/es/biodiversidad/temas/espacios-protegidos/red-natura-2000/lic.aspx>) to look for sites with occurrences of both Annex II and Annex IV bat species officially acknowledged. We considered SAC sites designated exclusively for bats when only appeared bats in the species lists of the technical report.

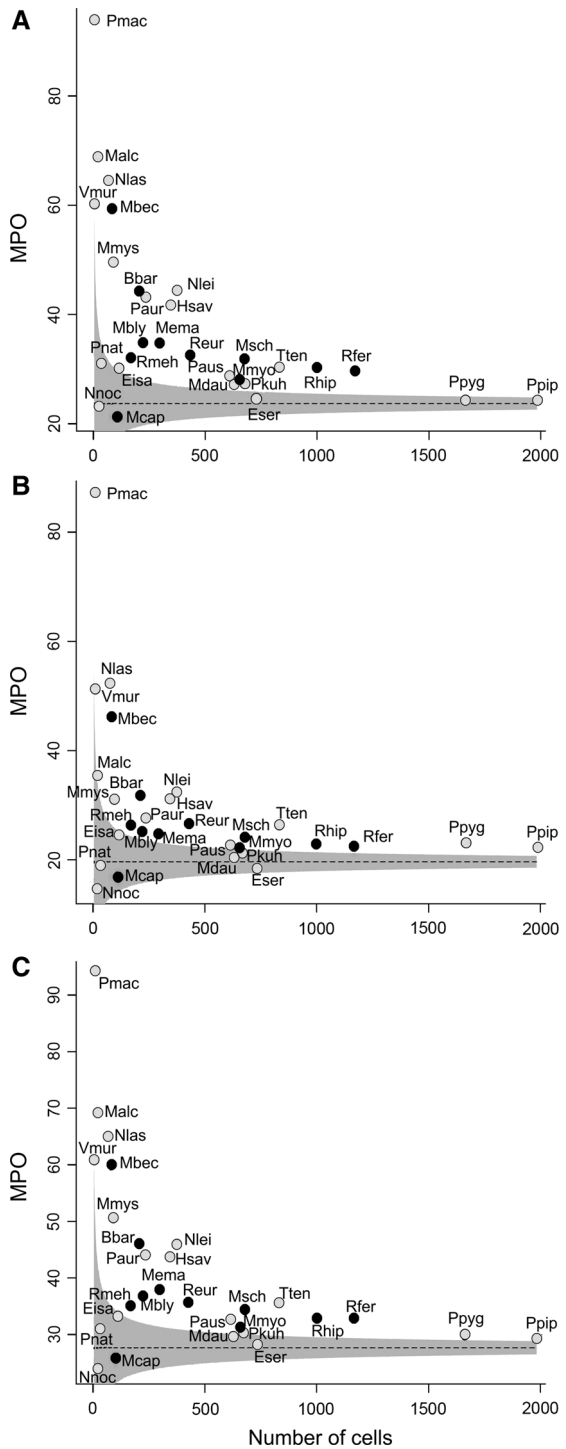
## Results

Of the 5436  $10 \times 10$  km UTM cells covering the study area, 3062 (56.3 %) showed the occurrence of at least one bat species. The species with the widest distributions in our study area were *Pipistrellus pipistrellus* (36.5 %), *Pipistrellus pygmaeus* (30.6 %) and *Rhinolophus ferrumequinum* (21.5 %). On the other hand, *Myotis alcaethoe* (0.3 %), *Vespertilio murinus* (0.09 %) and *Plecotus macrobullaris* (0.07 %) showed the narrowest distributions (Table 1).

The average MPO for all species with SACs, SPAs and N2000 was 38.5, 29.3 and 40.8 %, respectively (Table 1). In general, *Myotis capaccinii* and *Nyctalus noctula* showed the lowest MPO values, while *Myotis alcaethoe* and *Plecotus macrobullaris* showed the highest values of protection (Table 1; Fig. 1).

Comparing these values with those obtained at random (using the same number of cells), a total of 23, 22 and 23 out of the 29 species studied could be considered as efficiently represented by SACs, SPAs and N2000 respectively, while the remaining species could be considered as being randomly represented (Table 2). Thus, no species was found to be under-represented by any protected area network. Of the randomly represented species, all but *M. capaccinii* (Annex II) were species included in the Annex IV. However, the MPO values for the species included in Annex II were not significantly different from those obtained for the species included in Annex IV, regardless of the protected area network considered [SAC sites (LME:  $t = 0.72$ , d.f. = 27,  $P = 0.47$ ); SPA sites (LME:  $t = 0.42$ , d.f. = 27,  $P = 0.67$ ); N2000 (LME:  $t = 0.68$ , d.f. = 27,  $P = 0.49$ )]. However, the average MPO values for species included in Annex IV were higher in all protected area systems (Fig. 2). Only one target species (*M. capaccinii*) had MPO values higher than would be randomly expected, while there were five non-target species with MPO values higher than would be randomly expected (Fig. 1).

