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Co-occurrence patterns in a steppe bird community: insights into the role of dominance and competition

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Spatial co-occurrence patterns are determined by environmental factors, such as food availability or habitat characteristics and by biotic associations. When resources are limited, competition which implies a dominant hierarchy can shape species assemblage. Here, we study space and time co-occurrence of steppe passerines during the breeding season in a natural steppe habitat, its modulation by environmental filtering, potential biotic interactions and random processes. We applied the joint species distribution model of hierarchical modelling of species community (HMSC) to data on species presence–absence and environmental, temporal and spatial covariates acquired from seven plots in a natural steppe in central Spain during two consecutive years. Our results reveal the patterns of bird species co-occurrence and suggest that this assemblage might be competitively structured. The assemblage appears to be configured around one dominant species, the Eurasian skylark, which establishes principally negative associations with many of the coexistent species. Our results contribute to the understanding of how competition and dominance processes, together with ecological constraints and other biotic associations, shape bird assemblages.

Keywords: biotic associations, dominant hierarchy, ecological niches, resource partitioning, species co-occurrence, steppe passerines

Introduction

Disentangling the factors that influence community structure is a fundamental aspect of community and conservation ecology research (Bascompte 2010). Species co-occurrence patterns are shaped by abiotic factors (e.g. availability and dynamics of food resources or the type and structure of vegetation; Morris and Davidson 2000, Soberón 2007, Traba et al. 2015) and biotic factors (e.g. density of competitors, predators and pathogens and interspecific interactions; Rosenzweig 1981, Han et al. 2020). Although the relative contribution of these factors in structuring ecological assemblages has previously been addressed, the role of competition remains controversial and is a current topic of debate in ecology (Estevo et al. 2017, Blanchet et al. 2020).

Coexisting species compete for resources, especially when they are closely related and resources are limited. The competitive exclusion principle predicts that competitors for identical resources cannot coexist (Hardin 1960, Liu et al. 2014), and therefore coexisting species over evolutionary time should exhibit a partition of resources exploitation, whether spatial, temporal or trophic (Leibold et al. 2004, Leibold and Mcpeek 2006; but see Traba et al. 2017) to occupy different ecological niches (Hutchinson 1957, Soberón 2007, Chase and Leibold 2009, Levine and HilleRisLambers 2009, Salsamendi et al. 2012). Likewise, species may differ morphologically in order to reduce or eliminate competition (see 'character displacement' concept in MacArthur and Levins 1967, Levine and HilleRisLambers 2009). The existence of dominant species, often those larger than subordinate ones (Freshwater et al. 2014, Martin and Ghalambor 2014), could imply differential resources exploitation or even interference interactions between species (Morris 1989, Tarjuelo et al. 2017). When interferences are maintained in the same direction, a hierarchy of interspecific dominance is created (Drews 1993) with the dominant competitor excluding the subordinated ones by restricting the access to key resources (LeBrun 2005). Both potential outcomes of competition (partition of resources and/or interference interactions) ultimately may affect co-occurrence, potentially leading to negative species associations (Tarjuelo et al. 2017, Traba et al. 2017, but see Blanchet et al. 2020).

Passerines living in steppes and open habitats (de Juana 2005) are small, morphologically similar, insectivorous birds, with unique ecological and evolutionary characteristics: they nest on the ground and are subject to a high level of predation (de Juana 2005). Many of them are territorial and show a socially monogamous mating system (Billerman et al. 2022).

In this study, we analyse niche overlap and resource partitioning in a steppe passerine assemblage. Specifically, we study how a set of steppe passerines co-occur in space and time during the breeding season in a natural steppe habitat and how coexistence is modulated by environmental filtering, biotic associations and random processes through a joint species distribution model of Hierarchical modelling of species community (HMSC; Tikhonov et al. 2020b). The applied technique allows us to test predictions, both for the whole assemblage and for pairs of species. Firstly, we hypothesize that this assemblage, due to passerine features and its presumable long-time evolutionary coexistence, will exhibit food/habitat segregation to allow coexistence during the breeding season and thus, environmental filtering is expected to prevail in explaining co-occurrence patterns. Secondly, we expect that the more abundant species will be subject to a greater number of associations with cohabiting species and may be crucial to the configuration of the assemblage.

Methodology

The study system

The study area was located in the Soria province in central Spain (41°13′N, 2°28′W, Fig. 1) within two SPAs (Special protecting area) separated by 11 km, Altos de Barahona and Paramos de Layna, both included within the Sites of community importance (SCI) (ES4170148 and ES4170120 respectively). These SPAs were declared for their importance for steppe birds. These are characterized by flat areas dominated by shrubs and scrubs shorter than 50 cm, such as thyme *Thymus* spp., broom *Genista* spp. and lavender *Lavandula* spp., a high proportion of bare ground cover and a reduced extension of cultivated fields and scattered trees. The Iberian shrub-steppes are one of the most singular, rare and threatened habitats in the European Union (Sainz Ollero 2013) and represent an important habitat of Iberian steppes (Ollero and van Staalduinen 2012) due to the singular communities of plants, arthropods and birds they contain. They are considered a fundamental habitat for the protection of steppe birds, given the seriousness of their marked decline (Gómez-Catasús et al. 2018, Traba and Morales 2019). Detailed information about the typical habitat and climate in the study area can be found in Gómez-Catasús et al. (2019) and Zurdo et al. (2021).

