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Landscape Structure Shapes the Equilibrium Between Migratory and Sedentary Species in Avian Breeding Communities Along an Altitudinal Gradient

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ABSTRACT

Aim: Human land use shapes landscapes and threatens avian biodiversity, yet its interaction with altitudinal gradients and the consequences for the assembly of long-distance migratory and sedentary bird communities remain poorly understood.

Location: Southern France.

Taxon: Avian breeding communities.

Method: We examined the changes in the migratory–sedentary ratio (the relative proportion of migratory versus sedentary species) in avian breeding communities (5 × 5 km resolution) in response to a regional-scale altitudinal gradient (4000 m), in interaction with landscape structure (landscape heterogeneity and forest cover) and species richness.

Results: We detected interactions between altitude, landscape structure and species richness influencing the migratory: sedentary ratio. This highlights the complex responses of avian communities to both abiotic and biotic drivers. Reduced habitat diversity and evenness at lower altitudes promoted the occurrence of migratory species. While increasing forest cover generally promotes bird species richness, our results showed that its effect on the migratory: sedentary ratio differ between altitudinal belts. Specifically, forest cover was associated with a decrease in the proportion of migratory species at lower altitudes but with an increase at higher altitudes. Finally, increasing total bird richness altered the equilibrium at lower altitudes, where the richest communities (above ~117 bird species) hosted more migratory species than expected from the regional pool. We hypothesise that adding migratory rather than sedentary species to the richest communities reduces competitive interactions for resources and limits niche saturation.

Main Conclusions: Understanding interactions among environmental drivers is essential for predicting the assemblage of avian communities. Our results identify specific environmental conditions that promote or threaten the richness of migratory and sedentary bird species and thus provide insights to inform conservation actions and policy decisions aimed at mitigating the impacts of environmental change on avian communities.

Agathe Leriche and Alexandre Millon shared lead authorship.

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1 | Introduction

Landscapes are profoundly altered by anthropogenic pressures, the expansion and intensification of agriculture and urban areas, contributing to a global decline of biodiversity (Kong et al. 2021; Newbold et al. 2015; Powers and Jetz 2019; Rigal et al. 2023). These alterations mostly arise from habitat loss (i.e., the reduction in habitat extent) and fragmentation (i.e., the division of one habitat into smaller, more isolated patches), both of which are widely studied (Carrara et al. 2015; Fahrig 2003; Riva and Fahrig 2023). Habitat loss leads directly to a decline in populations and a reduction in species richness, and then to more vulnerable ecosystems, accelerating the loss of biodiversity (Brooks et al. 2002; Butchart et al. 2010; Pimm et al. 2014). As a widely monitored and ecologically diverse taxonomic group, birds are considered indicators of environmental change and are especially sensitive to alterations in habitat and climate. Accordingly, they are indeed heavily affected by ongoing environmental changes, with up to 21% of the 8750 land bird species potentially threatened with extinction by 2100 (Jetz et al. 2007; Lees et al. 2022). While landscape structure is expected to be a notable driver of biodiversity spatial patterns, its effect likely interacts with other environmental drivers, such as climate (Maestre et al. 2022; Newbold et al. 2015; Rillig et al. 2019). However, the role and estimation of these interactions in shaping avian communities remain poorly understood (Clavero et al. 2011; Eglington and Pearce-Higgins 2012; Gaüzère et al. 2022). Evaluating how avian communities respond to multiple environmental drivers, and their interactions, is therefore necessary to improve our understanding and prediction of avian diversity under global change (Ceresa et al. 2021; Eglington and Pearce-Higgins 2012; Pearce-Higgins et al. 2015).