**Fig. 1** Mean percentage overlap (MPO) between bat species distribution and protected area networks (**a** SAC; **b** SPA and **c** N2000). Species included in Annex II of the Habitat Directive are represented by *red dots*, and the remaining species (all included in Annex IV) are represented by *blue dots*. The *dashed lines* show mean percentage overlap from 10,000 randomizations at each range size level (number of cells), *grey surface* indicates the range of the 95th percentile of the randomized data. See species code in Table 1



**Table 2** Mean percentage overlap between bat species distribution and SAC, SPA, and N2000 networks

Species	SAC										SPA										N2000									
	MPO	MPO.r	CI.l	CI.u	Rank	P value	MPO	MPO.r	CI.l	CI.u	Rank	P value	MPO	MPO.r	CI.l	CI.u	Rank	P value	MPO	MPO.r	CI.l	CI.u	Rank	P value						
	Bbar	44.12	23.71	19.50	28.07	10,000	0	31.45	19.60	15.59	23.79	10,000	0	45.75	27.65	23.28	32.15	10,000	0											
Eisa	30.26	23.68	17.95	29.66	9846	0.0308	24.86	19.59	14.21	25.42	9637	0.0726	33.17	27.65	21.71	33.83	9603	0.0794												
Eser	24.69	23.71	21.58	25.87	8129	0.3742	18.42	19.62	17.53	21.77	1291	0.2582	28.04	27.67	25.43	29.93	6268	0.7464												
Hsav	41.74	23.69	20.51	26.96	10,000	0	31.15	19.60	16.49	22.75	10,000	0	43.99	27.67	24.35	31.10	10,000	0												
Maal	68.96	23.61	9.42	40.41	10,000	0	35.31	19.56	6.03	35.60	9725	0.055	68.97	27.52	12.23	44.64	10,000	0												
Mbec	59.32	23.66	16.87	30.93	10,000	0	46.20	19.60	13.20	26.53	10,000	0	59.56	27.69	20.69	35.17	10,000	0												
Mbly	35.00	23.69	19.71	27.83	10,000	0	25.31	19.62	15.77	23.69	9966	0.0068	36.93	27.68	23.39	32.03	10,000	0												
Mcap	21.55	23.69	17.87	29.68	2429	0.4858	16.99	19.57	14.10	25.51	1900	0.38	25.48	27.68	21.55	34.15	2479	0.4958												
Mdau	27.31	23.70	21.39	26.02	9985	0.003	20.37	19.63	17.42	21.89	7446	0.5108	29.75	27.68	25.33	30.16	9511	0.0978												
Mema	34.80	23.68	20.14	27.30	10,000	0	24.70	19.66	16.33	23.16	9979	0.0042	37.87	27.64	24.07	31.43	10,000	0												
Mmyo	27.71	23.71	21.46	26.07	9994	0.0012	21.82	19.62	17.42	21.88	9709	0.0582	30.84	27.66	25.31	30.07	9942	0.0116												
Mmys	49.81	23.73	17.32	30.52	10,000	0	30.76	19.65	13.52	26.17	9997	0.0006	50.20	27.65	21.10	34.59	10,000	0												
Msch	31.82	23.69	21.47	25.94	10,000	0	23.74	19.65	17.45	21.89	9995	0.001	34.23	27.66	25.34	30.00	10,000	0												
Nlas	64.70	23.67	16.47	31.28	10,000	0	52.29	19.66	12.76	27.10	10,000	0	65.15	27.68	20.15	35.69	10,000	0												
Nlei	44.24	23.71	20.64	26.91	10,000	0	32.21	19.64	16.65	22.80	10,000	0	45.85	27.64	24.50	30.92	10,000	0												
Nnoc	23.32	23.69	10.71	38.65	4971	0.9942	14.83	19.70	7.42	34.19	2523	0.5046	24.04	27.66	14.00	42.81	3212.5	0.6425												
Paur	43.12	23.76	19.89	27.80	10,000	0	27.29	19.66	15.88	23.64	10,000	0	44.25	27.68	23.56	31.94	10,000	0												
Paus	28.37	23.69	21.34	26.04	9997	0.0006	22.42	19.61	17.38	21.93	9905	0.019	32.50	27.64	25.26	30.12	9999	0.0002												
Pmac	93.95	23.78	0.61	59.78	9999	0.0002	87.28	19.66	0	53.78	9999	0.0002	93.96	27.48	1.40	63.57	9999	0.0002												
Pkuh	27.60	23.72	21.50	26.05	9997	0.0006	21.21	19.63	17.39	21.90	9180	0.164	30.16	27.66	25.34	30.03	9803	0.0394												
Pnat	31.14	23.76	13.71	35.23	9054	0.1892	18.99	19.71	10.02	30.72	4657	0.9314	31.20	27.62	17.02	38.93	7397	0.5206												
Ppip	24.23	23.70	22.56	24.82	8251	0.3498	22.10	19.63	18.56	20.71	10,000	0	29.33	27.67	26.49	28.85	9971	0.0058												
Ppyg	24.13	23.70	22.43	24.98	7374	0.5252	23.26	19.62	18.40	20.90	10,000	0	29.51	27.67	26.34	29.03	9957	0.0086												
Reur	32.61	23.70	20.87	26.61	10,000	0	26.49	19.63	16.89	22.46	10,000	0	35.80	27.65	24.66	30.63	10,000	0												

