

# Divergent altitudinal distributions of bird and bat species richness in a Mediterranean mountain range: patterns and prospects

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## Abstract

*Divergent altitudinal distributions of bird and bat species richness in a Mediterranean mountain range: patterns and prospects.* We studied the distribution of bird and bat species richness in Sierra de Guadarrama (Spain). We observed that bird richness had the highest scores at mid-elevations while bat richness increased monotonically with altitude. Both bird and bat richness were positively related to primary productivity but decreased and increased respectively with woodland cover. In addition, birds tracked vegetation complexity and shrub richness while bats did not track these fine-grained habitat traits. These differences could be related to the spatial scale of habitat use by birds and bats. While birds occur in small home ranges, bats can fly many km away from breeding sites in search of food. The tracking by bats of productive areas would thus blur the effect of fine-grained habitat traits. Our results suggest the need for further research on how the changes observed in productivity and tree cover in these mountains could affect distribution of bird and bat richness.

**Key words:** Habitat effects, Resource tracking, Spatial scale, Species density

## Resumen

*Distribución altitudinal divergente de la riqueza de especies de aves y murciélagos en una cordillera mediterránea: pautas y perspectivas.* En este trabajo analizamos la distribución de la riqueza de especies de aves y murciélagos en la Sierra de Guadarrama (España). Observamos que la riqueza de aves fue máxima en elevaciones medias, mientras que la de murciélagos aumentó con la altitud. La riqueza de aves y murciélagos se relacionó positivamente con la productividad primaria, pero disminuyó y aumentó respectivamente con la cubierta forestal. Además, la riqueza de aves estaba directamente relacionada con la complejidad de la vegetación y la riqueza de arbustos, mientras que la riqueza de murciélagos no guardaba ninguna relación con estas características del hábitat a pequeña escala. Estas diferencias podrían estar relacionadas con la escala espacial de uso del hábitat, ya que, mientras que las aves se desenvuelven en áreas pequeñas, los murciélagos pueden volar a muchos kilómetros de distancia desde los lugares de cría en búsqueda de alimento. De esta forma, el rastreo de las áreas productivas por los murciélagos desdibujaría el efecto de otras características del hábitat de menor escala. Los resultados sugieren la necesidad de realizar más investigaciones sobre cómo los cambios en la productividad y la cubierta forestal observados en estas montañas podrían afectar a la distribución de la riqueza de aves y murciélagos.

**Palabras clave:** Efectos del hábitat, Rastreo de recursos, Escala espacial, Densidad de especies

## Introduction

In a context of global change and biodiversity loss, it is important to unravel the factors shaping the distribution of species hotspots to launch conservation guidelines (Tilman et al 2017). However, the idiosyncratic requirements of species can make it difficult to design common management approaches to protect different taxonomic groups at the same time (Wolters et al 2006, Van Klink et al 2022). To meet this challenge, it is necessary to have prior knowledge of how different taxa react to the environmental setting of each managed region (Prendergast et al 1993, Lund and Rahbek 2002, Rodrigues and Brooks 2007).

In this study we compared the effect of several environmental drivers on bird and bat species richness within a mountain range in the Mediterranean region (Sierra de Guadarrama, Spain), a warm and dry geographical setting strongly affected by changes in climate and land use (Lionello and Scarascia 2018, Vega-Cañás et al 2020). In this setting, mountains are important biodiversity hotspots because several environmental factors related to elevation (e.g., decreasing temperatures) and long-term biogeographical processes (e.g., Pleistocene ice retreat) have led to the occurrence of northern and montane organisms that augment the regional pool of species (Rahbek et al 2019). In addition, the Sierra de Guadarrama shows increasing heterogeneity of human-made landscape if compared to the piedmont, a feature that strengthens its regional effect on species richness (Atauri and de Lucio 2001, Stein et al 2014). Due to these effects, the altitudinal range of the study area is home to many species of birds and bats that differ in biogeographic origin and habitat preferences (Tellería 1987, Tena and Tellería 2022).

Birds and bats are flying vertebrates that mainly feed on invertebrates during the breeding period in temperate regions. These similarities could be related to parallel habitat preferences and produce, all else (scale, sampled area), similar altitudinal patterns of species richness (McCain and Grytnes 2010). However, birds show differences to bats (e.g., activity rhythms, feeding behaviour, thermoregulation, etc.) that could blur any parallel response to a common environmental setting (Lund and Rahbek 2002, Willig and Presley 2016, Renner et al 2018, Barbaro et al 2019). The potential effect of these differences thus underlines the importance of exploring the reactions of bird and bat richness to the environment of each study area. Here we aimed to meet this objective in the Sierra de Guadarrama using two complementary approaches.

### Altitudinal distribution of species richness

Changes in the number of species along elevation gradients have been studied over a long-time frame (Rahbek 1995, 2005, Lomolino 2001, McCain and Grytnes 2010). According to patterns observed, species richness may decrease monotonically with altitude, decrease just after reaching an elevation threshold, or show a unimodal, bell-shaped pattern with the highest scores at mid elevations. In this context, several studies have observed that bird and bat richness fol-

low different altitudinal models (McCain and Grytnes 2010), making it difficult to predict their patterns a priori in each mountain range. These differences can be explained by the fact that trends in species richness are not caused by altitude per se but result by the idiosyncratic effect of environmental drivers that change with elevation in each taxonomic group (Rahbek 1995, Willig et al 2003).

