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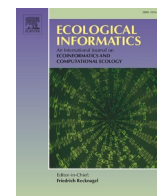
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A case study on joint species distribution modelling with bird atlas data: Revealing limits to species' niches

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ABSTRACT

Growing interest in biodiversity mapping has spurred the development of species distribution atlases, often mainly based on citizen-science projects. Atlas data have been frequently exploited to model species' ecological niches and distributions on a species-by-species basis. However, spatial autocorrelation and phylogenetic relatedness among species complicate the statistical description of species' niches. Also, the effects of species' traits and co-occurrences on species-habitat relationship are commonly disregarded. In this work, we build a hierarchical multi-species model based on a major citizen-science project (the third Spanish breeding bird atlas) that simultaneously accounts for spatial, phylogenetic and trait-based dependencies. We predict the distributions of species niches, species richness and community traits along regional ecological gradients. Climate, habitat associations and species' traits all contribute (in this order) to structuring species' distributions. Species richness increases towards intermediate climatic conditions and with aquatic habitat cover and decreases with increasing forest and woody agricultural land cover. Species were distributed along regional climate gradients in accordance with their global thermal niches. Forest habitats favoured assemblages dominated by generalist, small-sized and cold-dwelling species with limited migratory behaviour. Increasing sampling effort augmented the model performance. Model performance was weaker for rare species and those with decreasing population sizes, likely due to their low niche saturation. Overall, we show that ecological relationships generalize from local to large scales and may be elucidated from atlases based on citizen-science mapping efforts.

1. Introduction

Ongoing biodiversity loss has bolstered global interest in monitoring biodiversity and its ecosystem impacts (Jetz et al., 2019; Pereira et al., 2013). Diverse monitoring schemes have been implemented and the resulting data are habitually used to compile species distributional atlases (Keller et al., 2020; Robertson et al., 2010; Sillero et al., 2014). Atlas data have subsequently been analyzed with single-species distribution models to, for example, fill sampling gaps, assess population sizes and to describe species-environment relationships (e.g.: Estrada and Arroyo, 2012; Seoane et al., 2003), including dimensions of species' environmental niches (Elith and Leathwick, 2009).

Atlases do not represent the full distribution of the species, thus ecological models built from them must take into account the fact that species' distributions are spatially and temporally structured by environmental conditions, biotic interactions (e.g.: Kosicki, 2022, 2021), intrinsic processes such as dispersal (Estrada et al., 2015; Guisan et al., 2017; Sillero et al., 2021), and historical contingencies (Guisan et al., 2017; Sillero et al., 2021). Species' ecological traits (such as, for animals, average body size, resource and environmental specialization, and migratory behaviour) modulate their responses to biotic and abiotic drivers and dispersal, and are also expected to affect the predictive success of models of species distributions and ecological niches (Estrada et al., 2016; Guisan et al., 2017; McPherson and Jetz, 2007). For

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instance, specialist species occupy small ranges that are more easily described by distribution models than those of generalist species, and migratory species may be more challenging to model than sedentary species due to seasonally shifting habitat preferences (e.g.: Estrada and Real, 2021; Moreno-Zarate et al., 2020). Species' prevalences and their temporal population trends may also influence model performance. Rare species may be difficult to model due to insufficient observations, while ubiquitous species may show no clear associations with any predictor variable (Thibaud et al., 2014; van Proosdij et al., 2016). Species with temporally shifting abundances or ranges are not at environmental equilibrium and do not fill their potential distributions, and hence models of such species are hampered by commission and omission errors (Peterson et al., 2011). If ecological traits tend to be shared by close relatives, there may furthermore be phylogenetic structure in species' distributions and niche similarity (Wiens and Graham, 2005). Other largely unresolved complications in understanding current species distributions from biodiversity atlases, which are mentioned here for completeness but are not the focus of this study, are the role of historical events and dispersal in determining current ranges (Barve et al., 2011; Holt, 2003), and the scale-dependence of contributing factors (Chave, 2013). The former has long been recognized as a most relevant source of differences between the occupied and invadable niches and geographical areas (Peterson et al., 2011; Soberón, 2007). Including barriers to dispersal as model predictors (e.g.: Aliaga-Samanez et al., 2020) and a thorough consideration of the study area background and extent have been suggested to address this issue (Guisan et al., 2017; Sillero et al., 2021). Finally, the grain and extent of observations and the environmental descriptors are known to affect our understanding of ecological phenomena (Willis and Whittaker, 2002). Modelling exercises have tackled this by using predictors defined at several alternative scales (e. g.: Azcárate et al., 2023; Pérez-Granados et al., 2017) or implementing hierarchical frameworks (e.g.: Lomba et al., 2010; Mateo et al., 2019).

Most species atlases are based on citizen-science, that is, on the collection of data by non-professionals for scientific purposes (McKinley et al., 2017). These have greatly extended basic and applied research initiatives, and public support for these, despite their quality limitations (Galván et al., 2021). Atlas monitoring programs typically apply simple structured sampling to secure large numbers of participants over large areas (Tulloch et al., 2013). However, it is unclear whether the resulting data are of sufficient quality to describe species' niches (McKinley et al., 2017).

Here, we explore the niche determinants and other correlates of species' distributions for entire bird assemblages across Spain (one of the most biodiverse countries in Europe). To do so, we build a joint species distribution model, where a multivariate model is fitted to the species' co-occurrences to explore species-specific responses to environmental variables and simultaneously account for interactions across taxa. Correlations among species are captured by including a random effect (Warton et al., 2015). The model is based on observational data from the newest Spanish Breeding Bird Atlas (Molina et al., 2022). Specifically, we apply the hierarchical model of species communities framework (Ovaskainen et al., 2017), which compares favourably to other modelling techniques (Norberg et al., 2019). Thus, our description of niches is spatially structured and integrates information on species-environment relationships, and the potential effects of species interactions, species' traits and phylogenetic relatedness. We also test the hypotheses that species' prevalence, average specialization and body size, and population stability augment model performance, while migratory behaviour has a negatively impact. Overall, our study explores the usefulness of atlas data in combination with our modelling methodology for describing species' niches and gaining insight into niche determinants, species richness and trait-based patterns along ecological gradients.