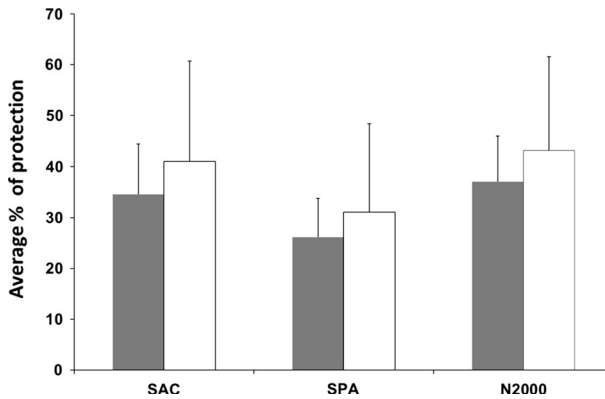


**Table 2** continued

Species	SAC					SPA					N2000							
	MPO	MPO.r	CI.l	CI.u	Rank	P value	MPO	MPO.r	CI.l	CI.u	Rank	P value	MPO	MPO.r	CI.l	CI.u	Rank	P value
Rfer	29.83	23.70	22.07	25.34	10,000	0	22.52	19.64	18.07	21.22	9999	0.0002	32.74	27.66	25.95	29.37	10,000	0
Rhip	30.33	23.70	21.94	25.50	10,000	0	23.03	19.63	17.91	21.40	9999	0.0002	32.58	27.66	25.82	29.52	10,000	0
Rmeh	32.25	23.67	18.98	28.62	9994	0.0012	26.29	19.59	15.04	24.34	9969	0.0062	35.17	27.62	22.85	32.60	9979	0.0042
Tten	30.43	23.70	21.73	25.71	10,000	0	26.36	19.62	17.76	21.56	10,000	0	35.25	27.65	25.56	29.75	10,000	0
Vmur	60.31	23.60	1.26	55.04	9884.5	0.0231	51.32	19.61	0	50.56	9774	0.0452	60.31	27.76	2.69	60.19	9754	0.0492

Summary of the values expected from 10,000 random draws of an equal number of grid cells (i.e. equivalent range size) selected from the entire study area. See species code in Table 1

MPO mean percentage overlap, MPO.r MPO random, CI.l lower 95 % confidence interval, CI.u upper 95 % confidence interval



**Fig. 2** Average percentage of protection (mean  $\pm$  SD) offered by each protected area systems. Grey bars represent Annex II bat species and white bars Annex IV bat species

On the other hand, for a total of 1249 SAC sites, we found that technical reports of 546 (43.7 %) included an Annex II bat species, while only 137 (11.0 %) included an Annex IV bat species. A total of 81 SAC sites (6.5 %) were designated exclusively for bats.

## Discussion

In general, high overlapping values were found between protected areas and species distributions. Our results showed that most bat species in Spain are effectively represented in N2000 sites. This agrees with the results of previous studies demonstrating a relatively good performance of the whole N2000 network to protect species included in the Annex II of the Habitat Directive (Gruber et al. 2012) or threatened species (Trochet and Schmeller 2013). However, contrary to what we expected, N2000 sites did not offer higher protection levels for species included in the Annex II than for the remaining species (Annex IV), despite the fact that SACs were designated specifically to protect the former species. This strategy of designating reserves to cover target species usually leads to the under-representation of many other important components of biodiversity (e.g. Dimitrakopoulos et al. 2004; Sánchez-Fernández et al. 2008). However, in our case, non-target species enjoyed a similar level of protection to the species for which these protected areas were designated; more specifically, species in both groups were generally over-represented by N2000 network.

A possible explanation for the high overlapping values found for both sets of bat species is that many protected areas are located in mountainous areas of scarce interest for agriculture or other human uses (e.g. urban development), and where there are a large number of caves available for bats. This would also explain why several species from Annex IV (*Plecotus macrobullaris*, *Nyctalus lasiopterus*, *Myotis alcaethoe*, and *Vespertilio murinus*) and two from Annex II (*Barbastella barbastellus* and *Myotis bechsteinii*), all with forest-dwelling habits, showed the highest protection values in SAC sites. Also, this phenomenon could be due to sampling bias. These species are difficult to detect and recognize, and they were probably only detected in the most intensively surveyed areas, i.e., within protected

areas, which reinforces the need to make detailed inventories in areas outside the protected areas (Hochkirch et al. 2013).