### Environmental drivers

It is commonly agreed that the number of species is shaped by a combination of climate, landscape, and fine-grained drivers (Ricklefs 2004), and that patterns observed may be strongly affected by the survey effort and the spatial scale of approach (Rahbek 2005). Accordingly, we performed a multivariate analysis to detect the effect of several scale-dependent environmental drivers on bird and bat species richness. We explored the effect of net primary productivity, a large-scale driver of species richness (Mittelbach et al 2001, Cusens et al 2012) that changes with elevation (Rahbek 2005, Rahbek et al 2019). In addition, because it has been observed that vegetation complexity shapes the spatial patterning of bird and bat species richness (Charbonnier et al 2016, Renner et al 2018, Barbaro et al 2019, Basile et al 2020), we tested the effect of landscape composition (e.g., relative contribution of woodland cover vs. open habitat) and some fine-grained habitat drivers (e.g., floristic diversity and vegetation complexity of sampling plots) on the altitudinal distribution of the observed patterns.

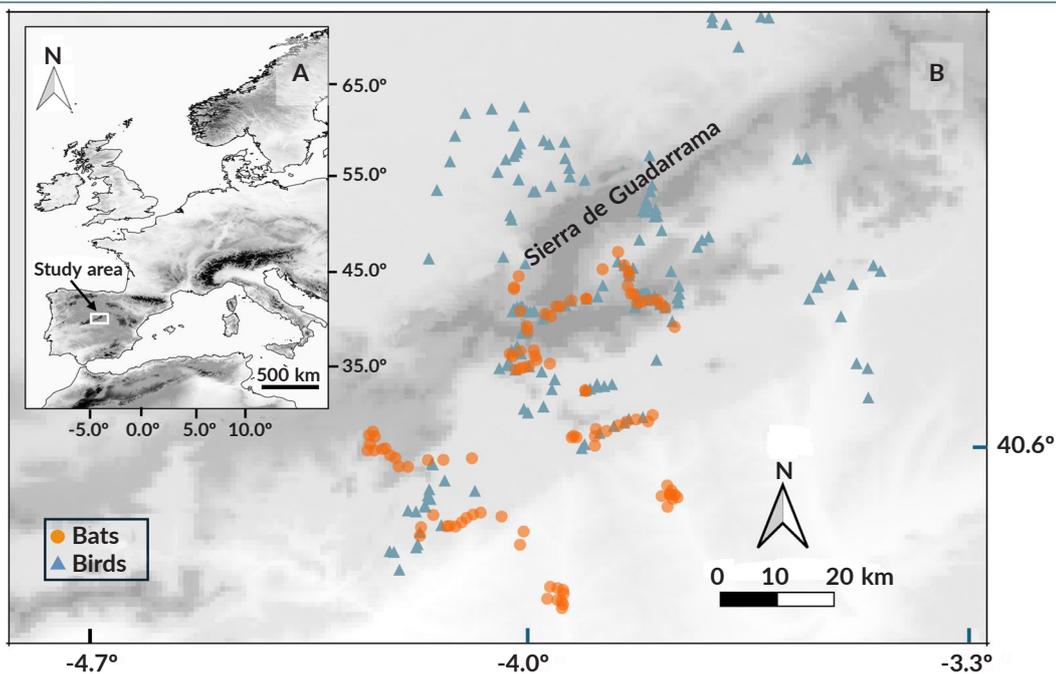
## Material and methods

### Study area

The Sierra de Guadarrama lies in the central Iberian Peninsula (fig. 1) along a NE-SW oriented 60 x 140 km belt, and ranges from around 550 m a.s.l. in the piedmont to 2,428 m asl at the highest peak of Mount Peñalara (40.85°N, -3.96°W). Along the elevation range, the Sierra is covered by a succession of vegetation belts that range from hot lowlands in spring and summer to colder highlands. Cereal fields, grasslands, and sclerophyllous trees and shrubs *Quercus ilex* L. and *Cistus ladanifer* L. occur in the piedmont (under 1,000). Scrublands *Cistus laurifolius* L. and less drought-tolerant wooded pasturelands *Quercus pyrenaica* Wildl. and mowing meadows covered by ash *Fraxinus excelsior* L. occur at mid elevations. Mountain pastures, shrublands (*Juniperus communis* L., *Cytisus oromediterraneus* Rivas Mart. et al) and Scots pine *Pinus sylvestris* L. woodlands are present at the highest elevations (above 1,500 m). These mountains are managed for extensive cattle rearing, except in the case of pinewoods, which are managed for timber production. Since 2013, the upper parts of these mountains (33,960 ha) have been declared a National Park.

### Bird and bat sampling

During May and June in 2014 and in 2015 we counted birds in 166 circular sampling points distributed at various elevations (550 to 1,900 m asl, fig. 1) and habitats



**Fig. 1.** Distribution of the Sierra de Guadarrama within the Western Palearctic (A) and location of sampling points for birds (blue triangles) and bats (red points) within the study area (B). Darkest sectors show the areas over 1,500 m asl.

**Fig. 1.** Distribución de la Sierra de Guadarrama dentro del Paleártico Occidental (A) y ubicación de los puntos de muestreo de aves (triángulos azules) y murciélagos (puntos rojos) en el área de estudio (B). Los sectores más oscuros muestran las áreas que se encuentran a más de 1.500 m snm.

(we excluded urban areas). The number of species detected during 10 minutes within a 100-m radius was recorded at each sampling point. We considered only the presence of passerines (O. Passeriformes) and other birds (e.g., woodpeckers, doves, etc.) commonly sampled using this method, and we excluded large birds such as storks, raptors, and crows (Johnson 2010). This method provides species density (Lomolino 2001), an index of species richness free of the effects of sampled area and sampling effort (Rahbek 1995, Gotelli and Colwell 2001). The same sampling protocol was carried out for bats in 99 sampling points recorded during the breeding season (June and July) of 2014 and 2015 (fig. 1). In this case, as the number of species recorded in 10-minute sampling periods was small, we repeated the counts three times each year to increase the number of detected species per sampling point. Since bat activity varies throughout the night (Vaughan et al 1997), we only sampled this group for three hours after dark. In addition, each sampling point was distributed evenly along this three-hour block to prevent any systematic effect of sampling time. All sampling points were geo-referenced (latitude and longitude) with GPS devices during field work.