2. Materials and methods

2.1. Study design and sampling protocol

2.1.1. Bird data

The Third Spanish Breeding Bird Atlas (Molina et al., 2022), a citizen-science project, recorded the occurrences of 450 breeding bird species in almost five thousand 10 km × 10 km UTM grid cells across Spain from 15 April to 15 June in 2014 to 2018. Most observations were by private individuals (amateur ornithologists), but information from species-specific monitoring programmes, occasional sightings (gathered from electronic platforms) and professional surveys of undersampled areas were also incorporated. Around 1400 volunteers selected a survey cell and engaged in one of three progressively more involved schemes (species lists, timed species-count in 15-min transects, and linear transects with two distance bands), aiming at a minimum of 10 h of field effort, either cross-country or by footpaths trying to survey every habitat in the grid cell. The data used in this study encompasses the occurrences of 191 terrestrial species within 817 UTM cells in mainland Spain (Fig. 1). This subset includes cells with a surface area > 50 km^2 that were judged to be well sampled by expert coordinators and to provide relatively even spatial coverage. Extremely rare and common species (those with prevalences outside the range 3–97%), introduced species without self-sustaining populations and pelagic species were excluded from analysis (see Table A.1 for the species list and inclusion criteria).

2.1.2. Explanatory variables

We selected eleven environmental covariates to represent climatic and habitat conditions in each UTM cell (Table B.1). First, 16 climatic variables describing temperature, radiation and water availability were synthetized into two PCA axes explaining 89% of variation in climate. PCA1 (68%) contrasts warm and dry Mediterranean conditions (roughly the southern three-quarters of Spain) to the cool, high rainfall Eurosiberian conditions in the north (Table B.2). PCA2 (21%) describes a continentality gradient, on which mean winter temperature and the number of days below freezing have large, opposite loadings (Figs. B.1-B.2). Habitat variables were the land covers (%) of seven main vegetation types. These were woodlands dominated by either coniferous (pine), broadleaf (deciduous oak, beech and riparian tree species), or evergreen (Holm and Cork oak) trees, open agriculture or woody crops, shrubland and aquatic environments. Aquatic habitats are generally rare but attract specialized species. Terrain ruggedness was captured by average slope (in degrees). Average human population density (log inhabitants / km^2) was included to represent anthropogenic impacts on birds and density-associated biases in sampling effort. Second order terms for the climatic and human population variables were included to describe potential curvilinear relationships. The number of sources of bird occurrence information per cell was included as an additional indicator of sampling effort.

2.1.3. Species traits

We selected five traits with established links to species' niches and to the range-shift capacities of species (Estrada et al., 2016). These were migratory behaviour (which also relates to the range-shift process), body mass, reproductive effort (average annual egg mass relative to body size), an index of species' habitat and trophic specialization (after Morelli et al., 2019) and a species-specific thermal index (e.g.: Gaüzère et al., 2015), which are related to both establishment and proliferation (Table 1).

2.1.4. Statistical analyses

We used Hierarchical Modelling of Species as our modelling framework (HMSC, Ovaskainen et al., 2017; Ovaskainen and Abrego, 2020). HMSC is a joint species distribution model (Warton et al., 2015) that includes a hierarchical structure allowing us to ask how species' responses to environmental covariates depend on their traits and
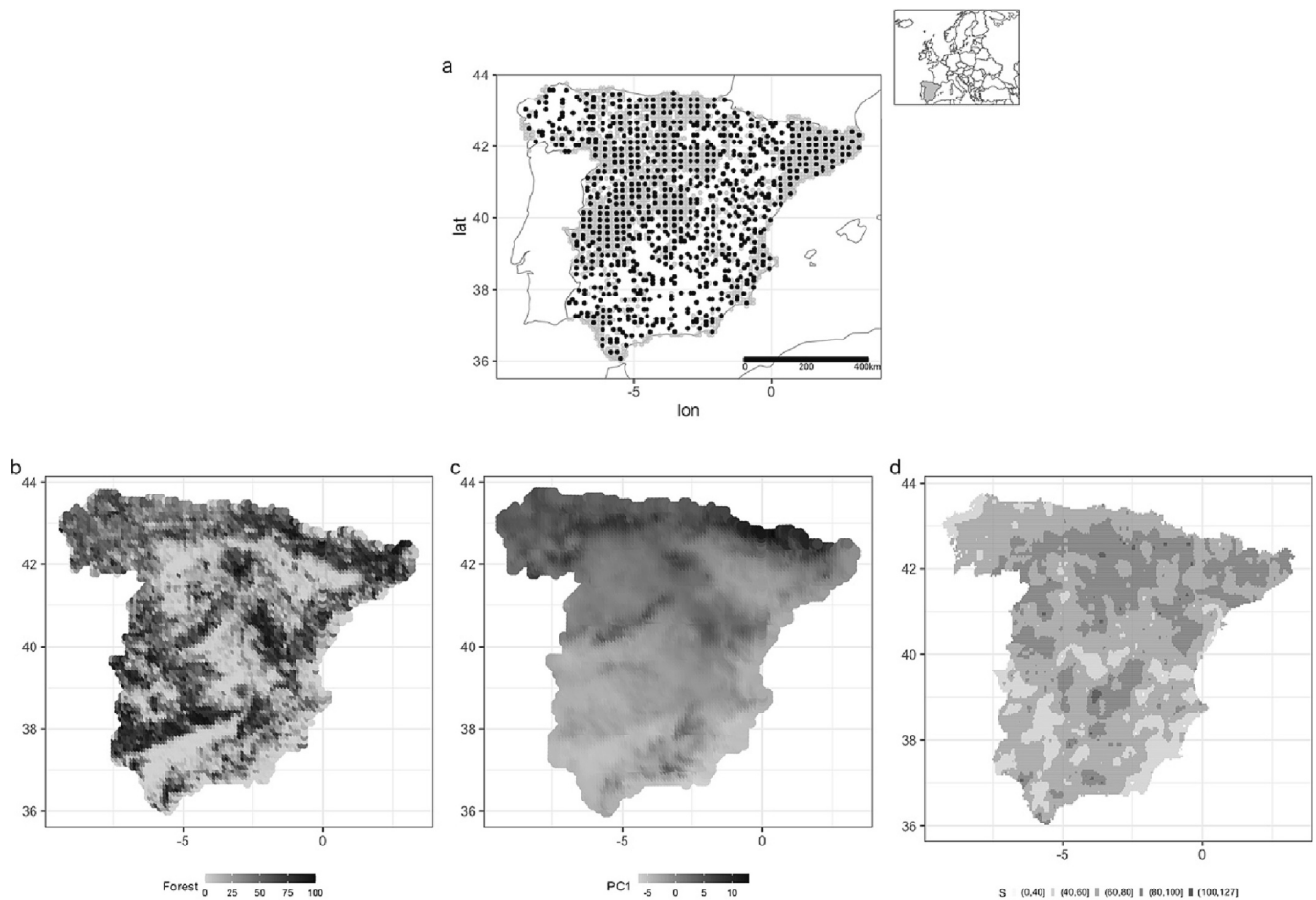
Fig. 1. **(a)** Study area. Black dots show the set of 10 × 10 km UTM square grids selected for the analyses (*n* = 817) out of the complete set available that was judged to be well sampled according to the expert opinion of regional and national survey coordinators (*n* = 2638, in gray). The inset shows the location of the study area within Europe. We show the following as examples of ecological gradients: **(b)** forest cover (in %) and **(c)** scores in the first PCA axis describing variation in climate (dry and warm Mediterranean climate vs wet and cool Eurosiberian conditions). **(d)** Predicted species richness. Richness was estimated by assuming median sampling effort in each sampled cell and stacking individual species' probabilities of occurrence (each being the average of 1000 posterior samples). These were interpolated with inverse squared distance and categorized in five classes for display (see Fig. C.6 for a colour map with a continuous palette).