As expected, widely distributed bats, such as *Pipistrellus pipistrellus* and *P. pygmaeus*, had very similar MPO values to those that would have been obtained if the same number of cells were chosen randomly. Surprisingly, the only bat considered as “Endangered” under Spanish legislation (Palomo et al. 2007), *Myotis capaccinii*, showed the lowest MPO values in all cases. This species is not effectively represented by any protected area system (Fig. 1), probably because it is a cave-dwelling bat that shows a preference for riparian habitats (Almenar et al. 2006, 2009; Biscardi et al. 2007). SACs designated to protect cave-dwelling species are limited to the entrances of caves. In most cases, these caves are small in size and cannot guarantee the conservation of suitable habitats for these species, which would normally be beyond the scope of the SACs (Lisón et al. 2013; Rainho and Palmeirim 2013). Also, some cave-dwelling bats are flexible in the selection of their roosts and may use other types of roost (Knight and Jones 2009; Dietz et al. 2009; Lisón et al. 2013), usually not far away from their optimal habitats (Daniel et al. 2008; Dietz et al. 2009), since the distance to the roost would probably condition their use (Rainho and Palmeirim 2011). Furthermore, the protection of riverine habitats usually creates social conflict, especially in the Mediterranean countries, where water is a scarce resource and riparian zones are threatened by intense human pressure (Martínez-Fernández et al. 2000, 2013; Bruno et al. 2014). Such riparian zones have a great importance for bats because they are used for feeding and drinking, as well as serving as corridors and landscape landmarks (e.g. Verboom and Huitema 1997; Russo and Jones 2003; Monadjem and Reside 2008; Lundy and Montgomery 2010; Akasaka et al. 2012; O’Keefe et al. 2013). Furthermore, conservation policies do not usually take into account the importance of ecological processes between rivers and their adjacent zones (Abellán et al. 2007; Bruno et al. 2014; Ormerod 2014).

The Habitat Directive states that “This network composed of sites hosting the natural habitat types listed in Annex I and habitat of the species listed in Annex II, shall enable the natural types and the species’ habitat concerned to be maintained or, where appropriate, restored at a favourable conservation status in their natural range”. We have demonstrated that there are no differences in the representation provided by N2000 to species of Annex II and the remaining species. This merits two reflexions: (i) species from the Annex II could have acted as effective umbrella species for the remaining bat species as they have similar ecological requirements and (ii) the management measures taken within N2000 would be expected to focus on protecting species included in the Annex II, at least. However, surprisingly, the two horseshoe bats whose populations are in pronounced decline (*Rhinolophus euryale* and *R. mehelyi*), especially in Mediterranean areas (Almenar et al. 2007; Flaquer et al. 2010; Lisón et al. 2011), also showed a high percentage of overlap with protected areas. This indicates that the presence of a species within an N2000 site (even with multiple records) is not a guarantee of long-term survival (even for Annex II species); in this case there is certainly an absence of specific management measures to ensure the conservation of these species in N2000 areas. It is likely that both species were affected by other factors, such as human disturbance of their roosts or the absence of insect-prey as a consequence of intensive agricultural practices or global warming (Maes et al. 2012). In this sense, it should be noted that only the 11 % of SAC sites officially recorded a bat species listed in Annex IV. A total of 81 SAC sites (6.5 %) were designated exclusively for bat species.

Due to the high cost that the management and maintenance of protected areas involves, it seems logical to evaluate their effectiveness for biodiversity protection in general and, especially, for the most threatened groups, like bats. To ensure that the N2000 network

achieves its goal of preserving the biodiversity in general and bats in particular, and to establish a coherent protected areas network, it is necessary to: (i) maximize our knowledge of biodiversity and its distribution (Amorim et al. 2014); (ii) establish the degree to which species are threatened by means of objective criteria (e.g. IUCN Red List) and identify areas with high conservation value; (iii) prioritize management measures to conserve bat species with a high risk of extinction and their habitats; (iv) take into account the cryptic diversity of bats (Ibáñez et al. 2006); (v) include suitable habitat for bat populations (Lisón et al. 2013; Rainho and Palmeirim 2013); and (vi) regularly examine the threatened categories and prioritization processes (Abellán et al. 2007; Loucks et al. 2008; McDonald and Boucher 2010; Cox and Underwood 2011; D’Amen et al. 2013; Hochkirch et al. 2013). This is very important if we are to improve and develop more effective management plans, bring together cultural services and values, improve connectivity and consider future environmental scenarios (Maiorano et al. 2007; McDonald and Boucher 2010; Araújo et al. 2011; Alagador et al. 2012; Rodríguez-Rodríguez and Martínez-Vega 2012; Crouzeilles et al. 2013; Piquer-Rodríguez et al. 2012; Skokanová and Eremiášová 2013; Venter et al. 2014; Kati et al. 2015), and also avoid social conflicts (Grodzinska-Jurczak and Cent 2011). In sum, government should remove redundant protection areas, assign more resources to obtaining comprehensive inventories of biodiversity, and approve integral management plans for these protected areas. It is also necessary to negotiate with and compensate those owners with properties adjacent to Natura 2000 network or the owners of cave-dwelling bats roosts.