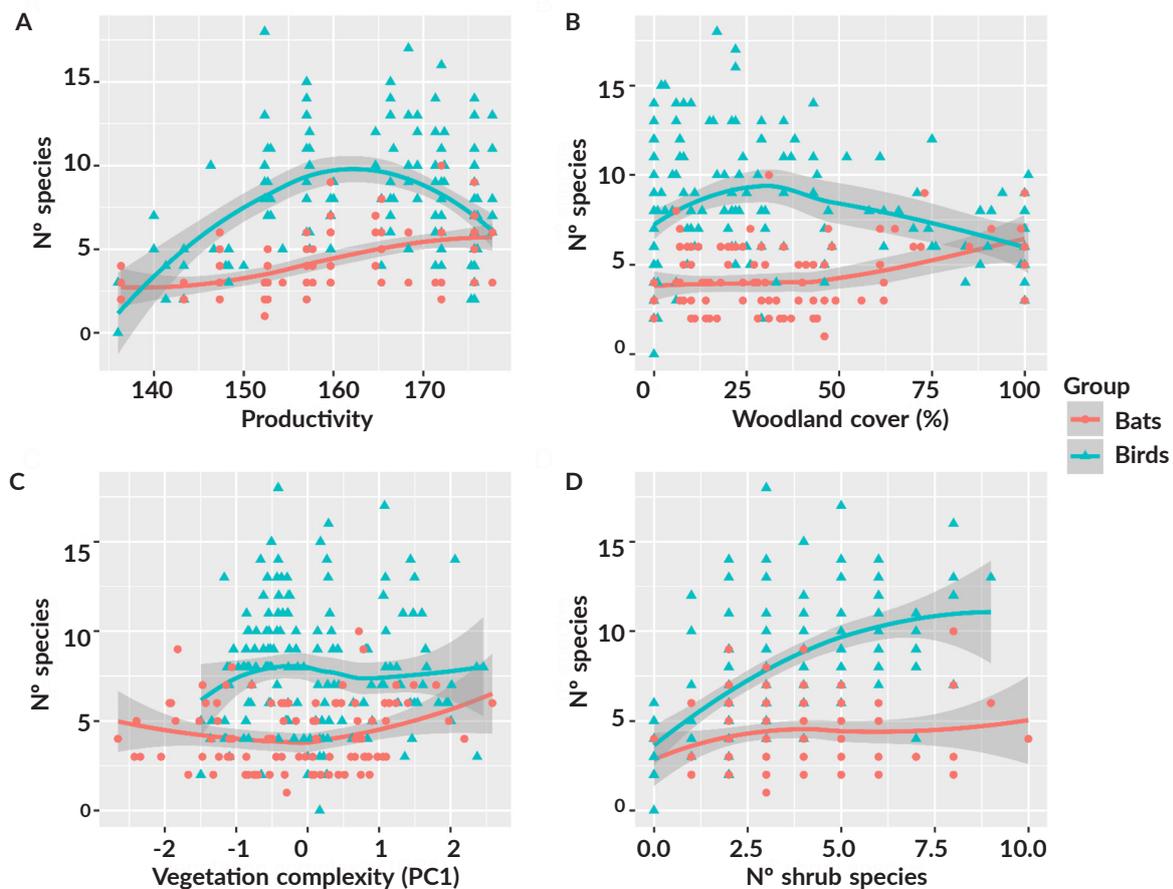
Birds were identified by visual and sound cues by one of the authors (JLT). Bats were recorded by ultrasound bat detectors (Echo Meter 3, Wildlife Acoustics) by another author (ET). All ultrasound bat sequences were recorded as full-spectrum in WAV format and filtered using Kaleidoscope (Wildlife Acoustics, Inc.). The filter settings were specified between 8 and 120 kHz

and 2 to 500 ms and each sequence for 5 seconds. We then analysed the WAV files by using the Bat-Sound 4 program (Pettersson Elektronik AB, Uppsala). The sequences were analysed using a sampling frequency of 44.1 kHz, with 16 bits/sample and a 512 pt. power spectrum (Fast Fourier Transform) with a Hamming window. At least two bat calls were analysed at random from each sequence. The resulting spectrograms were explored manually (following Rydell et al 2017) by assessing a set of parameters (call structure, start frequency, end frequency, frequency of maximum energy, duration, and inter-pulse interval) currently used to identify bat species (Russo and Jones 2002, Barataud 2012). It is commonly agreed, however, that spectrograms do not provide sufficient information to identify some individual species (Rydell et al 2017). We therefore ascribed the calls to different sonotypes in the case of *Nyctalus-Eptesicus* and two different groups in *Myotis* and *Plecotus* respectively.

### Environmental drivers

#### Primary productivity

We downloaded net primary productivity (the difference between plant photosynthesis and autotrophic respiration) from NASA Earth Observations (<https://neo.gsfc.nasa.gov/>). This programme provides a worldwide assessment of annual primary productivity (gC/m<sup>2</sup>/year). Because the previous year's productivity could affect reproductive success and, therefore, the abundance of birds and bats the following breeding



**Fig. 2.** Relationships between bird and bat species density and net primary productivity (A), woodland cover (B), vegetation complexity (C) and shrub species richness (D). Smoothed lines ( $\pm$  SE) have been added to show the dominant patterns in birds and bats.

**Fig. 2.** Relaciones entre la densidad de especies de aves y murciélagos y la productividad primaria neta (A), la cubierta forestal (B), la complejidad de la vegetación (C) y la riqueza de especies de arbustos (D). Se han agregado líneas suavizadas ( $\pm$  EE) para detectar las pautas dominantes en aves y murciélagos.