Table 1
Species' traits used to explore their role in determining ecological niches and the range-shift stage process to which they correspond. The metric and source of each trait is also given.

Trait	Range-shift stage	Metric	Source
Migratory behaviour	Emigration	Sedentary, short- and long-distance migrants	According to Storchová and Hořák (2018) amended and extended with information in De Juana and Garcia (2015)
Body mass	Movement	Log-transformed mean body mass (g)	Wilman et al. (2014)
Reproductive effort	Establishment and proliferation	Residuals of a linear regression of log(number of broods per year x clutch size per brood x mean weight per egg) on log (body mass)	Data from Storchová and Hořák (2018), extended with data from BWP (Cramp and Perrins 1977–1996), and HBW (Del Hoyo et al., 1992–2013).
Species' specialization index	Establishment and proliferation	Average specialization index across five habitat and trophic niche dimensions (range 0 [absolute generalist] to 1 [maximum specialist])	Methods and data in Morelli et al. (2019), amended and extended with data from BWP (Cramp and Perrins 1977–1996) and HBW (Del Hoyo et al., 1992–2013)
Species' thermal index	Establishment and proliferation	Mean long-term temperature in its global (breeding) distribution	Distributional data provided by BirdLife International and (2019) [version 2019.1] overlaid with WorldClim climatic rasters (1970–2000, Fick and Hijmans, 2017)

phylogenetic relationships (Abrego et al., 2017).

The sampling units in our model (n_y = 817) were the selected 10 × 10 km UTM cells described above. The response variables (the matrix n_y × n_s **Y** of HMSC; see Ovaskainen et al., 2017), were the binary occurrences of each of the n_s = 191 species. We built a probit regression of species occurrences including as fixed effects the 14 environmental terms described above and sampling effort per UTM cell (the n_y × n_c matrix **X** of HMSC; where n_c is the number of species-specific regression

parameters to be estimated).

We included the five species traits described above (Table 1). Closely related species in a phylogeny may share niche characteristics beyond those accounted for by the traits considered here and thus have correlated distributions. To assess whether such a phylogenetic signal was apparent in our data we included a 50% majority-rule consensus tree based on 100 phylogenetic trees downloaded from BirdTree.org (Jetz et al., 2012). To account for the spatial structure of the study design, we

included a spatially explicit random effect, implemented through the predictive Gaussian process for big spatial data (Tikhonov et al., 2020a). This random effect models spatial variation among sampling units that is not directly accounted for by the environmental covariates.

We fitted the model with the R-package Hmsc (Tikhonov et al., 2020b) using the default prior distributions (for details, see Ovaskainen and Abrego, 2020). We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each run for 375,000 iterations, and removed the first 125,000 as burn-in. The chains were thinned by 1000 to yield 250 posterior samples per chain and 1000 posterior samples in total. We assessed MCMC convergence based on the potential scale reduction factors (PSRFs) of the model parameters (Gelman and Rubin, 1992). We performed 10-fold crossvalidation based on models thinned by 100.

Model performance for each bird species was quantified in terms of Tjur's R^2 and AUC values (Pearce and Ferrier, 2000; Tjur, 2009). These metrics give complementary information on the ability of individual species' models to correctly discriminate between species presences and absences. Tjur's R^2 is asymptotically equivalent to the coefficient of determination R^2 and AUC summarizes model accuracy. To quantify the drivers of bird community structure, we ran variation partitioning quantifying the fractions of variance in species occurrences (in terms of Tjur's R^2) explained by each environmental covariate, by sampling effort and by the spatial random effect (see Chapter 5 of Ovaskainen and Abrego, 2020). We also quantified species' predicted responses to each model covariate (i.e., their predicted β parameters), and calculated the proportions of species that showed a positive or negative predicted responses to each covariate with at least 95% posterior probability.

We tested for relationships between model performance in terms of Tjur's R^2 and AUC and species' 1) prevalence (total number of occupied cells), 2) population trends over time and 3) traits (log body mass, species' specialization, thermal affinity and migratory behaviour). Species populations were coded as stable, strongly or moderately declining, or strongly or moderately increasing during the last decade (following Escandell and Escudero (2019) and monitoring reports from https ://www.seo.org/resultados-seguimiento-de-aves/). Migratory behaviour was coded as sedentary, short-distance or long-distance. Linear models for Tjur's R^2 and AUC were built with each of these properties in turn as predictors (continuous variables were included as second-order polynomials). Statistical significance and the relative importance of each term was assessed using log-likelihood ratio tests and type-II variance decomposition. The species' predicted occurrence probabilities were clustered to identify regions of common profile by partitioning around medioids, a robust alternative to k-means partitioning (Kaufmann and Rousseeuw, 1990).