A majority of works on avian communities have mainly focussed on the species richness of bird communities, but fewer have considered key aspects of their structure, such as species interactions, or movement behaviours (Basile et al. 2021; Flynn et al. 2009; Morelli et al. 2021). Among them, enhanced movement capacities of birds enabled by flight have allowed the evolution of long-distance migration, a defining characteristic of birds (Berthold 1999). The migratory behaviour implies the sequential use of two distinct environments throughout the biological cycle of individuals, and is more prevalent in birds than in any other taxonomic groups (with over 20% of compulsory migratory species worldwide; Somveille 2016). In this context, examining the equilibrium between migratory and sedentary species within communities may offer a complementary perspective to species richness. We define this as the migratory: sedentary ratio (R_{ms}). The maintenance of migratory species is therefore further complicated by the need for appropriate biotic and abiotic conditions across breeding and wintering habitats (Newton 2004; Ratikainen et al. 2008; Sherry and Holmes 1996). Evidence of migratory bird species decline, particularly long-distance ones, is accumulating, raising conservation concerns (Berthold 2001; Blount et al. 2021; Lemoine, Bauer, et al. 2007; Runge et al. 2015). Changes in migration timing and distribution have also already been observed in response to environmental changes, such as climate change (Ahola et al. 2007; McCain 2009). Migratory and sedentary species may thus respond differently to landscape structure, which could directly alter their relative abundance (Newton 2008; Ponti et al. 2020; Zurell et al. 2018). Exploring the variations in the R_{ms} may provide information on the underlying mechanisms shaping avian community structure such as niche partitioning, community saturation and species interactions. For instance, changes in species distribution may alter the outcome of competitive or positive interactions (facilitation) between migratory and sedentary birds. First, changes may intensify interspecific competition for shared resources, particularly in saturated communities (Macarthur and Levins 1967). Alternatively, competition may be alleviated if species partition resources in space or time (Ahola et al. 2007; Macarthur and Levins 1967). Finally, coexistence may be promoted if migratory species use sedentary species as indicators of suitable breeding habitats, as suggested by the heterospecific attraction hypothesis (Mönkkönen et al. 1997; Mönkkönen and Forsman 2002). Although previous studies have examined these processes (Böhning-Gaese and Lemoine 2004; Böhning-Gaese and Oberrath 2003; Hurlbert and Haskell 2003; Kim et al. 2018, 2022; Lemoine, Schaefer, and Böhning-Gaese 2007), they were often restricted to specific habitats, limited in geographic scope, or focused solely on migratory species or a small subset of species. A macroecological perspective appears then as a useful complement to understand how migratory and sedentary species respond jointly to environmental gradients and community processes (Kelly and Horton 2016; Somveille 2016; Somveille et al. 2015).

Among these gradients, altitude constitutes a major constraint to any community assemblages, as it encompasses environmental drivers such as climate and vegetation structure. Because of steep changes in both biotic and abiotic conditions, altitudinal diversity gradients have been widely studied across a wide range of taxa (Akhrorov et al. 2022; Körner 2007; Machac et al. 2011; Wang et al. 2023). Species richness often declines with increasing altitude, a pattern commonly attributed to environmental filtering, where only species with specific traits can tolerate harsher climatic conditions typically found at higher elevations (e.g., Graham et al. 2009; Grime 2006). While altitude serves as a geographic gradient, it is frequently used as a proxy for multiple climatic factors, such as temperature and oxygen availability, which can constrain species distributions (Körner 2007). Bird species richness typically decreases with altitude, with a restricted number of clades occupying the highest elevations (phylogenetic clustering; Graham et al. 2009; Webb et al. 2002). We may also expect that altitude can modulate the R_{ms}. Indeed, altitude can lead to shifts in habitat types or food sources, all of which then affect species occurrences. Given that migratory species are capable of exploiting short-lived resource peaks, we hypothesise they may be more prevalent in higher elevation breeding communities, where spring conditions offer temporary resource abundance and cooler temperatures (Boyle and Martin 2015; Kim et al. 2022). Since their presence is limited to the most favourable period of the year, they avoid the harsh winter conditions that filter out species unable to persist. In contrast, we hypothesise that sedentary birds, which have to endure environmental constraints throughout the year, are expected to breed at lower altitudes, where climatic conditions remain milder and resources more stable. This year-round persistence may, however, lead to more competition for resources, further influencing species distribution and community structure (Guillaumet and Russell 2022; Kim et al. 2022).

These distinct strategies illustrate different adaptations to environmental constraints and resource availability and suggest a gradual shift in the migratory–sedentary ratio, with a potential transition from a bias towards sedentary species in lowland areas to a predominance of migratory species in higher altitudes.