We located six and seven sampling areas (hereafter plots) in 2017 and 2018, respectively. Plot size range between 47.6 and 72.3 ha (mean ± SD = 60.0 ± 9.6), and they were 1–20 km apart (8.03 ± 6.77; Fig. 1). Plots were all similar in landscape or physical features: altitude (around 1150 m a.s.l.), plain relief (slope < 10%), and plant communities (majority presence of scrub steppe dominated by *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Linum suffruticosum*). See Zurdo et al. (2021) for a whole plant community description.

Steppe birds surveys

We focused on eleven passerine species that occur in sympatry during the breeding season in shrub steppes, and that make up most of this bird community: the Dupont's lark *Chersophilus duponti*, Eurasian skylark, greater short-toed lark *Calandrella brachydactyla*, Thekla lark *Galerida theklae*, tawny pipit *Anthus campestris*, Calandra lark *Melanocorypha calandra*, woodlark *Lullula arborea*, black-eared wheatear *Oenanthe hispanica*, northern wheatear *Oenanthe oenanthe*, rock sparrow *Petronia petronia* and common stonechat *Saxicola rubicola*. These species were present in at least four (of the seven) plots and with a minimum abundance of 20 individuals per species (Supporting information).

We carried out two different types of bird censuses in each plot to determine bird occurrence and spatial location, according to species characteristics and behaviour: Dupont's lark and passerine censuses. Dupont's lark territories were mapped between April and June of both sampling years using the census methodology commonly employed (Pérez-Granados and López-Iborra 2016). We located one transect through the center of each plot, and we georeferenced with GPS (error ± 5 m) all singing and calling males within a 500 m belt on each side of the line (Fig. 1). Censuses were carried out approximately 1 h before sunrise, when the Dupont's lark singing activity peaks, and they spanned around 40 min. Transects were repeated three times alternating the starting