3. Results

Individual species' models had good to excellent fit according to their AUC values (AUC > 0.90 and AUC > 0.80 respectively, Araújo et al., 2005) and their explanatory ability when assessed with Tjur's R2 was substantial (> 0.5) for a third of species. Although, performance varied widely among species (mean Tjur's R^2 0.44 ± s.d. 0.14, range 0.09–0.83; AUC 0.92 ± s.d. 0.05, range 0.79–0.99, Fig. C.1). Ten-fold cross-validation results based on models thinned by 100 for Tjur's R^2 ranged from 0.02 to 0.78 (mean 0.32 ± s.d. 0.14) and for AUC ranged from 0.66 to 0.99 (mean 0.86 ± s.d. 0.07). Note that the performance of models thinned by 1000 and by 100 was highly correlated ($\rho = 0.992$ and $\rho = 0.998$ for Tjur's R^2 and AUC, respectively). Total environmentally explained variance averaged 25% and additional variance captured by the spatial random effect averaged 18%. Sampling effort was a positive predictor of occurrence in 86% of species. It accounted for just 1% of total variance on average, but for >4% of variance in some models, e.g., of raptors like the Peregrine Falcon *Falco peregrinus* and the Red Kite *Milvus milvus*, that are recorded in multiple schemes (Table A.3).

The two climatic PCs contributed most, on average, to explained

variance (14%), followed by slope (3%), the three forest types (summed mean 2%), and the two agricultural habitat types (summed mean 2%, Table A.3).

The explanatory power of the models was significantly associated with species' prevalence and population trends (Table 2). The relationship with prevalence was downward concave for Tjur's R^2 and upward concave for AUC, with partial $R^2 = 10\%$ and 39% respectively (Figs. 2 and Fig. C.1). Average explanatory power was similar among the population trend classes, except that strongly declining species had lower values (partial $R^2 = 9\%$ and 11% respectively). Only the contrast of strongly declining to moderately increasing species remained significant at $\alpha = 0.05$ after Tukey adjustment for multiple comparisons. Tjur's R^2 values were also curvilinearly associated with species' specialization (partial $R^2 = 3\%$, Table 2). Model explanatory power was not related to body mass, species' thermal affinity or to migratory behaviour.

3.1. Species' environmental responses

Parameter convergence was satisfactory (PSRFs <1.05 for 97% of parameters, with a maximum value of 1.2). There was strong posterior support for phylogenetically correlated residuals: $E[\rho] = 0.73$ ($Pr[\rho > 0] = 1$) indicating that closer relatives tended to have more similar environmental niches.

In relation to climate, there was statistical support for a positive response (with >95% posterior probability) to PC1 in 45% of species (e. g., the Eurasian Bullfinch *Pyrrhula pyrrhula* and Yellowhammer *Emberiza citrinella*) and a negative response in 30% of species (such as Sardinian Warbler *Curruca (Sylvia) melanocephala*). The square term was furthermore negative for 45% of species, indicating intermediate optima or other curved responses to the gradient. For climatic PC2, the equivalent values for the linear term were 22% positive, 19% negative, and 24% negative for the square term (Fig. C.2).

Associations with habitat types were statistically supported in 83% of species, and these generally matched our prior understanding of regional species-habitat relationships. For example, we found posterior support for positive associations with forest types in 19% of the species. Among these, the Coal Tit *Periparus ater* and Crested Tit *Lophophanes cristatus* had the largest positive coefficients for coniferous forests, while the Eurasian Jay *Garrulus glandarius* and Eurasian Nuthatch *Sitta europaea* had the largest coefficients for broadleaf and evergreen forests

Table 2

Deviance table (type II tests) for the effects in linear regressions with Gaussian errors of data properties and ecological traits on the explanatory power (a: Tjur's R^2, b: AUC) of individual species' models. Degrees of freedom (Df), F-test (F), partial R^2, and *p*-values per term. *P*-values after type II tests with heteroscedasticity-corrected covariance matrices by hc3 correction (Long and Ervin, 2000). Partial R^2 based on nested comparisons to full model and the improvement on residual sum of squares. Prevalence, log body mass specialization and thermal affinity were modelled as second-order polynomials.