Forest cover and landscape heterogeneity are well-known drivers of bird species richness. Reduced forest cover, often a consequence of intensive land use, typically lowers overall richness and disproportionately affects forest specialists and generalist species (Carrara et al. 2015; Vargas-Cárdenas et al. 2022). Landscape heterogeneity arises from the diversity of available habitats (i.e., the number of distinct habitat types; habitat diversity hereafter) and their evenness (i.e., the relative proportion of each habitat type in a given landscape; habitat evenness hereafter), which also influence resource availability such as food and shelter, especially for species with narrow ecological niches (MacArthur 1972). These effects are not uniform across space: altitudinal gradients are likely to modulate the influence of landscape structure by amplifying environmental filtering processes (Sreekar et al. 2021). Along steep gradients in climate and vegetation, the impacts of habitat loss or simplification may differ across elevational belts, affecting the balance between specialist and generalist species. In turn, variations in species richness along altitudinal gradients may alter competitive interactions and shape the R_{ms}. In more diverse communities, increased biotic interactions may favour migratory species, which can temporarily exploit local resources without requiring year-round occupancy (Ahola et al. 2007; Forsman and Mönkkönen 2003; Pigot and Tobias 2013; Wiens 2011). For instance, higher bird species richness in a community may intensify competition, shaping the equilibrium between sedentary and migratory species, by potentially favouring species whose temporary presence is less restrictive, such as migratory species. Thus, the interplay between altitude, landscape structure and community richness may influence bird assemblages by filtering ecological strategies and behavioural responses (Elsen et al. 2021; Kim et al. 2018; La Sorte et al. 2015; McCain 2009). It therefore seems essential to understand these interdependent abiotic and biotic processes along altitudinal gradients in order to clarify the underlying processes driving species assemblages, and in particular the equilibrium between migratory and sedentary species.

Here we aimed to study the effects of a regional-scale altitudinal gradient (from 0 to ~4100 m), and its interactions with landscape structure on the migratory: sedentary ratio of avian communities during the breeding season in the south of France (Provence-Alpes-Côte d'Azur, hereafter the PACA region). The PACA region belongs to the Mediterranean biodiversity hotspot with wide environmental and anthropogenic gradients (e.g., altitude, human population density) and, consequently, a wide array of landscape structures. We expected a migratory: sedentary ratio at higher altitudes as a signature of environmental filtering, where migratory species can withstand the environmental conditions by benefiting from short-term resource peaks and avoiding harsh winter conditions (Boyle and Martin 2015; Kim et al. 2022). We further expected that higher diversity and evenness of habitats and higher species richness will promote niche availability due to resource partitioning (Macarthur and Levins 1967) or by the attraction of species whose temporary presence is less restrictive (Mönkkönen et al. 1997; Mönkkönen and Forsman 2002), and will therefore support communities with a higher R_{ms} (Kim et al. 2018, 2022). Also, since long-distance migratory species wintering in Africa are more associated with open habitats (Böhning-Gaese and Oberrath 2003; Kim et al. 2022; Mönkkönen and Helle 1989), we expected high forest cover to reduce the R_{ms}.

2 | Materials and Methods

2.1 | Study Area

The study area took place in the PACA region (Provence-Alpes-Côte d'Azur; 43°57′ N, 6°03′ E; WGS 84—EPSG:4326; Figure S1), and covers an area of 31,400 km^2 in the southeast of France, between the Alps mountains and the Mediterranean Sea. As part of an internationally recognised biodiversity hotspot (Myers et al. 2000), this region provides an ideal context for studying ecological patterns due to its pronounced gradients in land use, altitude, and bird community composition. Indeed, the region covers a wide range of climatic (mean annual temperatures ranging from 3°C to 15°C, mean annual precipitation from 400 to 1200 mm; Karger et al. 2020) and altitudinal gradients (from 0 to 4102 m). It also exhibits a large gradient of human population densities ranging from 30 to $>16{,}000$ inhabitants · km^{-2}, and is under growing pressures of increasing aridity and human footprint (Berdugo et al. 2022; D'Odorico et al. 2013; Pörtner et al. 2021; Underwood et al. 2009).

2.2 | Avian Community Data

The bird occurrence data were extracted from the Faune-PACA database managed by the LPO-PACA (upload from https://www.faune-paca.org/, in December 2022). Faune-PACA is a participatory database, with observations exhaustively checked in real-time by a network of local ornithological experts, thus minimising the risk of misidentification. The original dataset contained 7,751,862 observations (N_o) from 684 bird species, with 87%, 12% and 1% of opportunistic, semi-protocoled and protocoled observations respectively, and recorded between 2009 and 2022. However, the temporal distribution of records is uneven, with a marked increase over time and more than 30% of observations collected during the last 3 years (2020–2022). Overall, 30% of the observations included information on the species' breeding status (named 'Atlas Code'), allowing us to clearly identify the breeding avian communities in the region. As this type of database generally suffers from an under-representation of common species, observers have been encouraged to carry out protocol-based surveys in the form of checklists since 2016, i.e., to record all detected species in a given location, including the most frequent ones.