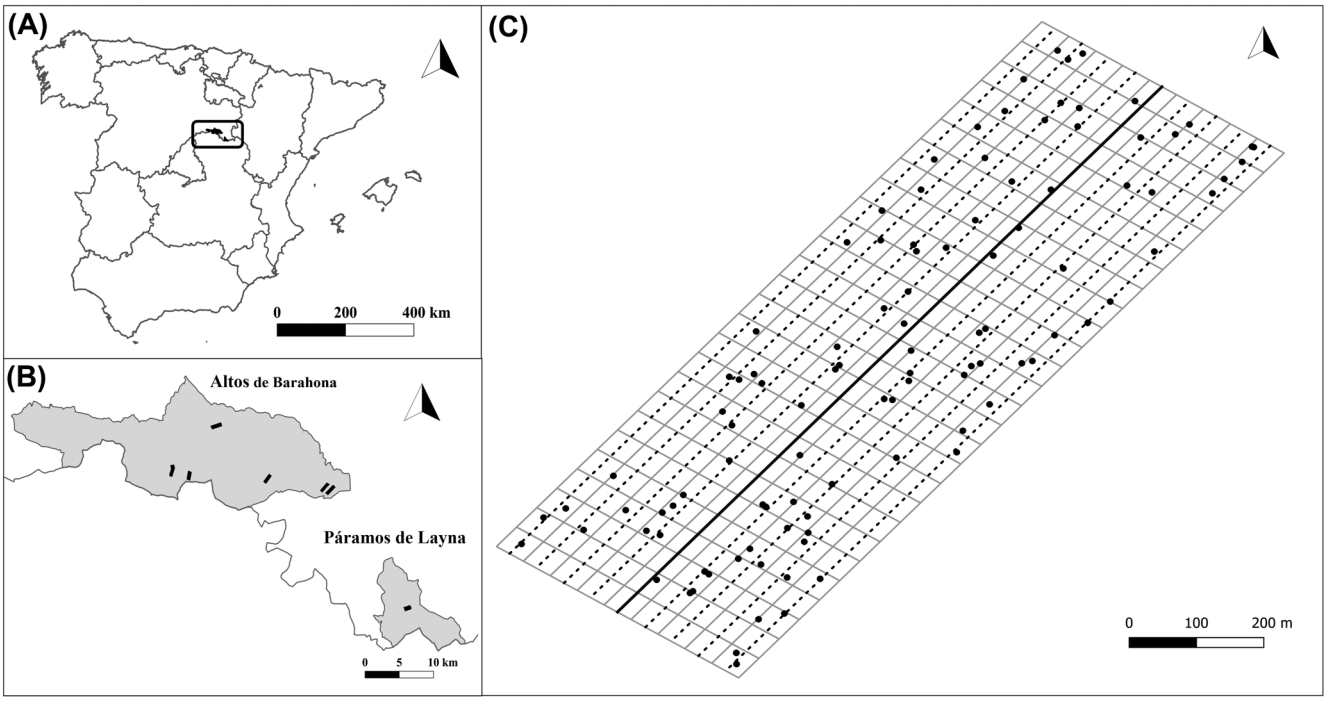

Figure 1. (A) Location of the study area in the Soria province, central Spain (rectangle). (B) Zoom to the study area in southern Soria. Sampling plots (black rectangles) are depicted. The name of the Special Areas of Conservation (SAC) and Special Protection Areas (SPA) for birds of the European Union's Natura 2000 Network (ES4170148 and ES4170120, respectively) are indicated in bold, and their limits are depicted (grey background). (C) Zoom to one sampling plot, with sampling grids of 50 × 50 m (grey line). The dashed line represents passerine census tracks. The solid black line in the middle represents the Dupont's lark census track. The black dots are all bird sightings collected during the two types of censuses.

point in each visit. Dupont's lark territories were located using the territory mapping method, gathering observations from different visits, and considering birds heard simultaneously.

The other passerine species were surveyed using the Finnish transect method (Järvinen and Väisänen 1976) in mid-late April, once per plot and year. We located between 8 and 11 linear transects per plot (proportional to patch size) of length equal to the length of the plot and with a bandwidth of 25 m on each side, so that they covered the entire plot (Fig. 1). Censuses were carried out just after sunrise, and they spanned around 1 h. Four observers walked simultaneously in parallel separated by 50 m, ultimately mapping all birds within each plot after carefully excluding double contacts.

Unmanned aerial vehicle (UAV) imagery

We used UAV flights to obtain aerial imagery to later estimate plant productivity and characterize the microhabitat structure. UAV flights were carried out during the middle of the breeding season (early June), coinciding with the optimum of vegetation vigorousness in the study area. Each plot was completely covered in a single flight to homogenize the meteorological conditions. UAV flights were made with a fixed wing drone (SRPAS model A2) flying at 120 m above the ground (equivalent to a focal length of 5.2 mm) offering a resolution on the ground (GSD) of about 50 cm pixel^{-1}. The UAV carried a Canon S100 camera with a 1/1.7″ CMOS sensor with 12 MP resolution, modified to make it sensitive to the near-infrared spectrum (approx. 770 nm; with filter marketed by Event38). This sensor provided images along three discrete spectral bands (red edge (RE), green and blue), useful to calculate vegetation indices such as the blue normalized difference vegetation index (BNDVI) (Lebourgeois et al. 2008, Salami et al. 2014).

Images post processing consisted mainly of 1) fine-scale georeferencing; and 2) elaboration of a terrain elevation model (DEM) and creation of the orthophoto mosaic by means of the photogrammetry software Agisoft Metashape Professional ver. 1.4 (Agisoft LLC 2018). Image georeferencing was done through a series of 4–6 control permanent points on the ground per plot, determined with submetric precision by a GNSS system with real-time differential correction (Emlid Reach). Finally, when performing the vegetation index calculations, the orthophoto's resolution was downscaled to 50 × 50 cm pixels, to reduce the size of the files, facilitating data processing but maintaining a high spatial resolution.

Environmental predictors

We characterized the plots using environmental predictors that describe the habitat quality and structure through the UAV

imagery. Firstly, we calculated the vegetation index BNDVI, which has previously been successfully used as a proxy of arthropod biomass (food availability, Table 1; Fernández-Tizón et al. 2020, Traba et al. 2022). Secondly, we characterized the microhabitat structure in each plot through aerial images, which were used to create our environmental predictors at a 50 × 50 cm spatial scale grouped into three sets of variables: abiotic features, vegetation types and land uses (see Table 1 for the composition of the groups and the description of the variables). To obtain the values of these variables we carried out a supervised classification through the maximum likelihood classification in the ArcGIS 10.4 software (ESRI 2016), which executes classification on a set of raster bands and creates a classified raster as output (Supporting information). This application allows users to distinguish between the classes selected in the analysed section, as well as to extrapolate the modal percentages associated with each class.

We used a 50 × 50 m grid to extract response (bird presence) and environmental predictors. We calculated the average BNDVI and the area (sum of pixels) of each of the ten classes of habitat structure per 50 × 50 m cell (Table 1). This grid size shows a compromise between reflecting the territorial behaviour of each species (Billerman et al. 2022) and allowing us to disentangle species-specific microhabitat preferences (Pulliam 2000) given that individually important ecological variables, such as behaviour, are generally measured at small and high-resolution scales (Whittaker et al. 2001). Prior to the analysis, all variables were logarithmically transformed and were z-transformed to standardize their scales as we considered their effect to depend on their proportional rather than absolute differences.

Joint species distribution modelling

The HMSC framework is a hierarchical Bayesian joint species distribution model that facilitates the formulation of data-driven hypotheses regarding the processes that structure communities. It addresses environmental filtering at the species level by measuring how the occurrence of each species depend on environmental variation. In addition, the HMSC captures co-occurrence patterns created by biotic interactions by species-to-species association matrices that can be estimated at multiple spatial or temporal scales. Such, residual species-to-species associations can be considered as hypotheses of interspecific interactions (see Ovaskainen et al. 2017 for a more detailed discussion).