Explanatory variable	Df	F	R^2	p-value
a) Tjur's R^2				
Prevalence	2	5.96	0.10	0.003
Population trend	4	3.62	0.09	0.007
Body mass (log)	2	0.48	0.01	0.622
Species specialization index	2	3.37	0.03	0.037
Species thermal index	2	0.94	0.01	0.394
Migratory behaviour	2	1.90	0.02	0.153
Residuals	176			
b) AUC				
Prevalence	2	45.79	0.39	<0.001
Population trend	4	4.12	0.11	0.003
Body mass (log)	2	1.09	0.01	0.338
Species specialization index	2	2.59	0.03	0.078
Species thermal index	2	0.12	0.01	0.886
Migratory behaviour	2	1.41	0.02	0.248
Residuals	176			
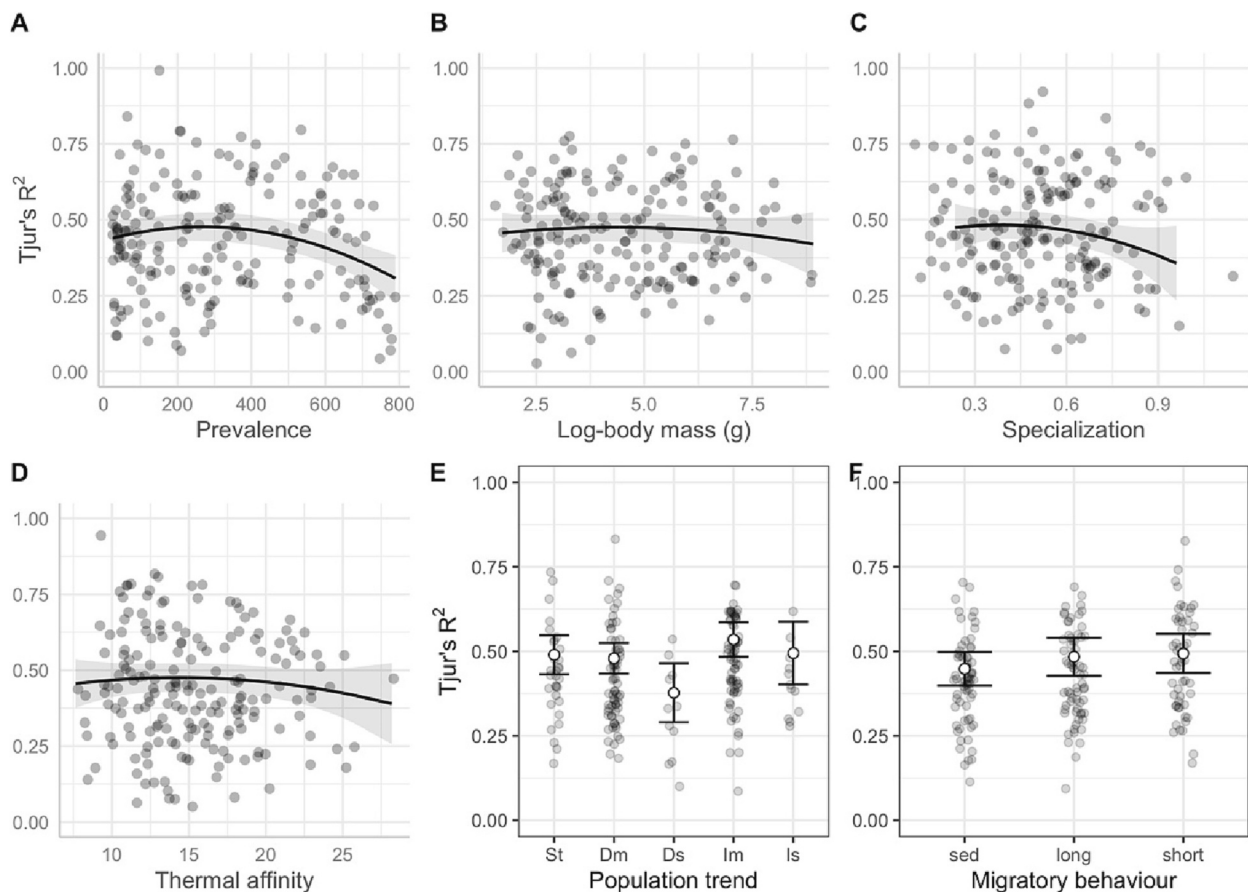
Fig. 2. Relationship between the explanatory power of individual species models (Tjur's R^2) and species' prevalences across sample sites, recent population trends and traits (A: prevalence, B: log-body mass, C: species specialization index, D: thermal affinity, E: population trend, F: migratory behaviour). Solid lines with polygons for continuous variables, and open circles with whiskers for factors, represent mean marginal effects and their 95% confidence intervals for each model term (see Table 2a). Raw data points are shown in the background, slightly jittered, for reference. Population trend: St: stable, Dm: decreasing moderate, Ds: decreasing strong, Im: increasing moderate, Is: increasing strong. Migratory behaviour: sed: sedentary, long: long-distance migration, short: short-distance migration. Relationships with log-body mass and migratory behaviour had $p > 0.05$ (see Table 2).

(Fig. C.3).

Positive responses to terrain slope were detected in 24% of species and negative responses in 39% of species. Mountain-dwelling species such as the Water Pipit *Anthus spinoletta* and Common Rock Thrush *Monticola saxatilis* were among those with large positive coefficients for slope, while steppe birds (e.g., Stone-curlew *Burhinus oedicnemus*, Mediterranean Short-toed Lark *Alaudala rufescens*) had large negative coefficients (Fig. C.4). Finally, there was posterior support for a positive effect of an intermediately high human population density for 16% of species.

There were positive residual correlations among most taxa. This and the fact that the spatial random effect accounted for 17% of total variance implies that our environmental covariates did not include all the relevant drivers of bird distributions.

Species richness was predicted to increase towards intermediate climatic conditions, extensive aquatic habitats, and with increasing human population density, but was predicted to decrease with increasing forest and woody agricultural land covers (Fig. C.5). Maps of predicted richness broadly coincide with earlier reports (Carrascal and Lobo, 2003; Moreno-Rueda and Pizarro, 2009) and highlight as hotspots the border between the Mediterranean and Eurosiberian biomes, the northwestern Iberian temperate forests, major wetlands (Doñana, La Mancha Húmeda) and particular mountain ranges (i.e., the Pyrenees, Central and Iberian ranges, but not the southern Sierra Nevada and Baetic ranges; Fig. 1, Fig. C.6).

Three bioregions ('regions of common profile') were identified by clustering the species' predicted occurrence probabilities. These highlight distinct bird communities in the Eurosiberian domain, the Mediterranean North and mountains in the Mediterranean South, and the Mediterranean South and dry interior basins (Fig. C.14).

3.2. Trait-mediated niche differences

Species' traits explained 16% of variation in their occurrences and were related to several environmental covariates (Fig. 3, Figs. C.6-C.7). Many specialized species (with high SSIs) had a strong Mediterranean climate affinity and often an intermediate optimum on the continentality gradient. Species with warm thermal preferences (high STIs) were more frequently associated with a Mediterranean climate, and negatively associated with coniferous and broadleaf (but not evergreen) forests, than species with lower STIs (Fig. 4).