2.2.1 | Avian Occurrence Data Curation and Filtering

2.2.1.1 | List of Species Considered. The dataset was filtered to focus on native and terrestrial bird species, but also included five introduced species now considered as established (*Columba livia f. domestica*, *Euodice malabarica*, *Leiothrix lutea*, *Phasianus colchicus*, *Psittacula krameri*). Additionally, we retained three marine species (*Morus bassanus*, *Phalacrocorax aristotelis desmarestii*, *Puffinus yelkouan*) that can occur on the mainland coastline or on small islands close by (<2 km from mainland) for breeding and/or foraging and therefore potentially interacting with terrestrial birds occurring on the coastline. These species were included because they contribute meaningfully to the regional breeding bird assemblages in these specific habitats, and their occurrences are spatially restricted, thus not influencing inland analyses. The breeding regional pool thus included 225 species (Table S1), leading to the exclusion of 398,300 records of vagrant, only wintering or accidental species ($N_o = 7,353,562$).

2.2.1.2 | Accuracy. The occurrences considered invalid by local ornithological experts were removed, i.e., data with unlikely combinations date and/or location mismatch or data concerning rare species with identification issues recorded with an insufficient description. This included data marked as 'Probably incorrect', 'Refused', or 'Incomplete', which accounted for less than 0.1% of the total observations ($N_o = 7,351,923$).

2.2.1.3 | Phenology. A temporal filter was applied on observation data following the region-specific breeding periods from Flitti et al. (2009): each occurrence was verified to eliminate the observations out of the breeding period, with the exception of the four marine species (the particularly long period in reproduction and residence justifies inclusion outside the periods). This filtering step consistently retained data with codes indicating nesting behaviour, resulting in the exclusion of 3,856,604 observations ($N_o = 3,495,319$). Among these, 70% included an explicit Atlas breeding code, providing direct evidence of breeding behaviour.

2.2.1.4 | Region. A total of 4069 occurrences of the Faune-PACA database were actually recorded outside of the study area and were consequently withdrawn ($N_o = 3,491,250$).

Together, these filters ensure that the dataset accurately represents actual breeding communities. This minimises the risk of including transient individuals and strengthens the ecological validity of subsequent analyses.

2.2.2 | From Point Specific Occurrence Data to Community Data

We divided the study area into a grid of 1449 cells (N_c) of 5 × 5 km, a size deemed optimal for mobile species that potentially use different environments for complementary activities (Figure S2; Andersen et al. 2023). We defined a community as the total number of species recorded in each cell, allowing us to adequately capture responses to both landscape structure and interactions among species (e.g., competition), while also accounting for species movements. This scale not only suits the ecological needs of the species but also aligns with those used in similar recent studies, facilitating broader comparisons (Andersen et al. 2023; Campbell et al. 2022; De Camargo 2023).

The avian community composition in a cell could be biased because:

i. Ornithologists may favour the reporting of rare and/or emblematic species but undermine the reporting of common ones, which leads to both the over-representation of rare species and the under-representation of common species in the dataset or,

ii. The cell may be under sampled (i.e., therefore missing out some species), due to access difficulties or remoteness from populated areas.

In order to ensure the representativeness of the community composition in each cell, we evaluated (i) the observed distribution of the 22 most common species of the regional pool throughout the study area (Figure S3) and (ii) computed the completeness of species richness.