In this study, we fitted two multivariate hierarchical generalized linear mixed models under the HMSC framework. We used species occurrence data (presence–absence) as response variables (Bernoulli distribution with probit link function, hereafter probit model) and the environmental predictors as fixed effects. Specifically, we fitted two probit models: 1) a null model, without fixed predictors; and 2) a constrained model, incorporating environmental predictors and bird sampling year as fixed effects. The aim of fitting both models is to differentiate between co-occurrence patterns that arise due to similar or differential habitat preferences (i.e. associations that appear in the null model but disappear in the constrained model), and those that could be due to species interactions (data-driven hypothesis of biotic interactions, i.e. associations that remain or appear in the constrained model, once we have controlled by the environmental factors). Both models included spatial random effects at two different scales, incorporating plot identity as an unstructured random effect and grid cell coordinates as a spatially structured random effect. The spatially structured random effect was constructed using the nearest neighbour gaussian process (NNGP; Tikhonov et al. 2020a). This approximation makes it possible to fit spatial models with tens or hundreds of thousands of sampling units, which would not be possible with the baseline implementation of the spatial models (Ovaskainen and Abrego 2020). We evaluated the predictive power of both models (null and constrained model) by ten-fold cross-validation.

We performed a variance partitioning to assess the relative importance of each set of predictors (Table 1) in explaining the occurrence of the species. The species environmental niches were obtained from the constrained model through assessing individual species responses to environmental covariates. To evaluate how the steppe bird community is structured in terms of species associations, we addressed raw co-occurrence (derived from the null-model) and residual

Table 1. Descriptive variables of the habitat quality and structure that were used as environmental predictors.

	Habitat predictors	Description
Food availability		
Food availability	Blue normalized difference vegetation index	Vegetation index used as a proxy of arthropod biomass
Microhabitat structure		
Abiotic features	Walls	Stony walls and constructions
	Stony ground	Gravel and small stones predominate
	Rocks	Medium–large rocks
	Bare ground	Stony bare ground. Bare soil predominates, with some small stones
Vegetation types	Short scrub	0–5 cm height woody or herbaceous chamaephytes
	Medium scrub	5–20 cm height shrub
	Tall scrub	20–50 cm height shrub
	Herbaceous	0–30 cm height herbaceous vegetation
	Trees and shrubs	> 1 m height phanerophytes
	Land uses/cereal	Arable land ploughed or sown

co-occurrence patterns (derived from the constrained-model) both at plot and grid levels. As explained above, raw co-occurrences (or raw associations) are not expected to primarily reflect biotic interactions, since they are also influenced by differential habitat preferences. In contrast, residual co-occurrences (or residuals associations) are controlled for those environmental variables that are included in the model, and thus, can be considered as hypotheses of biotic interactions. Negative co-occurrence means that two species co-occur less often than expected by chance, whereas positive co-occurrence means that they co-occur more often than expected.

Models were fitted using Markov chain Monte Carlo (MCMC) techniques (Ovaskainen and Abrego 2020). We ran four MCMC chains for 37 500 iterations, out of which the first 12 500 were removed as burn-in and the remaining were thinned by 100, yielding 250 posterior samples per chain, and thus 1000 posterior samples in total. MCMC convergence was assessed using the Gelman–Rubin convergence statistic (Gelman and Rubin 1992), where values close to 1 indicate convergence. Environmental predictors were considered to influence species occurrence with a strong statistical support if the 95% credibility interval was solely restricted to positive (or negative) values. Similarly, we considered that there was strong statistical support for positive or negative associations between species when the 95% credibility interval did not contain 0. Model fit was evaluated in terms of area under the curve (AUC) and Tjur R^2 (Pearce and Ferrier 2000, Tjur 2012). We used default prior distributions under the HMSC framework (Ovaskainen and Abrego 2020). We employed the packages Hmsc (Tikhonov et al. 2020b) and coda (Plummer et al. 2006) in the R software ver. 3.6.1 (www.r-project.org) for model fitting and MCMC converge checking, respectively. In addition, we used the package corrplot (Wei et al. 2017) to illustrate raw and residual association matrices.

Results

Species occurrence

In total, the data set consisted of 1871 records of 11 passerine species in 1846 grid cells within seven plots, and in two consecutive years. In general, species prevalence per cell was low (0–25%). The species with the highest prevalence were Eurasian skylark (22.05%), greater short-toed lark (8.65%), tawny pipit (5.58%) and Dupont's lark (4.43%). In terms of abundance, Eurasian skylark represented the majority (47.62%) of the records, followed by greater short-toed lark (18.44%), tawny pipit (10.69%) and Dupont's lark (8.39%).