Larger species were more likely to be negatively associated with coniferous and broadleaf forests, shrub cover and sloping terrain (roughly indicative of mountainous areas), and positively with human density and aquatic environments than smaller species. Short-distance migrants and sedentary species were more likely to be associated with coniferous and evergreen forests, respectively, than long-distance migrants. Also, short-distance migratory species were more likely to have affinities for Eurosiberian and continental climate, and for aquatic environments. In contrast, resident species were more likely in rugged areas, but less likely in populated areas rich in aquatic environments or open crops. Species with a higher reproductive effort were more likely to
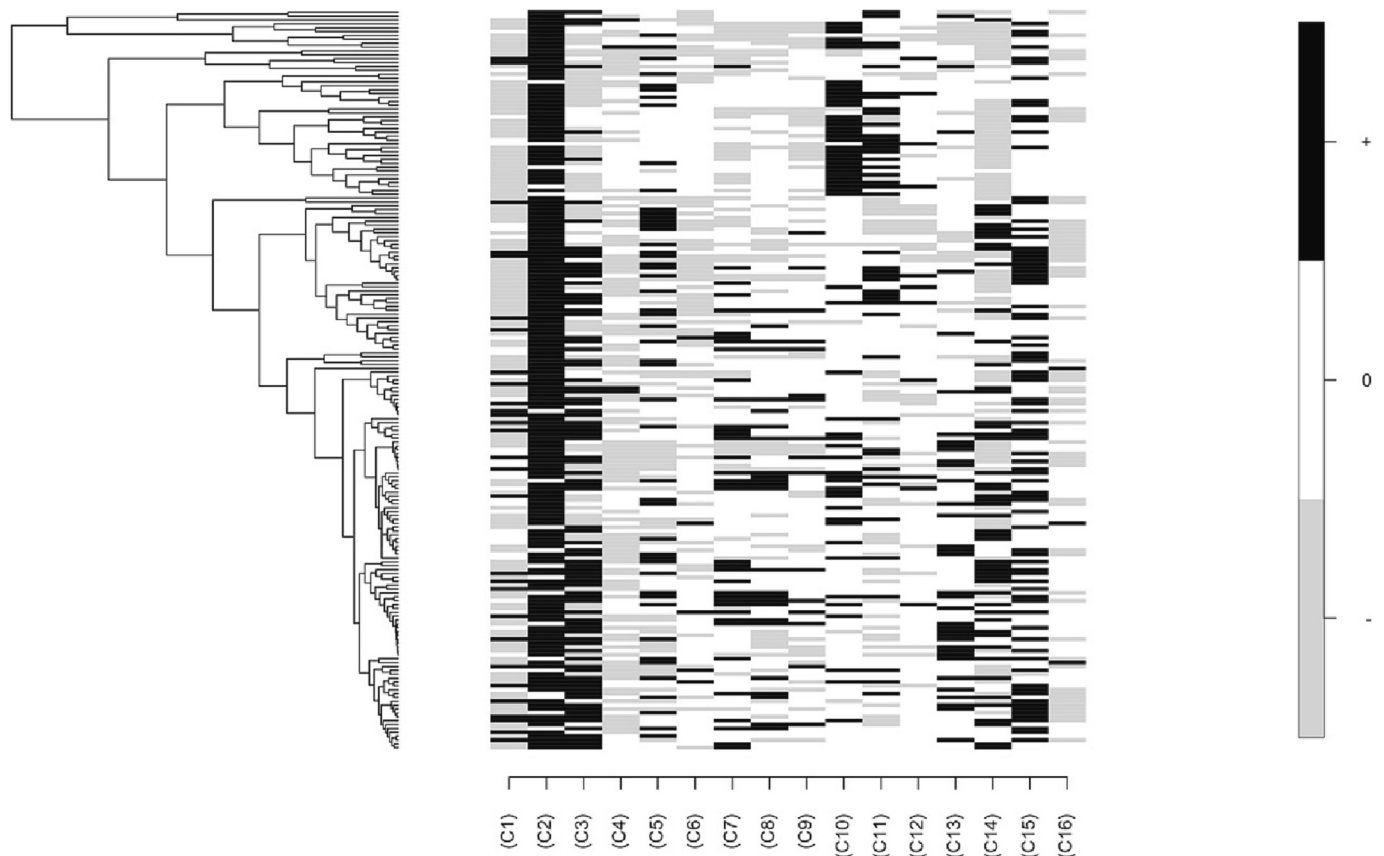
Fig. 3. Heatmap of estimated beta parameters for covariates describing species niches. Black and gray colours show the parameters that are estimated to be positive and negative, respetively, with at least 0.90 posterior probability. The phylogenetic relationship among species is shown to the left. Covariates are: C1, intercept; C2, sampling effort; C3 and C4, linear and second-order polynomial terms for first climatic PCA axis (Mediterranean to Eurosiberian climate), respectively; C5 and C6, linear and second-order polynomial terms for second climatic PCA axis (continentality), respectively; C7, C8 and C9 percentage cover of coniferous, broadleaf and evergreen forest, respectively; C10, percentage cover of aquatic environments; C11 and C12, percentage cover of open and woody crops, respectively; C13, percentage cover of shrubland; C14, average slope; C15 and C16, linear and second-order polynomial terms for log-human population density.

show positive response to continentality, aquatic environments, and populated areas, and negative response to sloping terrain, than those with a lower reproductive investment (Figs. C.8-C.13).

4. Discussion

4.1. Drivers of species' distributions

Our results demonstrate that citizen-science-based atlases provide valuable information on the abiotic (Grinellian) and functional (Eltonian) limits to the ecological niches of birds, and on regional biodiversity patterns. Joint modelling allows the ecological niches and regional distributions of entire assemblages to be successfully described, while simultaneously accounting for their inherent spatial and phylogenetic structure, although the task remains computationally challenging.

Climate is the major driver of species distributions across mainland Spain at our study grain and scale, followed by terrain slope and landcover. This is in line with previous modelling results at similar spatial grains and extents and with theoretical expectations based on a hierarchy of biodiversity drivers (Guisan and Thuiller, 2005; Luoto et al., 2007; Mateo et al., 2017). Most species showed directional climatic responses aligning with the major bioregions of the study area, from warm and dry Mediterranean areas to cooler and more humid Eurosiberian areas. Typical northern- and southern-European species were associated with opposite ends of this climatic gradient, matching expectations based on their continental ranges (Keller et al., 2020). Hence, our models captured their climatic responses successfully despite being

fitted with data from a subset of their entire range (Chevalier et al., 2022). All but one species showed associations with either climatic or habitat descriptors and these associations generally matched expert knowledge and the main reports on species' ecological preferences and distributions in Spain (e.g.: De Juana and Garcia, 2015; Telleria et al., 1999). The one revealing exception was the Common Kestrel *Falco tinnunculus*, the model for which had weak explanatory power and failed to indicate any environmental associations. This is a generalist species that favours fine-grained habitat features that were inadequately summarized by our environmental descriptors. Overall, species' responses to climate and habitat translate into three major bioregions with partially distinct bird communities (the Eurosiberian domain, Mediterranean north and Mediterranean south, Fig. C.14).