In conclusion, our results show that although the species of community interest listed in Annex II of the Habitat Directive do not enjoy a higher level protection in Spain than other species, both groups are generally over-represented in the N2000 network. This underlines the usefulness of some of conservation measures, such as the inclusion of species in Annex II of the Habitat Directive, at least in the cases like Spanish bats, as these species could act as effective umbrella species. However, this must be accompanied by integral measures of biodiversity management within protected areas (not focused only on the species by which these protected areas have been designated). In the absence of these management plans and/or recuperation plans, their inclusion in protected areas, in other words “virtual protection”, will not mitigate the decline in their populations.

**Acknowledgements** We are grateful for the important contributions of bat workers and SECEMU members to the development of the distribution of bat fauna of Spain. We are also grateful for the support and the comments of the people of “Ecosistemas Mediterráneos” and “Ecología Acuática” research groups (University of Murcia), especially Félix Picazo. We thank Philip Thomas and Ángeles Haz for correcting the English. The first version of the manuscript was considerably improved by the comments of anonymous reviewers and the editors. D. S.-F. was supported by a postdoctoral Grant (Juan de La Cierva programme) from Spanish Ministry of Economy and Competitiveness.

## References

- Abellán P, Sánchez-Fernández D (2015) A gap analysis comparing the effectiveness of Natura 2000 and national protected area networks in representing European amphibians and reptiles. *Biodivers Conserv*. doi:10.1007/s10531-015-0862-3
- Abellán P, Sánchez-Fernández D, Velasco J, Millán A (2007) Effectiveness of protected area networks in representing freshwater biodiversity: the case of a Mediterranean river basin (south-eastern Spain). *Aquat Conserv* 17:361–374. doi:10.1002/aqc.778
- Akasaka T, Akasaka M, Nakamura F (2012) Scale-independent significance of river and riparian zones on three sympatric *Myotis* species in an agricultural landscape. *Biol Conserv* 145:15–23. doi:10.1016/j.biocon.2011.08.017