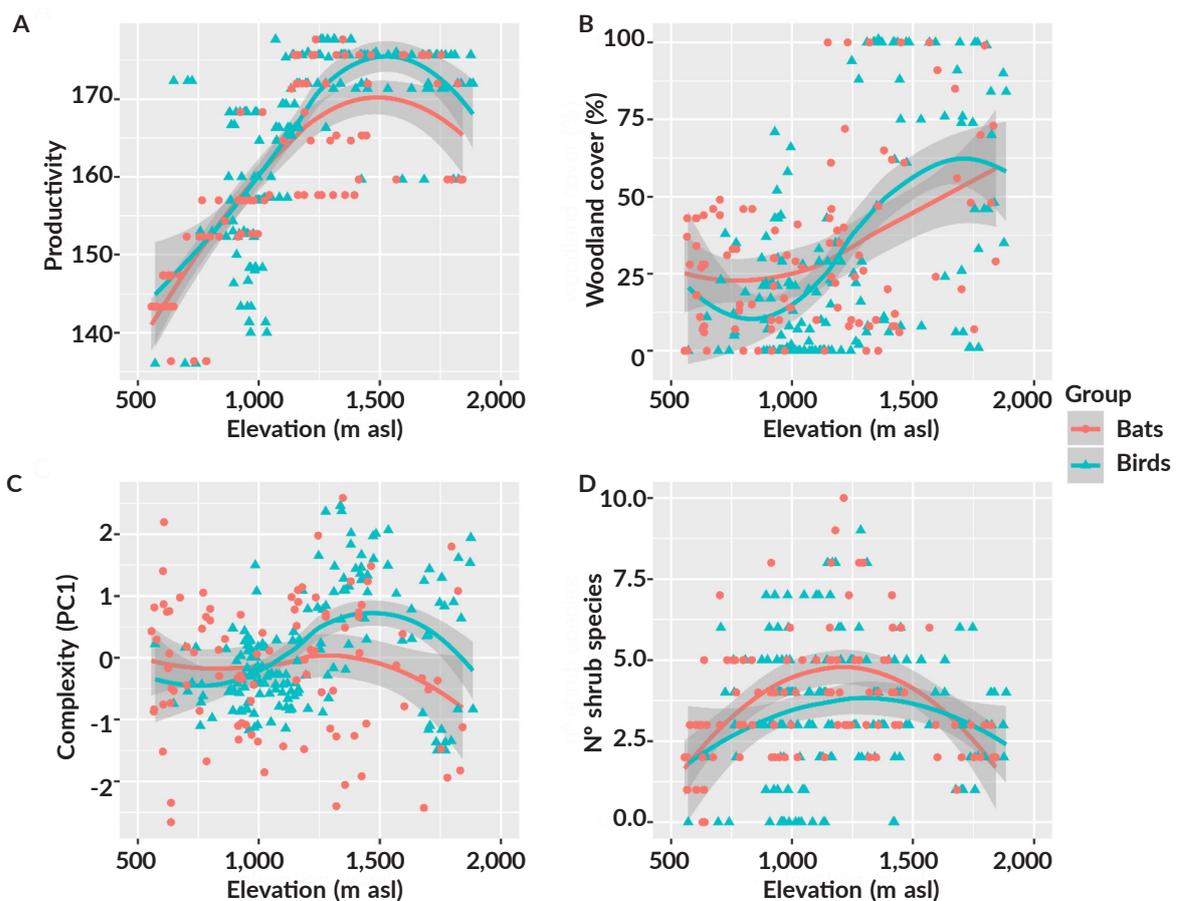
season, we calculated the average productivity for the years 2013, 2014 and 2015 to assess its effect on species richness immediately before and during the study period (2014-2015). These data were extracted in the 265 sampling points using the Point Sampling Tool of QGIS 3.22 (QGIS Development Team 2020).

#### Landscape composition

The regional distribution of open and woodland landscapes was obtained from EarthEnv (<https://www.earthenv.org/>, Tuanmu and Jetz 2014) by using QGIS (see above). Woodland cover was obtained by adding the covers of deciduous broadleaf trees, evergreen deciduous needle-leaf trees, evergreen broadleaf trees, and mixed other trees. Both variables were negatively correlated (Spearman  $r = -0.77$ ,  $p < 0.001$ ), suggesting that wooded landscapes were increasingly related to decreasing open covers. Thus, we finally elected woodland cover as a comprehensive index of landscape composition.

#### Fine-grained habitat drivers

We assessed habitat structure in 25 m radius circles around each sampling point. Cover (percentage) of grass, shrub (vegetation  $< 0.5$  m and between 0.5 and 2 m height), and tree (vegetation  $> 2$  m height) layers were visually assessed. In addition, we counted the number of shrub and tree species over 0.5 m height as an index of shrub richness. Covers were used to perform a principal component analysis to obtain a latent variable able to describe vegetation structure. We selected one component related to an increasing gradient of tree development (PC1, eigenvalue: 1.03; explained variance: 25.86%; factor loadings, grass layer: -0.329; shrub cover under 0.5 m: -0.491; shrub cover 0.5-2 m: 0.010; tree cover  $> 2$  m: 0.828). The factor scores of sampling points within this component were used as comprehensive indices of vegetation complexity. This index and shrub richness were not correlated (Spearman  $r = 0.07$ , n.s.).