Model fit

The potential scale reduction factors for all beta-parameters (i.e. parameters measuring the link from covariates to species occurrences; Ovaskainen and Abrego 2020) were smaller than 1.02, indicating satisfactory MCMC convergence (Supporting information). The null and constrained HMSC models yielded similar values of explanatory power, but the constrained model had higher predictive power. According to AUC, the restricted model had an explanatory power of 0.88 and predictive power of 0.73. The null model had an explanatory power of 0.88 and a predictive power of 0.68. According to Tjur's R^2, the constrained model had an explanatory power of 0.06 and a predictive power of 0.03. The null model had an explanatory power of 0.03 and a predictive power of 0.01. The greater predictive power in the constrained model indicates the importance of the fixed effects included in the constrained model (Supporting information).

Variance partitioning

In general terms, the vegetation type (31%; five variables) explained slightly more than abiotic features (20%; four variables), and habitat configuration as a whole (type and structure; sum of the nine variables) was the main factor explaining species occurrence (51%) (Fig. 2). The spatial random effects had an important role in explaining the occurrence of species (42%; two variables: plot: 22% and grid: 20%). Interannual variation played a minor role (2.6%; one variable), as well as food availability (4.3%; one variable) (Fig. 2, Supporting information).

Species niche

The variables that most influenced species occurrence were related to microhabitat structure (Table 1). The presence of natural (trees and shrubs) and human-made (walls) structures influenced the presence of up to five and six species, respectively (Fig. 3). On the other hand, those species whose occurrence was determined by a larger number of variables were the Eurasian skylark and the greater short-toed lark with five variables, while the rock sparrow presence was determined only by one variable (Fig. 3, Supporting information).

Community assembly

In the null model and at the plot level, we found strong statistical support (posterior probability of at least 95%) for positive co-occurrence between 15 out of 55 pairs of species (raw association matrix in Fig. 4, up left panel; green cells), and strong statistical support for negative association between 17 pairs of species (Fig. 4, up left panel; blue cells). The species with most associations (whether negative or positive) were the Eurasian skylark (three positive and five negative associations) and the woodlark (four positive and four negative associations). In the constrained model, after accounting for habitat preferences (residual association matrix in Fig. 4, up right panel), out of the 15 pairs of species showing positive co-occurrence in the null model, 10 pairs maintained strong statistical support for positive

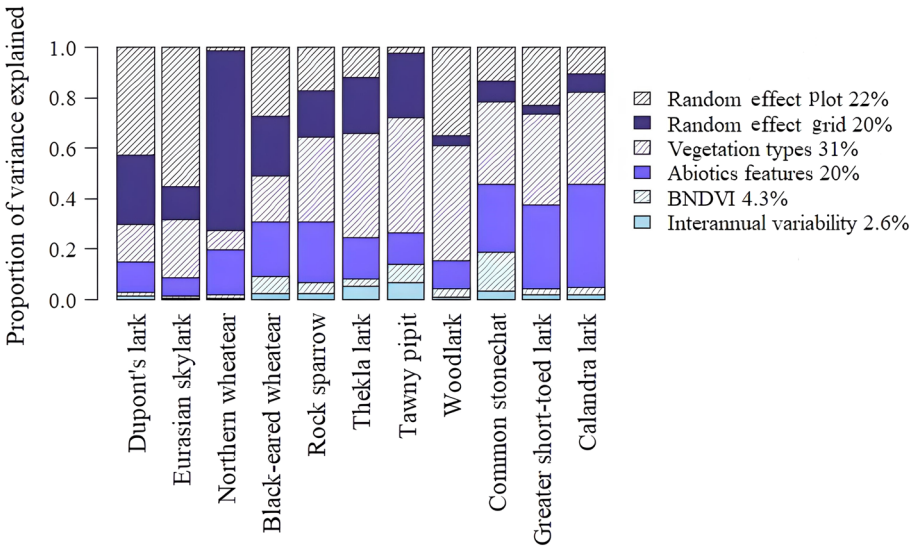

Figure 2. Variance partitioning among the fixed and random effects included in the probit model for each species. The percentages in the legend stand for the average values across species.

co-occurrence at the plot level (Fig. 4, up right panel; green cells). Out of the 17 pairs of species showing negative association in the null model, five pairs maintained strong statistical support for a negative co-occurrence at this spatial scale (Fig. 4, right panel; blue cells). The species with most associations was the Eurasian skylark (one positive and five negative associations).

At the grid level, we found strong statistical support (posterior probability of at least 95%) in the null model for positive co-occurrence between seven out of the 55 pairs of species (raw association matrix in Fig. 4, down left panel; green cells), and strong statistical support for negative association between eight pairs of species (Fig. 4, down left panel; blue cells). The species with most associations were the Eurasian skylark and the Dupont's lark (total of four associations, all of them negative). In the constrained model (residual association matrix in Fig. 4, down right panel), out of the seven pairs of species showing positive co-occurrence in the null model, four pairs maintained strong statistical support for positive co-occurrence at the grid level (Fig. 4, down right panel; green cells). Out of the eight pairs of species showing negative association in the null model, six pairs maintained strong statistical support for a negative co-occurrence at this spatial scale (Fig. 4, down right panel; blue