- Alagador D, Triviño M, Cerdeira JO, Brás R, Cabeza M, Araújo MB (2012) Linking like with like: optimising connectivity between environmentally-similar habitats. *Landsc Ecol* 27:291–301. doi:[10.1007/s10980-012-9704-9](https://doi.org/10.1007/s10980-012-9704-9)
- Almenar D, Aihartza JR, Goiti U, Salsamendi E, Garín I (2006) Habitat selection and spatial use by the trawling bat *Myotis capaccinii* (Bonaparte, 1837). *Acta Chiropterol* 8:157–167
- Almenar D, Monsalve MA, Alcocer A, Castelló AJ (2007) *Rhinolophus mehelyi* Matschie, 1901. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, pp 151–152
- Almenar D, Aihartza JR, Goiti U, Salsamendi E, Garín I (2009) Foraging behaviour of the long-fingered bat *Myotis capaccinii*: implications for conservation and management. *Endanger Species Res* 8:60–78. doi:[10.3354/esr00183](https://doi.org/10.3354/esr00183)
- Amorim F, Carvalho SB, Honrado J, Rebelo H (2014) Designing optimized multi-species monitoring networks to detect range shifts driven by climate change: a case study with bats in the North of Portugal. *PLoS One* 9:e87291. doi:[10.1371/journal.pone.0087291](https://doi.org/10.1371/journal.pone.0087291)
- Araújo MB (2004) Matching species with reserves: uncertainties from using data at different resolutions. *Biol Conserv* 118:533–538. doi:[10.1016/j.biocon.2003.10.006](https://doi.org/10.1016/j.biocon.2003.10.006)
- Araújo MB, Lobo JM, Moreno JC (2007) The effectiveness of Iberian protected areas in conserving terrestrial biodiversity. *Conserv Biol* 21:1423–1432. doi:[10.1111/j.1523-1739.2007.00827.x](https://doi.org/10.1111/j.1523-1739.2007.00827.x)
- Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecol Lett* 14:484–492. doi:[10.1111/j.1461-0248.2011.01610.x](https://doi.org/10.1111/j.1461-0248.2011.01610.x)
- Biscardi S, Russo D, Casciani V, Cesarini D, Mei M, Boitani L (2007) Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. *J Zool* 273:372–381. doi:[10.1111/j.1469-7998.2007.00337.x](https://doi.org/10.1111/j.1469-7998.2007.00337.x)
- Bosso L, Rebelo H, Garonna AP, Russo D (2012) Modelling geographic distribution and detecting conservation gaps in Italy for the threatened beetle *Rosalia alpina*. *J Nat Conserv* 21:72–80. doi:[10.1016/j.jnc.2012.10.003](https://doi.org/10.1016/j.jnc.2012.10.003)
- Boyles JG, Cryan PM, McCracken GF, Kunz TH (2011) Economic importance of bat in agriculture. *Science* 332:41–42. doi:[10.1126/science.1201366](https://doi.org/10.1126/science.1201366)
- Bruno D, Belmar O, Sánchez-Fernández D, Guareschi S, Millán A, Velasco J (2014) Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales. *Ecol Indic* 45:456–464. doi:[10.1016/j.ecolind.2014.05.051](https://doi.org/10.1016/j.ecolind.2014.05.051)
- Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genove P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández-Morcillo M, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear JR, Skolnik B, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R (2010) Global biodiversity: indicators of recent declines. *Science* 328:1164–1168. doi:[10.1126/science.1187512](https://doi.org/10.1126/science.1187512)
- Civantos E, Thuiller W, Maiorano L, Guisan A, Araújo MB (2012) Potential impacts of climate change on ecosystem services in Europe: the case of pest control by vertebrates. *Bioscience* 62:658–666. doi:[10.1525/bio.2012.62.7.8](https://doi.org/10.1525/bio.2012.62.7.8)
- Cox RL, Underwood EC (2011) The importance of conserving biodiversity outside of protected areas in Mediterranean ecosystems. *PLoS One* doi:[10.1371/journal.pone.0014508](https://doi.org/10.1371/journal.pone.0014508)
- Crouzeilles R, Lorini ML, Viveiros-Grelle CE (2013) The importance of using sustainable use protected areas for functional connectivity. *Biol Conserv* 159:450–457. doi:[10.1016/j.biocon.2012.10.023](https://doi.org/10.1016/j.biocon.2012.10.023)
- D'Amen M, Bombi P, Campanaro A, Zapponi L, Bologna MA, Mason F (2013) Protected areas and insect conservation: questioning the effectiveness of Natura 2000 network for saproxylic beetles in Italy. *Anim Conserv* 16:370–378. doi:[10.1111/acv.12016](https://doi.org/10.1111/acv.12016)
- Daniel S, Korine C, Pinshow B (2008) Central-place foraging in nursing, arthropod-gleaning bats. *Can J Zool* 86:623–626. doi:[10.1139/Z08-041](https://doi.org/10.1139/Z08-041)
- Dietz C, von Helversen O, Nill D (2009) Bats of Britain, Europe & Northwest Africa. A & C Black Publishers Ltd, London
- Dimitrakopoulos PG, Mentsas D, Troumbis AY (2004) Questioning the effectiveness of the Natura 2000 special areas of conservation strategy: the case of Crete. *Glob Ecol Biogeogr* 13:199–207. doi:[10.1111/j.1466-822X.2004.00086.x](https://doi.org/10.1111/j.1466-822X.2004.00086.x)
- Flaquer C, Puig X, Fàbregas E, Guixé D, Torre I, Ràfols RG, Páramo F, Camprodon J, Cumplido JM, Ruíz-Jarillo R, Baucells A, Freixas L, Arrizabalaga A (2010) Revisión y aportación de datos sobre quirópteros de Catalunya: Propuesta de lista roja. *Galemys* 22:29–61
- Gaston KJ, Jackson SF, Nagy A, Cantú-Salazar A, Johnson M (2008) Protected areas in Europe: principle and practice. *Ann NY Acad Sci* 1134:97–119. doi:[10.1196/annals.1439.006](https://doi.org/10.1196/annals.1439.006)