4.2. Model performance

Model performance in our study was comparable to that of other regional modelling efforts based on atlas data (González-Taboada et al., 2007; Ovaskainen et al., 2016). Our rudimentary proxy for sampling effort boosted explanatory performance for most species. Its contribution was generally small, but was more substantial for some owls, raptors and other relatively common species nesting in particular landscape features (cliffs, cavities). This suggests that adding occurrence information from multiple sources may counterbalance the imperfect detection of some moderately rare species (albeit not of the rarest species, which require targeted monitoring). We hence reiterate calls to record sampling effort in biodiversity monitoring (Barbosa et al., 2013;
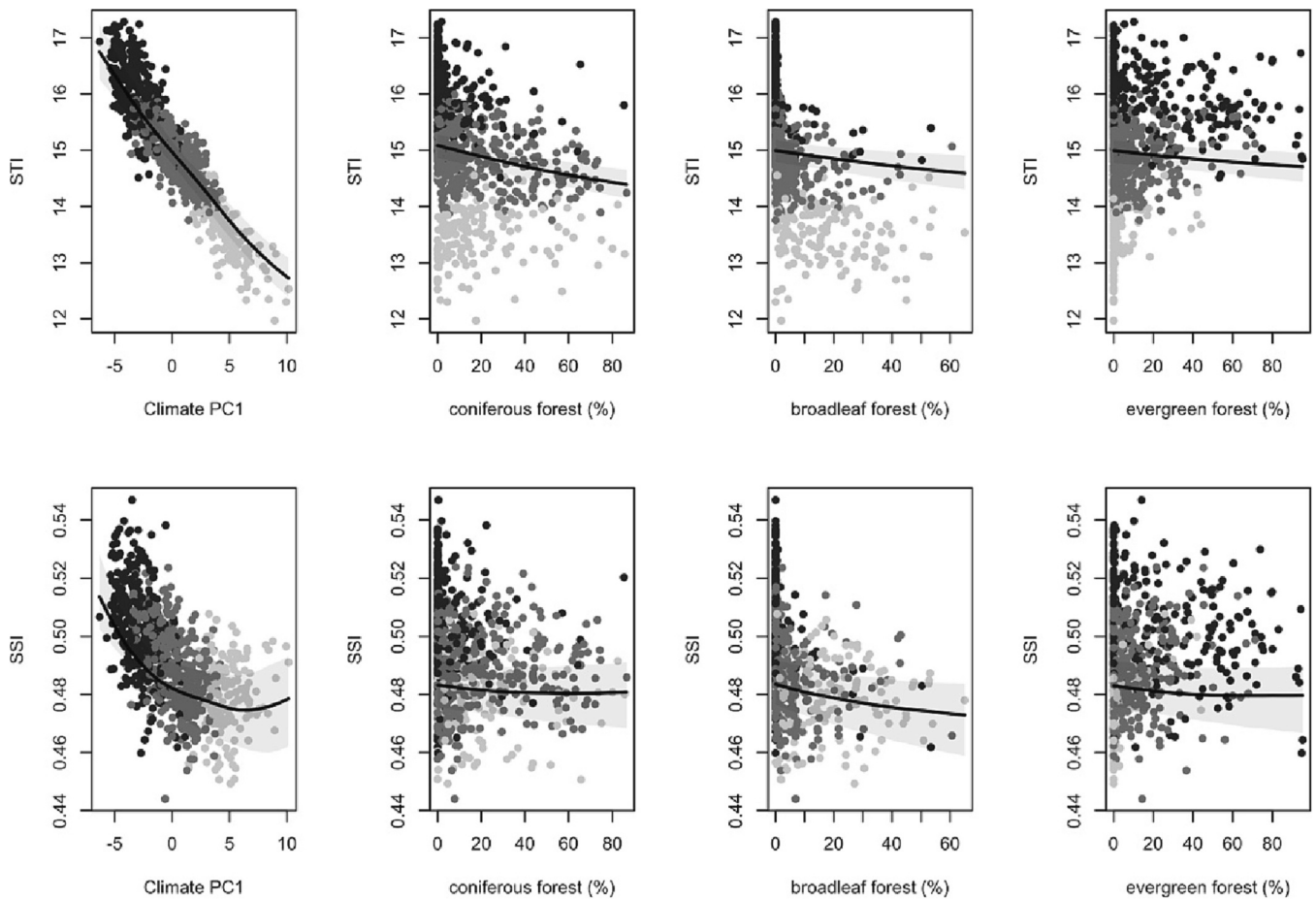
Fig. 4. Community-weighted mean (CWM) values for a selection of traits and environmental combinations. We show here as an illustration predictions of CWM of species' thermal preferences (STI top row; higher values for warm-dwelling species) and species' specialization (SSI bottom row; higher values for specialists) along gradients in climate (PCA1; higher values for Eurosiberian conditions) and percent of forest cover (second to fourth column: coniferous, broadleaf and evergreen). Points are coloured as three regions of common profile based on species' occurrence probabilities (see Fig. C.14): light gray for Eurosiberian domain, medium gray for Mediterranean North and mountains in the Mediterranean South, black for Mediterranean South and dry interior basins. The support of predicted change from gradient minimum to maximum was in all cases >95% except for SSI on coniferous and evegreen forest (0.73 and 0.77 respectively). Predictions are made fixing all other covariates except the focal one at their mean value. See Figs. C.8-C.13 for all the trait and environment combinations.

Calenge et al., 2015).