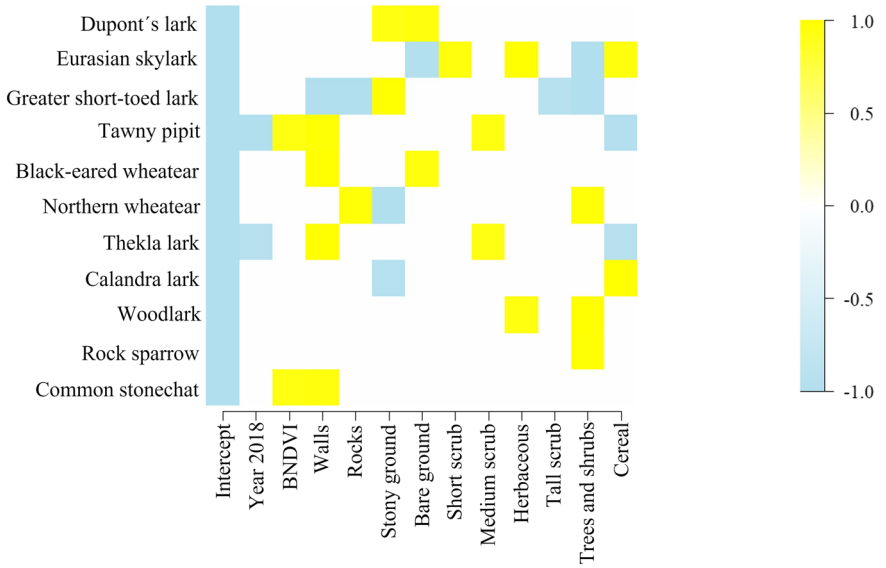

Figure 3. Heatmaps of the β parameters, i.e. species niches. It represents the results of the constrained model containing 12 environmental covariates. The baseline (intercept) of the categorical variable Year is the Year 2017. The colours indicate the parameters that are estimated to be positive (yellow) or negative (blue) with at least 0.95 posterior support. For numerical values, see the Supporting information.

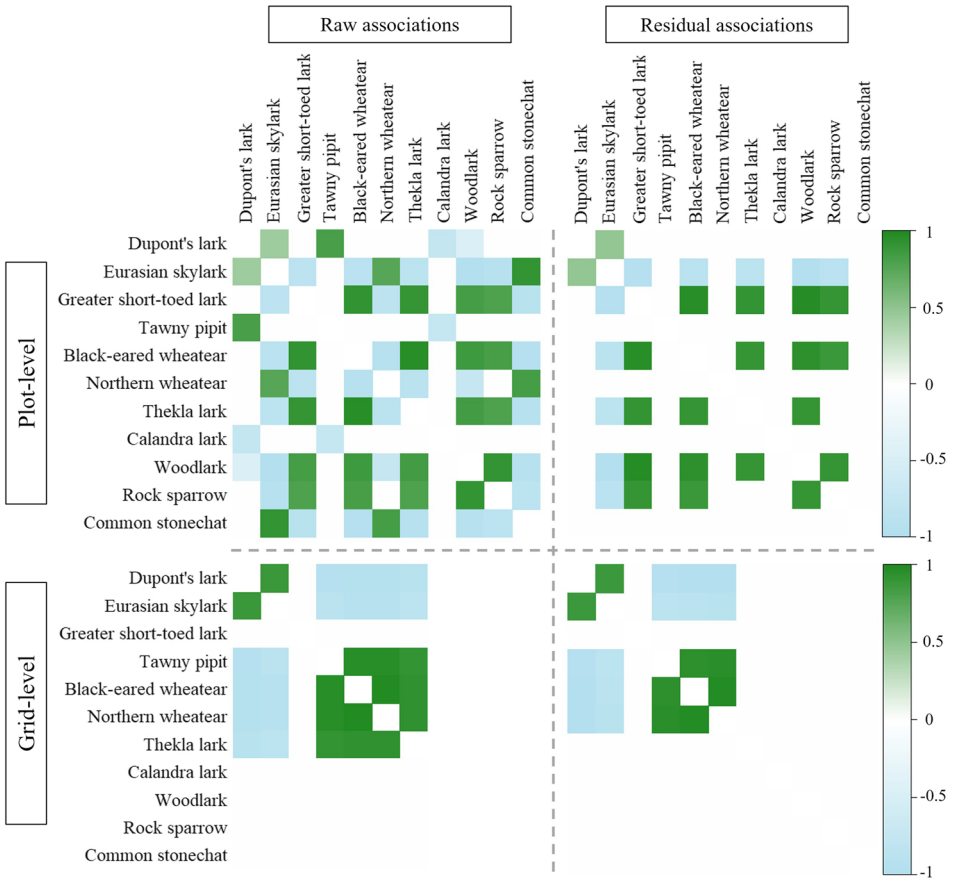

Figure 4. Raw (null model; left panels) and residual (constrained model with environmental predictors; right panels) species associations at the plot (upper panels) and grid (lower panels) levels. The panels show the results of the probit models to data on species presence–absences. In all panels, the associations that are estimated to be positive with at least 0.95 probability are shown in green, and associations that are estimated to be negative with at least 0.95 probability are shown in blue. The intensity of the colour represents the strength of the association, measured in units of correlation.

cells). The species with more associations were the Eurasian skylark and the Dupont's lark (total of three associations, all of them negative).