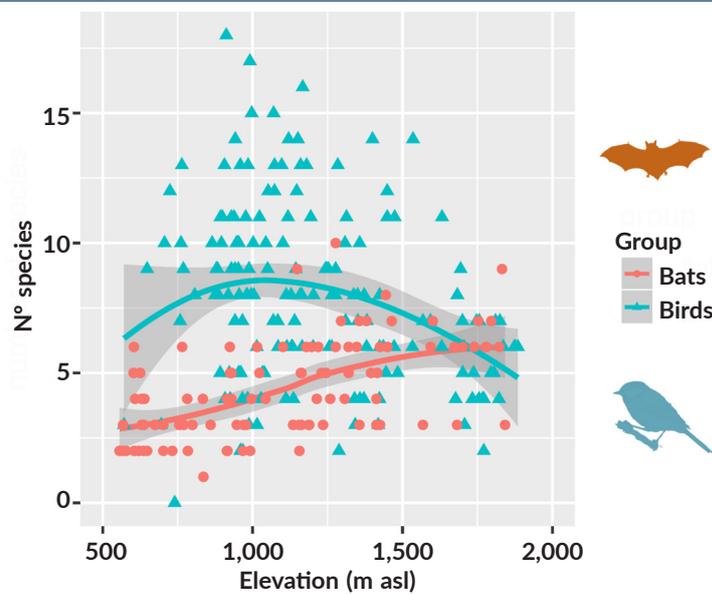
**Fig. 3.** Distribution of productivity (A), woodland cover (B), vegetation complexity (C) and shrub richness (D) along the elevation gradient of the Sierra de Guadarrama. Smoothed lines ( $\pm$  SE) have been added to detect the dominant patterns in birds and bats.

**Fig. 3.** Distribución de la productividad (A), la cubierta forestal (B), la complejidad de la vegetación (C) y la riqueza de arbustos (D) a lo largo del gradiente de elevación de la Sierra de Guadarrama. Se han añadido líneas suavizadas ( $\pm$  EE) para detectar las pautas dominantes en aves y murciélagos.

### Data analysis

We performed a preliminary analysis to detect whether species richness was spatially autocorrelated (SAC) by using Moran's I coefficient provided by the 'ape 5.0' library (Paradis and Schliep 2019). Results suggested that both bird (Moran's I: 0.164,  $p < 0.001$ ) and bat richness (Moran's I: 0.238,  $p < 0.001$ ) were spatially autocorrelated. As these patterns have practical effects on statistical inferences (Type I error; Gaspard et al 2019), we explored the residual spatial autocorrelation (rSAC) of the generalized linear models (GLM) initially used to model species richness. In these models, bird and bat richness were regressed on productivity, woodland cover, shrub richness and vegetation complexity. As bird richness displayed a hump-shaped relationship with productivity and vegetation complexity (fig. 2), we also included the squares of these two drivers when modeling this group. Furthermore, all environmental factors were standardized (mean = 0 and sd = 1) to favor a direct comparison of the coefficients in the resulting models.

Because we detected significant rSAC in GLM (see below), we used generalized least squares (GLS) models to repeat the analyses. These models allow us to directly model the spatial covariance structure contained in the variance-covariance matrix. In this way, although the residuals may be spatially autocorrelated, the model errors are not, which is ultimately what we need to correctly estimate the parameters. GLS models fit better with different spatial correlation structures (gaussian, exponential, spheric, linear, rationale; Dormann et al 2007) so that we selected one of them by using the Akaike information criterion (AICc, Burnham and Anderson 2002, Diniz-Filho et al 2003). In the selected models, as an averaged estimator is a more honest measure of precision and reduced bias than an estimator from just the best model, we averaged parameter estimates ( $\beta$ ) using model weights ( $W_i$ ) derived from all models with  $\Delta AICc < 7$  (Burnham et al 2011). These analyses were conducted in R 3.1.2 using the 'MuMIn' (Bartoń 2023) and 'nlme' (Pinheiro 2009) libraries (R Development Core Team 2017).



**Fig. 4.** Altitudinal distribution of density of birds and bat species along the elevation gradient of the Sierra de Guadarrama. Smoothed lines ( $\pm$  SE) have been added to bird and bat plots to show the dominant patterns in birds and bats.

**Fig. 4.** Distribución altitudinal de la densidad de especies de aves y murciélagos a lo largo del gradiente de elevación de la Sierra de Guadarrama. Se han agregado líneas suavizadas ( $\pm$  EE) para detectar las pautas dominantes en aves y murciélagos.

## Results

We recorded 73 bird species and 11 bat species or sonotypes (table 1) within the elevation gradient of the Sierra de Guadarrama, which displays sharp changes in environmental conditions (fig. 3). Productivity and the number of shrub species displayed a unimodal distribution, while woodland cover and vegetation complexity depicted the highest scores over 1,200 m asl (fig. 3). Within this geographical setting, birds displayed the highest species richness at mid-elevations while bat richness increased monotonically with elevation (fig. 4).

GLM models reduced rSAC in bat richness (Moran's I: 0.04,  $p = 0.084$ ) but not in bird richness (Moran's I: 0.06,  $p < 0.001$ ; appendix 1). GLS models reported similar results since rSAC continued to be spatially autocorrelated in birds (Moran's I: 0.11,  $p < 0.001$ ) but not in bats (Moran's I: 0.03,  $p = 0.163$ ). The selected GLS models (smaller AICc) fitted spherical (birds) and exponential (bats) spatial correlation structures. Both bird and bat richness were related to net primary productivity (table 2), but birds displayed a unimodal pattern while bats showed a monotonic increase within the observed range of productivity (table 2, fig. 2A). Woodland cover affected species richness but also differed between groups as it was negatively related to birds and positively (but weakly) related to bats (table 2, fig. 2B). In addition to the effect of productivity and woodland cover, bird richness was positively related to shrub richness and vegetation complexity (table 2, fig. 2C-2D).

## Discussion

### Altitudinal distribution of species richness

Our results show altitudinal patterns of bird and bat species richness within the study mountain range differed (fig. 4). The observed unimodal distribution of bird richness having highest scores at mid elevations has been reported previously from studies in mountains around the globe (McCain and Grytnes 2010). This pattern fits well with the 'dry mountain model' in which species numbers increase between the dry-hot conditions of lowlands and the humid-cold conditions of higher elevations (McCain 2009). It is interesting to note that this pattern has been also observed in other taxa of the Sierra de Guadarrama, such as shrubs (this study, fig. 3D), butterflies (Wilson et al 2007) and ants (Flores et al 2018). However, the monotonic increase of bat species richness is harder to explain because the altitudinal distribution of this group has usually been ascribed to decreasing or unimodal distributions (McCain and Grytnes 2010). In effect, the observed pattern of increasing species richness has been not considered in former models (McCain and Grytnes 2010), probably because it depicts the first half of a bell-shaped distribution or is an artifact related to the positive effect of increasingly large areas in upper elevations (e.g., Rahbek 1997, McCain 2007). This latter explanation does not apply within the hypsographic structure of the Sierra de Guadarrama, where the altitudinal reduction of land area (fig. 1) would produce, if at all, a negative trend of species richness (Elsen and Tingley 2015).