First, we divided the breeding period of each species into 10 equal-length time intervals. Then, for each species, all occurrences recorded within the same interval, same year, and same cell were grouped into a spatio-phenological statistical unit—i.e., a standardised sampling unit defined by time (interval × year) and space (cell). This process generated a maximum of 140 statistical units per species and per cell (14 years × 10 intervals), used for both evaluations. Given opportunistic data tend to favour the record of rare species and protocol-based data better capture common ones, we used these spatio-phenological units to evaluate the presence of common species across space. For each cell, we calculated how many of the 140 statistical units contained at least one detection of each common species. This frequency measure was used to examine the spatial patterns of common species distributions (Figure S3). Results showed similar trends across the 22 species, though with some variation. For example, *Sturnus vulgaris* had a median frequency of 1 record per cell (mean = 8.04), while *Parus major* had a median of 16 (mean = 22.43). Seven common species, such as *Garrulus glandarius* (max = 133), reached over 120 occurrences in some cells, while others had lower frequencies, with over 25% of cells showing fewer than five records. However, distribution maps for these 22 species were checked by local ornithological experts and were consistent with known regional patterns. We therefore considered that common species were not over-represented, and their sampling was overall reliable.

We evaluated the completeness of the avian community in each of the 5 × 5 km cell using the non-parametric 'Sample Coverage' estimator (SC; Equation 1; Chao et al. 2014; Chao and Jost 2012; see Figure S2 for spatial distributions of SC across the region). We considered all 140 (spatio-phenological) statistical units for all species present in the cell (*R SpadeR package*). The SC estimator was calculated as following:

$$SC = 1 - nf_1\left((n-1)f_1 + 2f_2(n-1)f_1\right) \quad (1)$$

where n is the total sample size (total number of individuals observed), f_1 is the number of species observed only once (frequency = 1, referred as 'singletons') and f_2 is the number of species observed exactly twice (frequency = 2, referred as 'doubletons'). This estimator is well suited for heterogeneous occurrence data, and is based on the frequency of singletons and doubletons, i.e., species observed only once or twice, respectively (Chao et al. 2014, 2020; Chao and Jost 2012). Cells for which the data were unlikely to be adequately represented in the model were first discarded: (when the number of total observations was insufficient to avoid singletons dominating the data), when the total number of species observations was equal to the number of singletons (i.e., no species was recorded in more than one statistical (spatio-phenological) sample), or when no species was observed exactly twice. SC was calculated for 1436 cells and cells with a SC under 90% were discarded (Troia and McManamay 2016, 2017), leaving 1275 cells (88% of the total number of cells covering the study area, i.e., 1449 cells). The bias induced by the under-sampling of common species in some cells (i.e., false singletons and doubletons for common species), could lead to overestimate the expected richness, thereby reducing completeness, meaning more stringent selection of cells.

We further evaluated the robustness of our cell selection based on spatio-phenological statistical unit definition by comparing it with an alternative method based on spatial-only statistical unit (Kusumoto et al. 2023). For this method, each 5×5km cell was subdivided into 25 1×1km cells, and observed data were converted into incidence data per 1km^2 cell. A 1×1km cell was considered a statistical unit, and the 25 cells were used to calculate the SC (Equation 1) per 5×5km cell. The number of 5×5km cells with a completeness of at least 90% was $N_c = 1118$ (77% of the total number of cells), and all of them were included in the 1275 cells selected using the previous method. In order to be as conservative as possible and to ensure representativeness of the avian communities, we selected this more stringent subset of $N_c = 1118$ (5×5km cells) in all subsequent analyses (with $N_o = 3{,}415{,}724$).

Finally, we excluded three cells for which terrestrial habitats are only composed of islands (Levant, Port-Cros, Porquerolles; typically, ≥2km from the mainland) because of their unique ecological features, making them unrepresentative of terrestrial avian communities and compromising comparability with mainland cells. This exclusion guaranteed methodological consistency, resulting in $N_c = 1115$ cells and $N_o = 3{,}406{,}986$.

2.2.3 | Calculating the Migratory: Sedentary Ratio From Community Data

First, we assigned to each of the 225 bird species a migratory behaviour corresponding to either sedentary, short-distance migrant or long-distance migrant, based on Flitti et al. (2009) and our own experts' knowledge (A.F. and A.M.). Long-distance migratory species included all the species for which most individuals migrate over the Mediterranean Sea to overwinter in Africa (either side of the Sahara Desert). This category also included *Platalea leucorodia* and *Plegadis falcinellus* primarily identified as long-distance migrants, but in which a significant proportion of individuals are sedentary. Finally, we considered two levels of migratory status: sedentary (including short-distance migratory species) vs. migratory species (including only long-distance migratory species). The avian regional pool was therefore made up of 225 breeding species with 149 of them considered as sedentary (66.2%) and 76 migratory species (33.8%; Table S1 and Figure S4). We then calculated the migratory: sedentary ratio as follows:

$$R_{ms} = \log\left(\frac{N_m}{N_s}\right) \quad (2)$$

where N_m and N_s are the number of migratory and sedentary species, respectively. The closer R_{ms} is to 0, the more migratory species there are in a community compared with sedentary species.