Indices of species' rarity and trend, and ecological characteristics were moderately to weakly related to model performance (Table 2). Species prevalence had a curvilinear relationship with model discrimination (Fig. 2 and Fig. C.1). In agreement with previous simulation studies, Tjur's R^2 peaked at intermediate prevalence (Jiménez-Valverde et al., 2009; Reese et al., 2005). The interplay of prevalence and sample size has complex effects on model performance (van Proosdij et al., 2016). Large sample sizes are beneficial if they improve geographical and environmental coverage (Tessarolo et al., 2014). However, logistic regression model predictions are biased towards presences or absences, depending on which category is more frequent. Studies indicate that model performance tends to decrease with increasing prevalence for a given sample size, and that the sample size of the rare category is of paramount importance (Jiménez-Valverde et al., 2009; van Proosdij et al., 2016). Here, overall, our models attained very good explanatory power and explained a substantial proportion of variance in species distributions irrespective of their prevalence.

Recent population trends were weakly related to model performance. The distributions of strongly declining species were least reliably predicted (Table 2). Temporally changing abundances and ranges violate the equilibrium assumption of species' distribution models (Peterson et al., 2011). Thus, we expected a lower fit for models of species with unstable population trends. The fact that reduced

explanatory power was only evident for strongly declining species suggests that occurrence data at this coarse spatial resolution may be insufficiently sensitive to accurately characterize less pronounced temporal trends.

Species' ecological specialization was negatively associated with model discrimination, albeit weakly: model performance decreased substantially with specialization above roughly intermediate values, against our prior expectations (Table 2). Earlier studies have found positive relationships between habitat specialization and model performance, as it facilitates the ability of modelling algorithms to distinguish between suitable and unsuitable habitats (McPherson and Jetz, 2007; Sillero et al., 2021). The effects of specialization on model performance can, however, easily be confounded with those of prevalence, because specialists tend to be rare and to have small range sizes, and are hence difficult to model successfully (Jiménez-Valverde et al., 2009). However, we tested the marginal effects of specialization and prevalence on model performance in a combined model and found that poor model performance for specialists was not a simple function of their rarity. In general, the available species' traits were not clearly related to model performance, perhaps because coarse-grained occurrence and environmental data decouples model performance from species' characteristics. However, the distributions of species with intermediate to high prevalences, and those with strongly declining populations, tended to be less successfully predicted than other taxa.

4.3. Patterns of species richness

Environmental trends in species richness matched previous observations and theoretical expectations linking diversity to broad-scale energetic constraints and habitat heterogeneity (Davies et al., 2007; Moreno-Rueda and Pizarro, 2009; Fig. C6). Richness was lower at both ends of the climatic gradients where temperature, water availability and continentality may strongly filter taxa (Moreno-Rueda and Pizarro, 2008).

Species richness is further limited in these areas by the interaction of habitat type with the constraints set by ambient energy and water availability (Seoane et al., 2017).

In accordance with the well-established positive relationship between habitat diversity and species richness (Tews et al., 2004) and the role of land use in shaping large scale richness patterns (Martins et al., 2014), larger extents of most habitat types were associated with lower bird species richness. Some specialists require large areas of specific habitats, but our findings suggest that these do not compensate for the absence of many species in more homogeneous landscapes. The notable exception was aquatic habitats, for which there was a positive relationship between extent and species richness over much of the gradient, highlighting the importance of wetland and riverine ecosystems for bird diversity (González-Taboada et al., 2007; Ramirez et al., 2018). Finally, the observed positive relationship of species richness with human density has been previously interpreted as a productivity effect, whether directly boosted by energy derived from human activity, or simply due to the coincidence of larger human and bird populations in high-energy areas (González-Taboada et al., 2007; Moreno-Rueda and Pizarro, 2009). However, residual correlations among species in our models were overwhelmingly positive, which implies that we failed to identify some relevant drivers of bird species distributions and richness. Likely candidates are fine-scale habitat structure, vegetation composition and human disturbance.

4.4. Species' traits and environmental variables

Correlations between species' traits and environmental variables provide insights into niche constraints to species distributions. Notably, species' thermal indices were correlated with their climatic and habitat distributions. Typically, cold-dwelling species avoided warm Mediterranean conditions and favoured pine and broadleaf forests, but not oak woodlands. Forest species may exhibit colder climatic niches in Europe than species of open habitats due to the broad latitudinal extent of postglacial forests and higher agricultural land conversion in southern than in northern Europe (Barnagaud et al., 2012).

Species' habitat and trophic specialization also correlated with climate and habitat gradients. Bird assemblages of Mediterranean environments were predicted to include high proportions of specialists. However, past-century forest expansion in Mediterranean areas, resulting from agricultural land abandonment and rural depopulation, is likely to have favoured generalists over these specialists, thereby promoting the functional homogenization of bird communities (Clavero and Brotons, 2010; Fusco et al., 2021). The observed trait-environment relationships also suggest contrasting changes in bird assemblages under projected climatic warming (i.e., increases in specialist bird species) and habitat change (increases in species with cooler thermal preferences with increasing forest cover). Two other relationships between habitat preferences and species' traits stand out. First, sedentary and short-distance migratory strategies were positively associated with non-seasonal evergreen forests and woodlands. This supports previous findings that trans-Saharan migrants are more frequent in seasonal environments (Telleria et al., 1999) and observations of large seasonal changes in bird assemblages in these areas (Villén-Pérez et al., 2013). Second, average body mass correlated negatively with forest cover, mainly because small-sized species were more frequent in woodlands, exemplifying variation among habitats in the eco-evolutionary constraints on body size (Polo and Carrascal, 1999).

4.5. Conclusions

Overall, this work illustrates the promise of joint species distribution models for capitalizing on the enormous efforts invested in compiling biodiversity atlases, and demonstrates that recognized aspects of climate- and habitat-driven structure in local bird assemblages generalize to the regional scale. Adding analytical value to citizen-based atlas projects promotes our ecological knowledge of entire regional communities and can also help to raise public awareness to fight the biodiversity crisis.

CRediT author statement

J. Seoane conceived the ideas and designed methodology; J. Seoane and M. Jones analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Raw data cannot be archived in a publicly available repository because it is owned by a third-party, the environmental NGO SEO/BirdLife (https://seo.org/). However, this NGO grants grant permission to access these data for research purposes. Requests should be addressed to seguimientodeaves@seo.org and a signed non-disclosure agreement is requested. Moreover, the data are already displayed in the form of maps of observed and predicted distributions on a dedicated website (https://atlasaves.seo.org/).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2023.102202.

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