Discussion

In this study we reveal, through joint species distribution modelling, the patterns of co-occurrence and assembly of a community of steppe passerines. Moreover, we show how species co-occurrences are explained by both environmental and abiotic factors, and residual associations with other species, which could reflect biotic associations. Although non-manipulative data on species occurrence do not allow conclusive inference on ecological interactions (Dormann et al. 2018, Freilich et al. 2018), our results allow us to infer interesting residual species-to-species associations, which can be considered as hypotheses of such interactions and can be tested in future research. Residual associations could also arise due to shared or differential responses to missing environmental factors, but this is unlikely given the detailed characterization of the habitat that was carried out in this study (UAV flights 50 cm pixel^{-1}). Therefore, the biotic interactions that could be explaining the residual associations are discussed hereafter, which should be taken as data-driven hypothesis for future studies aiming to provide causal inference on the processes that structure these communities.

Despite the apparent low bird density and high food availability in the study area during the breeding period, competition seems to play an important role in this bird assemblage with a slightly greater number of negative than positive associations in the raw model, and with all species exhibiting at least one negative association. This could be due to the effect of competition for resources not specifically considered in this study, such as nesting site or true diet preferences (Barrero et al. unpubl., Zurdo et al. unpubl.). Also, the assemblage could be configured around one dominant species, the Eurasian skylark, since it establishes principally negative associations with many of the coexistent species at both spatial scales (plot and grid).

Species occurrence

We found a general dominance of abundant species, not only in terms of bird numbers, but also in prevalence in our plots. This was the case of Eurasian skylark, greater short-toed lark,

tawny pipit and Dupont's lark. The rest of the species showed low values of both abundance and prevalence. Generally, low prevalence of species could be a sign of habitats with limited resources but, in this specific case, may be also reflecting the decline in recent decades of these steppe passerines, which were much more abundant in the past (Herranz 2013).

Resource partitioning and niche selection

Our models explained less than 10% of total variance, and ca 90% of the variance remained unexplained. The explanatory power is obtained at the grid level (grid size 50 × 50 m) and thus, the high proportion of unexplained variance shown by the models is because the difficulty in predicting species occurrence at such small scale. The variance partitioning among the fixed and random effects (Fig. 2) revealed that, in most species, > 50% of the explained variance was attributed to structural fixed effects, which suggests that habitat structure and fine-scale vegetation types are important factors to explain species occurrence patterns, in agreement with previous studies (Cody 1981, Kamp et al. 2012). The value of the spatial random effects in the variance partitioning was very important in three species (the northern wheatear, the Dupont's lark and the Eurasian skylark), for which they absorbed more than 60% of the variance explained by the model (Fig. 2). Overall, spatial random effects absorbed 42% of the model variance, which could help to explain why the null model without environmental variables was so similar to the constrained model (Tjur $R^2 = 2.5\%$ and 3.8%, respectively). Despite the restrictions in habitat requirements of some species, especially the Dupont's lark, these species can be considered generalists within our delimited study areas, as they are distributed throughout almost all the plots.

The small variation (4.3%) absorbed by our proxy for food availability (BNDVI) was striking. Food availability has been described as a key factor in many habitat selection studies (Schoener 1974), including birds (Cody 1985, Pachomski et al. 2021), and other works in this study area (Gómez-Catasús et al. 2019, Reverter et al. 2019). Assuming that vegetation indices such as BNDVI are good descriptors of arthropod biomass (i.e. food availability; Traba et al. 2022), and taking into account that true diets of these species are still unknown (Zurdo et al. unpubl.), we expected this variable to be more relevant in our models, since our bird assemblage is dominated by insectivorous species, at least during the breeding season (Cramp and Simmons 1980). Our results suggest that food availability, probably concomitant with the low bird density in the study area, may not be a limiting factor, allowing the coexistence of potential food competitors (Soberón 2007, Chase and Leibold 2009). Conversely, factors related with habitat structure and nesting requirements might be the drivers of the competitively structured community. However, another potential explanation for the poor predictive power of this variable might be the poor capacity of BNDVI to describe the diet of the studied species.

Our model allowed us to define the specific niche preferences of the steppe bird assemblage (Fig. 3). The niche competition theory postulates that species must differ in their ecological niches to achieve stable coexistence (Wang et al. 2005, Leibold and Mcpeek 2006), due to competitive exclusion (HilleRisLambers et al. 2012) or to evolutionary divergence in the habitat preferences of the species due to past competition (Connell 1980). Our results suggest low overlap in preferences, which could be associated with a niche partitioning after evolutionary time coexistence (Connell 1980, Leibold and Mcpeek 2006).