2.3 | Environmental Variables

To investigate the effect of abiotic and biotic drivers on R_{ms}, we extracted the value of 10 variables related to altitude, landscape structure and human-induced landscape modification, climate and species richness, for the 1115 cells (see Table 1). Two cells were discarded as not covered by all variables ($N_c = 1113$).

2.3.1 | Altitude

We extracted the mean altitude per 5×5km cell from a 5-m resolution Digital Terrain Model (DTM, https://geoservices.ign.fr/rgealti) and classified the cell within (1) one of three altitudinal belts, based on the Ozenda (1981) vegetation boundaries: hilly belt, below 900m (62% of N_c), mountain belt at 900–1600m (22%) and subalpine belt, above 1600m (16%).

2.3.2 | Landscape Heterogeneity

Corine Land Cover 2018 (here after CLC2018; U2018_CLC2018_V2020_20u1; Version 2020 20u1 (dated 02/2020); 100m grid, https://land.copernicus.eu/) with 14 sub-categories was used to calculate: (2) habitat diversity (i.e., the number of distinct habitats within a cell), (3) Shannon index (i.e., a measure integrating both the number of distinct habitats and their relative proportions within a cell) and (4) habitat evenness (i.e., the proportional distribution of habitats, calculated by normalising the Shannon index by its theoretical maximum value; Table S2) per 5×5km cell.

CLC2018 was used to extract (5) forest cover value per 5×5km cell, calculated as the proportion of the cell's surface covered by forest of any type (Table S2).

2.3.3 | Human Impact

We extracted (6) the median value of human-induced alteration per 5×5km cell developed from a cumulative measure of human modification of land around the world (1-km resolution raster data at https://doi.org/10.7927/edbc-3z60; Kennedy et al. 2019) together with (7) human population density value (from 1-km resolution raster; CIESIN—Columbia University 2015; data at https://doi.org/10.7927/H4F47M65).

2.3.4 | Climate

We extracted (8) the average mean annual temperature and (9) average total annual precipitation per cell between 2009 and 2018, from CHELSA-W5E5 v2.0 (1-km resolution raster; https://doi.org/10.48364/ISIMIP.836809.2; Karger et al. 2021).

TABLE 1 | Summary of environmental variables considered for the analysis of R_{ms}, N_m and N_s responses.

Variable name	Type	Source (Resolution)	Unit	Status	Reason for exclusion	Transformation
Altitude	Abiotic/Cont.	IGN RGE Alti (5 m)	meters	Excluded	High VIF; correlated with temp, precip, pop. density	—
Altitudinal belt	Abiotic/Cat.	Derived from altitude, based on Ozenda (1981) vegetation zones	Category (3 levels)	Retained	—	None
Temperature	Abiotic/Cont.	CHELSA-W5E5 v2.0 (1 km)	°C	Excluded	Correlated with altitude	—
Precipitation	Abiotic/Cont.	CHELSA-W5E5 v2.0 (1 km)	mm/year	Excluded	Correlated with altitude	—
Population density	Anthrop./Cont.	CIESIN (1 km)	people/km^2	Excluded	High VIF; correlated with human impact	—
Human impact	Anthrop./Cont.	Kennedy et al. (2019) (1 km)	Index (0–1)	Excluded	High VIF; correlated with pop. density	—
Forest cover	Landscape/Cont.	CORINE Land Cover 2018 (CLC2018, 100 m)	% surface	Retained	—	Log (N_m, N_s); Raw (R_{ms})
Habitat diversity	Landscape/Cont.	CLC2018 (100 m)	Number of habitat types	Retained	—	Quadratic
Habitat evenness	Landscape/Cont.	CLC2018 (100 m)	Evenness index (0–1)	Retained	—	Raw
Species richness	Biotic/Cont.	Derived from community data	Number of species	Retained	—	Log (R_{ms}); Quadratic (N_m, N_s)

Note: For each variable, the following information is provided: Type, source (and resolution), unit, inclusion or exclusion in the final models, reasons for exclusion (VIF > 5 or correlation $r > |0.70|$), and the transformation applied (raw, logarithmic or quadratic). The exact VIF values and correlation coefficients are available in Figure S5.