**Table 1.** List of bird and bat species recorded in the sampling points that have been considered in this study.**Tabla 1.** Lista de especies de aves y murciélagos registradas en los puntos de muestreo que se han considerado en este estudio.

Order	Birds
Passeriformes	<i>Aegithalos caudatus</i> , <i>Alauda arvensis</i> , <i>Anthus campestris</i> , <i>Anthus trivialis</i> , <i>Carduelis carduelis</i> , <i>Certhia brachydactyla</i> , <i>Cettia cetti</i> , <i>Chloris chloris</i> , <i>Coccothraustes coccothraustes</i> , <i>Curruca cantillans</i> , <i>Curruca communis</i> , <i>Curruca conspicillata</i> , <i>Curruca hortensis</i> , <i>Curruca melanocephala</i> , <i>Curruca undata</i> , <i>Cyanistes caeruleus</i> , <i>Cyanopica cooki</i> , <i>Emberiza calandra</i> , <i>Emberiza cia</i> , <i>Emberiza cirius</i> , <i>Emberiza hotulana</i> , <i>Erithacus rubecula</i> , <i>Ficedula hypoleuca</i> , <i>Fringilla coelebs</i> , <i>Galerida cristata</i> , <i>Galerida theklae</i> , <i>Garrulus glandarius</i> , <i>Hippolais polyglottal</i> , <i>Lanius meridionalis</i> , <i>Lanius senator</i> , <i>Linaria cannabina</i> , <i>Lophophanes cristatus</i> , <i>Loxia curvirostra</i> , <i>Lullula arborea</i> , <i>Luscinia megarhynchos</i> , <i>Luscinia svecica</i> , <i>Motacilla flava</i> , <i>Muscicapa striata</i> , <i>Oenanthe hispanica</i> , <i>Oriolus oriolus</i> , <i>Parus major</i> , <i>Passer domesticus</i> , <i>Passer montanus</i> , <i>Periparus ater</i> , <i>Petronia petronia</i> , <i>Phoenicurus ochruros</i> , <i>Phylloscopus bonelli</i> , <i>Phylloscopus collybita</i> , <i>Pica pica</i> , <i>Prunella modularis</i> , <i>Regulus ignicapilla</i> , <i>Regulus regulus</i> , <i>Saxicola rubicola</i> , <i>Serinus citrinella</i> , <i>Serinus serinus</i> , <i>Sitta europaea</i> , <i>Sturnus unicolor</i> , <i>Sylvia atricapilla</i> , <i>Sylvia borin</i> , <i>Troglodytes troglodytes</i> , <i>Turdus merula</i> , <i>Turdus philomelos</i> , <i>Turdus viscivorus</i>
Piciformes	<i>Dendrocopos major</i> , <i>Dryobates minor</i> , <i>Dryocopus martius</i> , <i>Jynx torquilla</i> , <i>Picus sharpei</i>
Columbiformes	<i>Columba palumbus</i> , <i>Streptopelia decaocto</i> , <i>Streptopelia turtur</i>
Galliformes	<i>Alectoris rufa</i>
Buceratiformes	<i>Upupa epops</i>
	<b>Bats</b>
Chiroptera	<i>Barbastella barbastellus</i> , <i>Hypsugo savii</i> , <i>Nyctalus/Eptesicus</i> sp., <i>Myotis</i> sp., <i>Pipistrellus kuhlii</i> , <i>Pipistrellus pipistrellus</i> , <i>Pipistrellus pygmaeus</i> , <i>Plecotus</i> sp., <i>Rhinolophus ferrumequinum</i> , <i>Rhinolophus hipposideros</i> , <i>Tadarida teniotis</i>

### Environmental drivers

Net primary productivity is a main driver of land-vertebrate richness (Mittelbach et al 2001, Cusens et al 2012, Rahbeck et al 2019), particularly when it is not constrained by temperature (ectotherms) and water availability (amphibians, Qian 2010, Buckley et al 2012, Gebert et al 2019). This parameter measures productivity at a first trophic level that in turn may predict the abundance and richness of the following trophic levels (Wright 1983, but see Currie et al 2004), a pattern detected in endothermic vertebrates (Gebert et al 2019, De Souza et al 2022). Within the altitudinal range of the Sierra de Guadarrama, net primary productivity increases up to 1,500 m, whereafter it decreases at the highest elevations (fig. 3A). Within this elevation interval, the relationship between productivity and species richness shows different patterns because birds fit a bell-shaped distribution and bats show a monotonic increase (fig. 2A). This pattern suggests that bird richness is constrained by the effect of other environmental drivers in the most productive sectors and bat richness does not experience a similar process within the study range of productivity (table 2, fig. 2A).

A putative explanation of these patterns could be related to the effect of different woodland cover, which increases in the upper, more productive parts of the mountains (fig. 3B) and negatively affects bird richness (table 2, fig. 2B). This negative relationship, previously detected in the Sierra de Guadarrama (Tellería 2020),

has been explained by the loss of bird species due to the effect of tree densification and understory loss resulting from rural abandonment or forestry practices in the Mediterranean region (Gil-Tena et al 2007). However, this pattern does not occur in bat richness, which increases slightly in wooded areas of the upper parts of mountains (table 2, fig. 2B), supporting the current view that bats crowd these Mediterranean highlands (Paz et al 2017, Hermida et al 2017, Tena and Tellería 2022, Alonso-Alonso et al 2022). Thus, although it has been observed that bats search the clearings within the dense forest matrix of the Sierra de Guadarrama (Tena et al 2020), this pattern does not support any negative effect of woodland cover on the regional distribution of species richness. Therefore, according to these results, woodland cover increasingly reduces bird richness but does not constrain bat richness in the most productive sectors of the upper part of these mountains. The combined effect of productivity and woodland cover could therefore explain the bell-shaped and monotonic altitudinal distribution of bird and bat richness.