Community assembly

The raw model showed a greater number of negative than positive associations at both plot and grid scale. This could reflect a community assembly structured in terms of present-day competition. Discerning whether present niche segregation comes from differential habitat selection or from responses to past competition is difficult (the ghost of competition past Connell 1980, Traba et al. 2017). In the past, this could have occurred through niche segregation in accordance with the competitive exclusion principle (Hardin 1960). Species would maintain a stable sympatric coexistence sharing limited resources but partitioning their niches to reduce interspecific competition (Chesson 2000, Chase and Leibold 2009).

When comparing inferred associations of null model versus constrained model, we differentiated two groups. In the first, raw associations (Fig. 4, left panel) not found in the residual association matrix (Fig. 4, right panel) would reflect species tending to co-occur more or less often than expected by chance due to similar or different habitat preferences (i.e. niche requirements) (Ovaskainen et al. 2017). A clear example in Fig. 4 is the negative associations that Calandra lark presents. This species in Spain is frequently found in open plains of steppes and pastures and in dry crops avoiding stony areas (de Juana and Suárez 2020), in agreement with our results (Fig. 3). In our study area, Calandra lark is limited to plots with cereal crops, where it uses field edges to nest (de Juana and Suárez 2020). Dupont's lark or tawny pipit, with which Calandra lark shows negative associations, either totally reject cereal crops or prefer bare and stony soils (Fig. 3), and thus negative associations are explained by differential habitat requirements. In the case of Dupont's lark, the high importance of spatial random effects of variance partitioning (Supporting information), could be masking its rejection of cereal crops in the β-parameter heat maps (Fig. 3; but see negative effect in Supporting information), as previous studies describe it as a species with a strong rejection towards crops, which are also one of the main causes of habitat loss and species decline (Gómez-Catasús et al. 2016, Reverter et al. 2021).

In the second group, those raw associations (Fig. 4, left panel) that were maintained in the residual association matrix (Fig. 4, right panel) could reflect: 1) missing relevant environmental variables, or 2) biotic interactions that cause either attraction or repulsion between species (Ovaskainen et al. 2017). An example of the latter could be reflected through

negative residual associations, especially those with Eurasian skylark. Eurasian skylark is a highly territorial species (Campbell et al. 2020), especially in the nest surroundings and in feeding areas, where the male is more aggressive (Green 1978). This could prevent other species from establishing their territories near Eurasian skylark territories to avoid aggressions. Territoriality could help to explain the numerous negative residual interactions with species such as greater short-toed lark, black-eared wheatear, Thekla lark, woodlark and rock sparrow (Fig. 4). Eurasian skylark is the most abundant species in the area, so these negative residual associations could be attributed to a dominant effect (the dominance hypothesis, Morse 2015): within a competitive assemblage structure, some species behave as dominant as they are commonly larger than subordinates (Martin and Ghalambor 2014). Results at the grid scale support this hypothesis, as the skylark maintains negative residual associations with other species. However, the persistence and asymmetry of these dominance associations between closely related species that coexist spatially and temporarily should be further investigated (Martin et al. 2017).

Agonistic relationships between species, as chasing individuals of other species trying to expulse them from skylark core areas, are often observed throughout the study area, usually associated with contention over a specific resource (Grether et al. 2013, Delius and Delius 2021). Territoriality can help to regulate demographic population pressure (Delius and Delius 2021) and habitat segregation facilitates the coexistence of species within the same landscape. Thus, if one species predominantly uses a space that is largely unoccupied by another, the probability of occurrence of a competing species can be negatively predicted by the presence of the other one (Fisher et al. 2013). Interspecific territoriality has often been recorded in birds belonging to the same guild (Bourski and Forstmeier 2000, Martin and Martin 2001), especially in simple, low-productivity environments, where there may be greater overlap in nesting sites, feeding or food availability (Orians and Willson 1964, Bourski and Forstmeier 2000).

Conclusion

Interspecific competition is an essential driver of species community organisation and evolutionary change. To understand these effects, it is necessary to assess ecological and evolutionary processes not only in terms of environmental filtering but also of biotic interactions between the species conforming the assemblage. Although manipulative experiments can provide more conclusive evidence to address patterns of competition, at the same time they can be difficult to perform for many taxa, in particular for species, and may not allow to quantify the size of the effect under natural conditions. In this sense, our results, though coming from purely observational data suggest that competition might be occurring at present time, through negative associations between species. The assemblage is apparently configured around a dominant species, the Eurasian skylark, which is the most abundant species in the community, and which establishes negative associations with many of the coexisting species. Our results contribute to understanding how bird assemblages are configured over evolutionary time in response to ecological constraints and biotic associations, reflecting how the relative position of a species within a hierarchy may have implications for the mechanisms underlying species distribution and the structure of biological assemblages.

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Author contributions

Adrian Barrero: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Writing – original draft (lead). **Otso Ovaskainen:** Formal analysis (equal); Software (equal);Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Juan Traba:** Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal). **Julia Gómez-Catasús:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Software (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – review and editing (equal).

Data availability statement

Scripts to fit models, landmark data and habitat structure data are available from the Github Digital Repository: https://doi.org/10.5281/zenodo.5903345.

Supporting information

The Supporting information associated with this article is available with the online version.

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