2.3.5 | Biotic Driver

We considered (10) total bird species richness as a biotic driver, indicating the overall avian diversity of species within communities and considering its potential influence on ecological interactions and community composition (Table S3).

From these 10 environmental variables under consideration, we kept a set of them that minimise both multicollinearity (i.e., with a Variance Inflation Factor (VIF) value < 5; Menard 2002) and correlations among pairs of variables ($|r| < 0.70$; Table 1 and Figure S5). Altitude was strongly correlated with temperature (negatively), precipitation (positively), and population density (negatively), while human impact was mainly associated with population density, and variables like species richness or habitat evenness displayed weak correlations with others. We thus considered (1) altitudinal belt (highly correlated with climatic and human impact variables), (2) habitat diversity, (3) evenness, (4) forest cover and (5) species richness in subsequent statistical analyses ($|r| < 0.35$ in all cases; Table 1 and Figure S5).

We then identified the most appropriate fit (raw, log-transformed, or quadratic) for the relationship between each response variable (R_{ms}, N_m, N_s) and each of the four selected continuous environmental variables (habitat diversity, habitat evenness, forest cover, and species richness) by comparing the Akaike Information Criterion (AIC) across a set of full models. For each response variable (R_{ms}, N_m, and N_s), multiple full linear models were tested in which the focal variable was alternately modelled in its raw, log-transformed, or quadratic form, while the other variables were retained in their raw form. For the model regarding the response of R_{ms}, species richness was log-transformed, forest cover and habitat evenness were considered as raw variables and habitat diversity was considered with a quadratic term (see Table 1). In the models for N_m and N_s, forest cover was transformed into a logarithm, the evenness of habitats was considered as a raw variable and habitat diversity and species richness were considered with a quadratic term (see Table 1).

2.4 | Statistical Analyses

We investigated how the migratory–sedentary ratio (R_{ms}), as well as the richness of both sedentary (N_s) and migratory species (N_m), responded to the five environmental variables selected across the 1113 cells of the study area. Habitat diversity, habitat evenness, forest cover and total bird species richness were all considered in interaction with altitude. The five environmental variables were z-scored. We performed linear regression models for each response variable, and used a stepwise selection procedure (*R MASS package, 'stepaic' function*) on the environmental variables based on the AIC criterion (Burnham and Andersson 2002). Four cells with extreme studentised residuals were removed from the analysis, which finally included $N_c = 1109$.

We then evaluated the spatial dependency of the model residuals using the Moran's Index (Legendre 1993) and found a spatial autocorrelation up to a distance of 37.5 km, with a Moran's Index maximum value of 0.16 (corresponding to the closer distance; Figure S6). Spatial autocorrelation in a model's residuals could lead to type 1 error, i.e., inflating the probability of a spurious significant effect of a predictor. Therefore, we corrected for this spatial autocorrelation using the simultaneous auto regression (SAR) model as implemented in the *spdep* package (Rangel et al. 2006),