- Grodzinska-Jurczak M, Cent J (2011) Expansion of nature conservation areas: problems with Natura 2000 implementation in Poland? *Environ Manag* 47:11–27. doi:[10.1007/s00267-010-9583-2](https://doi.org/10.1007/s00267-010-9583-2)
- Gruber B, Evans D, Henle K, Bauch B, Schmeller D, Dziock F, Henry PY, Lengyel S, Margules C, Dormann C (2012) Mind the gap!: How well does Natura 2000 cover species of European interest? *Nat Conserv* 3:45–62. doi:[10.3897/natureconservation.3.3732](https://doi.org/10.3897/natureconservation.3.3732)
- Haysom K, Dekker J, Russ J, van der Meij T, van Strien A (2013) European bat population trends: a prototype biodiversity indicator. EEA Technical report 19/2013. Brussels. <http://www.eea.europa.eu/publications/european-bat-population-trends-2013>
- Hochkirch A, Schmitt T, Beninde J, Hiery M, Kinitz T, Kirschev J, Matenaar D, Rohde K, Stofen A, Wagner N, Zink A, Lötters S, Veith M, Proelss A (2013) Europe needs a new vision for a Natura 2000 network. *Conserv Lett* 6:462–467. doi:[10.1111/conl.12006](https://doi.org/10.1111/conl.12006)
- Ibáñez C, García-Mudarra JL, Ruedi M, Stadelmann B, Juste J (2006) The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterol* 8:277–297. doi:[10.3161/1733-5329\(2006\)8\[277:TICTCD\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2006)8[277:TICTCD]2.0.CO;2)
- Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. *Endanger Species Res* 8:93–115. doi:[10.3354/esr00182](https://doi.org/10.3354/esr00182)
- Juste J, Benda P, García-Mudarra JL, Ibáñez C (2013) Phylogeny and systematics of Old World serotine bats (genus *Eptesicus*, Vespertilionidae, Chiroptera): an integrative approach. *Zool Scr* 42:441–457. doi:[10.1111/zsc.12020](https://doi.org/10.1111/zsc.12020)
- Kati V, Hovardas T, Dieterich M, Ibisch PL, Mihok M, Selva N (2015) The challenge of implementing the European network of protected areas Natura 2000. *Conserv Biol* 29:260–270. doi:[10.1111/cobi.12366](https://doi.org/10.1111/cobi.12366)
- Knight T, Jones G (2009) Importance of night roosts for bat conservation: roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*. *Endanger Species Res* 8:79–86. doi:[10.3354/esr00194](https://doi.org/10.3354/esr00194)
- Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. *Ann NY Acad Sci* 1223:1–38. doi:[10.1111/j.1749-6632.2011.06004.x](https://doi.org/10.1111/j.1749-6632.2011.06004.x)
- Lisón F, Yelo ND, Haz A, Calvo JF (2010) Contribución al conocimiento de la distribución de la fauna quiropterológica de la Región de Murcia. *Galemys* 22:11–28
- Lisón F, Aledo E, Calvo JF (2011) Los murciélagos (Mammalia: Chiroptera) de la Región de Murcia (SE España): distribución y estado de conservación. *Anales de Biología* 33:79–92
- Lisón F, Palazón JA, Calvo JF (2013) Effectiveness of the Natura 2000 Network for the conservation of cave-dwelling bats in a Mediterranean region. *Anim Conserv* 16:528–537. doi:[10.1111/acv.12025](https://doi.org/10.1111/acv.12025)
- Lisón F, Haz A, Calvo JF (2014) Preferencia de hábitat del murciélago hortelano meridional *Eptesicus isabellinus* (Temminck, 1840) en ambientes mediterráneos semiáridos. *Anim Biodivers Conserv* 37:59–67
- Loucks C, Ricketts TH, Naidoo R, Lamoreux J, Hoekstra J (2008) Explaining the global pattern of protected area coverage: relative importance of vertebrate biodiversity, human activities and agricultural suitability. *J Biogeogr* 35:1337–1348. doi:[10.1111/j.1365.2699.2008.01899.x](https://doi.org/10.1111/j.1365.2699.2008.01899.x)
- Lundy M, Montgomery I (2010) Summer habitat associations of bats between riparian landscapes and within riparian areas. *Eur J Wildlife Res* 56:385–394. doi:[10.1007/s10344-009-0330-z](https://doi.org/10.1007/s10344-009-0330-z)
- Maes J, Paracchini ML, Zulian G, Dunbar MB, Alkemade R (2012) Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. *Biol Conserv* 155:1–12. doi:[10.1016/j.biocon.2012.06.016](https://doi.org/10.1016/j.biocon.2012.06.016)
- Maiorano L, Falcucci A, Garton AEO, Boitani L (2007) Contribution of the Natura 2000 Network to biodiversity conservation in Italy. *Conserv Biol* 21:1433–1444. doi:[10.1111/j.1523-1739.2007.00831.x](https://doi.org/10.1111/j.1523-1739.2007.00831.x)
- Maiorano L, Falcucci A, Zimmermann NE, Psomas A, Pottier J, Baisero D, Rondinini C, Guisan A, Boitani L (2011) The future of terrestrial mammals in the Mediterranean basin under climate change. *Philos Trans Roy Soc B* 366:2681–2692. doi:[10.1098/rstb.2011.0121](https://doi.org/10.1098/rstb.2011.0121)
- Martínez-Fernández J, Esteve MA, Calvo JF (2000) Environmental and socioeconomic interactions in the evolution of traditional irrigated lands: a dynamics system model. *Hum Ecol* 28:279–299. doi:[10.1023/A:1007024204961](https://doi.org/10.1023/A:1007024204961)
- Martínez-Fernández J, Esteve MA, Baños-González I, Carreño F, Moreno A (2013) Sustainability of Mediterranean irrigated agro-landscapes. *Ecol Model* 248:11–19
- McDonald RI, Boucher TM (2010) Global development and the future of the protected area strategy. *Biol Conserv* 144:383–392. doi:[10.1016/j.biocon.2010.09.016](https://doi.org/10.1016/j.biocon.2010.09.016)
- Monadjem A, Reside A (2008) The influence of riparian on the distribution and abundance of bat in an African savanna. *Acta Chiropterol* 10:339–348. doi:[10.3161/150811008X414917](https://doi.org/10.3161/150811008X414917)
- O’Keefe JM, Loeb SC, Gerard PD, Lanham JD (2013) Effects of riparian buffer width on activity and detection of common bats in the southern Appalachian Mountains. *Wildlife Soc Bul* 37:319–326. doi:[10.1002/wsb.267](https://doi.org/10.1002/wsb.267)