Birds and bats differ in the way fine-grained habitat structure affects species richness. Bird richness is reinforced by its positive relationships with vegetation complexity and shrub richness, which reach the highest scores at mid-elevations (table 2, fig. 2). This pattern agrees with the well-known positive effect of fine-grained habitat complexity on bird species

**Table 2.** Results of generalized least squares mixed models in which the bird and bat species richness has been regressed against productivity (Prd), woodland cover (Wdc), vegetation complexity (Vgc) and shrub richness (Shr) according to a spherical (birds) and exponential (bats) correlation structure (see text). To assess the importance of variables in the full set of selected models we use the weighted averages of coefficients (Mean  $\beta$ ) and the sum the Akaike weights of each selected variable ( $\Sigma$  Weight).

**Tabla 2.** Resultados de los modelos mixtos de mínimos cuadrados generalizados en los que se ha realizado una regresión de la riqueza de especies de aves y murciélagos en función de la productividad, la cubierta forestal, la complejidad de la vegetación y la riqueza de arbustos según una estructura de correlación esférica (pájaros) y exponencial (murciélagos) (véase el texto). Se ha evaluado la importancia de las variables en el conjunto de los modelos seleccionados mediante la media ponderada de los coeficientes (Mean  $\beta$ ) y la suma de los pesos de Akaike de cada variable seleccionada ( $\Sigma$  Weight).

Birds	Intercept	Prd	Prd <sup>2</sup>	Wdc	Vgc	Vgc <sup>2</sup>	Shr	df	AICc	Delta	Weight	R <sup>2</sup>
Model 1	7.68	28.05	-27.82	-0.71	2.20	-1.25	1.73	10	736.9	0.00	0.664	0.499
Model 2	7.69	27.05	-26.98	-0.70	0.94	-	1.80	9	738.7	1.83	0.266	0.450
Model 3	7.67	25.28	-25.35	-	0.80	-	1.74	8	741.4	4.52	0.069	0.413
Mean $\beta$		27.56	-25.65	-0.66	1.71	-0.83						
$\Sigma$ Weight		1	1	0.93	1	0.66	1					

Bats	Intercept	Prd	Prd <sup>2</sup>	Wdc	Vgc	Vgc <sup>2</sup>	Shr	df	AICc	Delta	Weight	R <sup>2</sup>
Model 1	4.20	0.71	-	-	-	-	-	5	372.3	0.00	0.522	0.335
Model 2	4.29	0.96	-	0.34	-	-	-	6	374.1	1.77	0.215	0.363
Model 3	4.15	0.73	-	-	-	-	-0.14	6	375.6	3.26	0.102	0.335
Model 4	4.20	0.70	-	-	0.02	-	-	6	376.5	4.14	0.066	0.335
Model 5	4.21	-	-	-	0.07	-	-	5	377.7	5.41	0.035	0.010
Model 6	4.29	0.98	-	0.33	-	-	-0.08	7	377.9	5.56	0.032	0.365
Model 7	4.29	0.96	-	0.34	-0.01	-	-	7	378.3	5.96	0.027	0.363
Mean $\beta$		0.75	-	0.09	0.00	-	-0.02					
$\Sigma$ Weight		0.96	-	0.27	0.13	-	0.13					

richness (Wiens 1992), which has also been tested in the Sierra de Guadarrama (Díaz 2006, Tellería 2020). The positive relationships between bird and plant richness have been linked to the concomitant variety of functional interactions on birds of nesting and feeding substrates linked to various plant species (Wiens 1992, Dehling et al 2014). However, our results do not support any effect of fine-grained habitat structure on the distribution of bat richness. This lack of microhabitat tracking by bat richness disagrees with the fact that bats show hunting strategies adapted to habitat structure (e.g., they are classified in open, edge, and gleaner species, Schnitzler and Kalko 2001), which could favor the presence of more species in heterogeneous landscapes. In summary, although it has been observed that tree-related microhabitats can shape bat distribution at smaller spatial scales (Mendes et al 2017, Jung et al 2012, Charbonnier et al 2016, Renner et al 2018, Barbaro et al 2019, Basile et al 2020, Novella-Fernández et al 2022), the regional distribution of bat richness in the Sierra de Guadarrama mainly tracks productivity and woodland cover and is not sensitive to fine-grained habitat drivers.

### Bird and bat differences

A main conclusion of this study is that the richness of bird and bat species does not similarly track the environmental setting of the Sierra de Guadarrama. The most obvious approach to these differences is to consider that birds are not bats and vice versa, and that despite some similitudes (flight, diet, etc.), they show biological differences that affect their response to environmental variability (Lund and Rahbek 2002).

One main difference is related to the dispersal capabilities of birds and bats during the breeding period, a trait that could affect their multi-scale perception of the environment (Rahbek 2005). The spatial distribution of both groups is related to the availability of nesting/roosting sites from where they move in search of food. Small passerines, the dominant bird group herein (table 1), are linked to small home ranges around the nest from where they come and go in search of food for nestlings (Odum and Kuenzler 1955, Schoener 1968). As a result, in this study, the number of species is related to the regional patterning of productivity and the local availability of feeding and nesting substrata depicted by fine-grained drivers. However, bats can fly many

kilometers away from roosting sites to reach distant watering and feeding areas (Popa-Lisseanu et al 2009, Rainho and Palmeirim 2011, Nado et al 2019). In this context, the regional tracking of the most productive areas would blur the effect of other fine-grained habitat requirements (e.g., roost, feeding microhabitats) related to breeding areas. As a result, any sampling of active bats will mainly depict the environmental features of activity areas, and these may not overlap with breeding sectors (Rainho and Palmeirim 2011). The Sierra de Guadarrama extends over an area in which the piedmont occurs at less than 10 km of the most elevated and productive sectors (fig. 1), suggesting that many bats could move each night in search of the most productive feeding patches (e.g., Georgiakakis et al 2010). We can then suggest that the bird and bat assemblages studied here do not represent equivalent situations. Bird data display the sites where they feed and breed while bat data mainly refer to the regional distribution of feeding areas.

### Prospects

Species richness is a subrogate of taxonomic diversity and number of individuals (Carnicer et al 2012) which, within a multicriteria decision framework, is a proper conservation target (Fleishman et al 2006). Most of the study area in the Sierra de Guadarrama National Park is subject to management guidelines, so it seems appropriate to highlight possible improvements in conservation of bird and bat species richness. As for other species hotspots in the Mediterranean region, the Sierra de Guadarrama is under the effect of ongoing climate and habitat changes (Kuemmerle et al 2016, Vegas Cañas et al 2020) that are shifting the distribution of many species (Wilson et al 2005, Tellería 2019, Caro-Miralles and Gutiérrez 2023). Although the relative contribution of both processes to changes is hard to assess (Sirami et al 2017), results in this paper suggest delving into two complementary approaches:

First, in a context of an increasing number of heat waves and persistent droughts affecting productivity (Bastos et al 2014, Soares et al 2023), it is key to monitor how the most productive sectors will shift within the elevation gradients of the Sierra de Guadarrama. If productivity shifts uphill, the hypsographic structure of the Sierra de Guadarrama will reduce the extent of the most productive sectors (Elsen and Tingley 2015), with the concomitant negative effect on bird and bat species assemblages. We acknowledge, however, that this prediction requires further research to detect the most vulnerable sectors as it has been observed that interannual trends in productivity differ among nearby areas in central Spain (Aragón et al 2019).

Second, bird richness is also driven by the interacting effects of landscape and fine-grained habitats traits. Woodland encroachment and densification resulting from rural abandonment and forestry have reduced bird richness in the upper part of the Sierra de Guadarrama, a process that could be reversed by managing floristic and physiognomic heterogeneity (Tellería 2020). Our results, nevertheless, do

not support such effects on the richness of active bats, and that suggest further studies are required to assess the environmental drivers of bat richness in resting areas.

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#### Author contributions

E Tena and JL Tellería designed the study, conducted the fieldwork, analyzed the data, wrote the paper and read and approved the final manuscript.

#### Conflicts of interest

No conflicts declared.

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**Appendix 1.** Results of general lineal models (family: Poisson, link: log), in which the bird and bat species richness has been regressed against productivity (Prd), woodland cover (Wdc), vegetation complexity (Vgc) and shrub richness (Shr) according to a spherical (birds) and exponential (bats) correlation structure (see text). To assess the importance of variables in the full set of selected models we use the weighted averages of coefficients (Mean  $\beta$ ) and the sum the Akaike weights of each selected variable ( $\Sigma$  Weight).  $D^2$ , explained deviance.

**Apéndice 1.** Resultados de los modelos lineales generalizados (familia: Poisson, vínculo: log) en los que se ha realizado una regresión de la riqueza de especies de aves y murciélagos en función de la productividad, la cubierta forestal, la complejidad de la vegetación y la riqueza de arbustos según una estructura de correlación esférica (pájaros) y exponencial (murciélagos) (véase el texto). Se ha evaluado la importancia de las variables en el conjunto de los modelos seleccionados mediante la media ponderada de los coeficientes (Mean  $\beta$ ) y la suma de los pesos de Akaike de los modelos de cada variable seleccionada ( $\Sigma$  Weight).  $D^2$ , desviación explicada.

Birds	Intercept	Prd	Prd <sup>2</sup>	Wdc	Vgc	Vgc <sup>2</sup>	Shr	df	AICc	Delta	Weight	D <sup>2</sup>
Model 1	2.01	6.43	-6.39	-0.16	0.12	-	0.22	6	744.4	0.00	0.528	0.510
Model 2	2.01	6.49	-6.43	-0.16	0.27	-0.15	0.22	7	745.0	0.67	0.377	0.556
Model 3	2.01	6.25	-6.22	-0.16	-	0.11	0.22	6	747.8	3.42	0.095	0.542
Mean $\beta$		6.44	-6.39	-0.16	0.17	-0.05	0.22					
$\Sigma$ Weight		1	1	1	0.91	0.47	1					

Bats	Intercept	Prd	Prd <sup>2</sup>	Wdc	Vgc	Vgc <sup>2</sup>	Shr	df	AICc	Delta	Weight	D <sup>2</sup>
Model 1	1.43	0.26		-	-		-	2	374.2	0.00	0.293	0.342
Model 2	1.43	0.23		0.07	-		-	3	374.5	0.27	0.256	0.366
Model 3	1.43	0.26		-	-		-0.02	3	376.2	1.99	0.108	0.344
Model 4	1.43	0.26		-	-0.00		-	3	376.3	2.13	0.101	0.343
Model 5	1.43	0.23		0.06	-		-0.01	4	376.6	2.38	0.089	0.367
Model 6	1.43	0.23		0.07	-0.00		-	4	376.6	2.44	0.086	0.366
Model 7	1.43	0.26		-	-0.00		-0.02	4	378.4	4.17	0.037	0.344
Model 8	1.43	0.24		0.06	-0.00		-0.01	5	378.8	4.60	0.029	0.367
Mean $\beta$		0.25		0.03	-0.00		-0.01					
$\Sigma$ Weight		1		0.46	0.25		0.26					