- Ormerod SJ (2014) Rebalancing the philosophy of river conservation. *Aquat Conserv* 24:147–152. doi:10.1002/aqc.2452
- Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General de la Biodiversidad-SECEM-SECEMU, Madrid
- Pellissier V, Touroult J, Julliard R, Siblet JP, Jiguet F (2013) Assessing the Natura 2000 network with a common breeding birds survey. *Anim Conserv* 16:566–574. doi:10.1111/acv.12030
- Piquer-Rodríguez M, Kuemmerle T, Alcaraz-Segura D, Zurita-Milla R, Cabello J (2012) Future land use effects on the connectivity of protected area networks in southeastern Spain. *J Nat Conserv* 20:326–336. doi:10.1016/j.jnc.2012.07.001
- R Core Team. (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rainho A, Palmeirim JM (2011) The importance of distance to resources in the spatial modeling of bat foraging habitat. *PLoS One* 6:e19227. doi:10.1371/journal.pone.0019227
- Rainho A, Palmeirim JM (2013) Prioritizing conservation areas around multispecies bat colonies using spatial modeling. *Anim Conserv* 16:438–448. doi:10.1111/acv.12013
- Rodríguez-Rodríguez D, Martínez-Vega J (2012) Proposal of a system for the integrated and comparative assessment of protected areas. *Ecol Indic* 23:566–572. doi:10.1016/j.ecolind.2012.05.009
- Rosati L, Marignani M, Blasi C (2008) A gap analysis comparing Natura 2000 versus National protected area network with potential natural vegetation. *Commun Ecol* 9:147–154
- Russo D, Jones G (2003) Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26:197–209
- Sánchez-Fernández D, Abellán P (2015) Using null models to identify under-represented species by protected areas: an example with European amphibians and reptiles. *Biol Conserv* 184:290–299. doi:10.1016/j.biocon.2015.02.006
- Sánchez-Fernández D, Bilton DT, Abellán P, Ribera I, Velasco J, Millán A (2008) Are the endemic water beetles of the Iberian Peninsula and the Balearic Islands effectively protected? *Biol Conserv* 141:1612–1627. doi:10.1016/j.biocon.2008.04.005
- Sánchez-Fernández D, Abellán P, Picazo F, Millán A, Ribera I, Lobo JM (2013) Do protected areas represent species optimal climatic conditions? *Divers Distrib* 19:1407–1417. doi:10.1111/ddi.12104
- Santos H, Juste J, Ibáñez C, Palmeirim JM, Godinho R, Amorim F, Alves P, Costa H, de Paz O, Pérez-Suarez G, Martínez-Alos S, Jones G, Rebelo H (2014) Influences of ecology and biogeography on shaping the distributions of cryptic species: three bat tales in Iberia. *Biol J Linn Soc* 112:150–162. doi:10.1111/bij.12247
- Scott JM, Davis F, Csuti B, Noss R, Butterfield B, Groves C, Anderson H, Caicco S, D’Erchia F, Edwards TC, Ulliman J, Wright RG (1993) Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monograph* 123:1–41
- Skokanová H, Eremiášová R (2013) Landscape functionality in protected and unprotected area: case studies from the Czech Republic. *Ecol Inform* 14:71–74. doi:10.1016/j.ecoinf.2012.11.007
- Trochet A, Schmeller DS (2013) Effectiveness of the Natura 2000 network to cover threatened species. *Nat Conserv* 4:35–53. doi:10.3897/natureconservation.4.3626
- Venter O, Fuller RA, Segan DB, Carwardine J, Brooks T, Butchart SHM, Di Marco M, Iwamura T, Joseph L, O’Grady D, Possingham HP, Rondinini C, Smith RJ, Venter M, Watson JEM (2014) Targeting global protected areas expansion for imperiled biodiversity. *PLoS Biol* 12:e1001891. doi:10.1371/journal.pbio.1001891
- Verboom B, Huitema H (1997) The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and serotine *Eptesicus serotinus*. *Landscape Ecol* 277:494–499
- Vimal R, Rodrigues ASL, Mathevet R, Thompson JD (2011) The sensitivity of gap analysis to conservation targets. *Biodivers Conserv* 20:531–543. doi:10.1007/s10531-010-9963-1
- Zehetmair T, Müller J, Runkel V, Stahlschmidt P, Winter S, Zharov A, Gruppe A (2014) Poor effectiveness of Natura 2000 beech forests in protecting forest-dwelling bats. *J Nat Conserv* 23:53–60