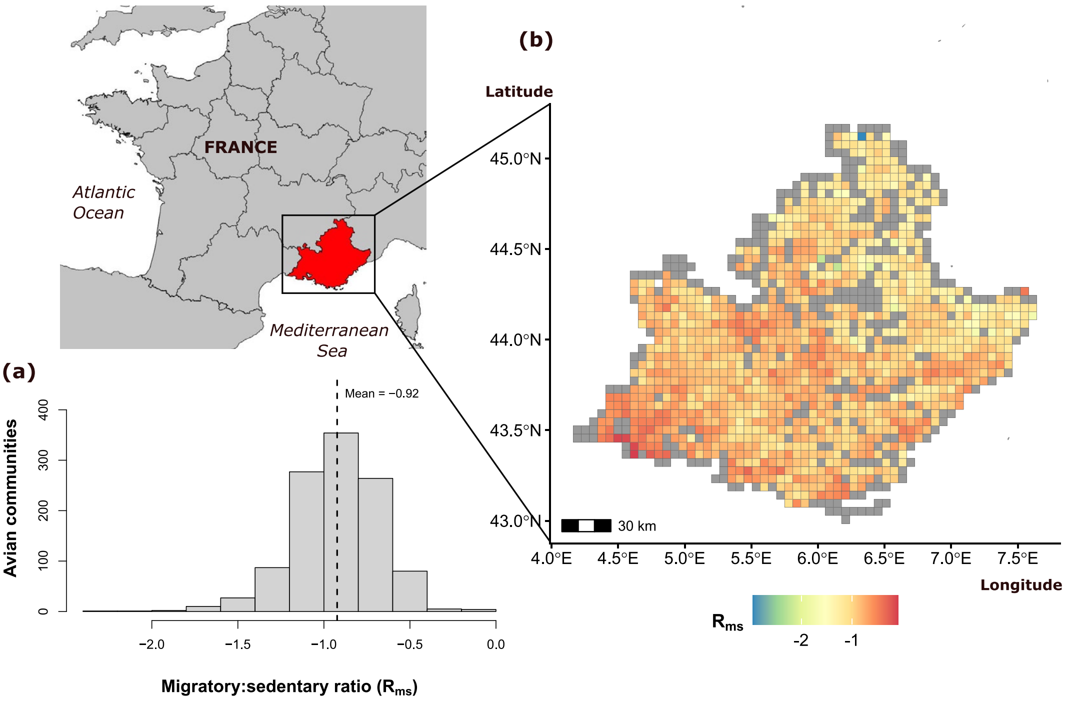

FIGURE 1 | Distribution of the migratory: Sedentary ratio R_{ms} in the PACA region (France). (a) Histogram illustrating the distribution of the R_{ms} values across all avian communities ($N_c = 1109$); (b) Spatial distribution of the R_{ms} across avian communities in the study region. We defined an avian community as all bird species occurring within a 5 × 5 km cell.

TABLE 2 | Results of the spatial auto regressive (SAR) model exploring the variations in migratory: Sedentary ratio R_{ms} in response to altitude (three altitudinal belts: Hilly, Mountain, Subalpine) and to the interactions between altitude and habitat diversity, habitat evenness, forest cover and species richness.

Variable	Estimate	SE	*z* value	*p*
(Intercept)	**−0.875**	**0.013**	**−66.692**	**< 0.001**
Mountain Belt	**−0.063**	**0.021**	**−2.995**	**0.003**
Subalpine Belt	**−0.232**	**0.027**	**−8.469**	**< 0.001**
Log (Species Richness)	**0.090**	**0.008**	**11.520**	**< 0.001**
Forest Cover	**−0.016**	**0.008**	**−1.966**	**0.049**
Habitat diversity	**−0.029**	**0.007**	**−4.154**	**< 0.001**
(Habitat diversity)^2	**0.013**	**0.004**	**3.269**	**0.001**
Habitat Evenness	**−0.016**	**0.006**	**−2.628**	**0.009**
Mountain Belt * Log (Species Richness)	0.028	0.015	1.882	0.060
Subalpine Belt * Log (Species Richness)	−0.010	0.016	−0.596	0.551
Mountain Belt * Forest Cover	−0.034	0.017	−1.951	0.051
Subalpine Belt * Forest Cover	**−0.044**	**0.019**	**−2.320**	**0.020**
Mountain Belt * Habitat diversity	**−0.037**	**0.018**	**−2.028**	**0.043**
Subalpine Belt * Habitat diversity	**0.061**	**0.022**	**2.786**	**0.005**
Mountain Belt * Habitat evenness	0.021	0.014	1.540	0.123
Subalpine Belt * Habitat evenness	−0.007	0.016	−0.429	0.668

Note: Significant effects are shown in bold.

accounting for the fact that the response variable is influenced by the values of other observations based on their geographic proximity (neighbourhood). The implementation of SAR models involves decisions regarding the definition of neighbourhood (distance) and ponderation. As in (Kissling and Carl 2008), we tested multiple combinations of distance and types of weighting and selected the one which maximised the correction of spatial autocorrelation using AIC. The optimal configuration corresponded to a row-standardised weighting matrix ('W') with a distance threshold of 10 km. The use of the SAR model significantly reduced the spatial autocorrelation of the residuals to a value of 0.06, up to 2.5 km, compared with the initial linear model (Figure S6).

For the description of model results, we considered Nagelkerke pseudo-R^2 as a measure of explained variance (Nagelkerke 1991).

3 | Results

3.1 | Variation of Landscape Structure and Species Richness According to Altitudinal Belts of the PACA Region

Both the average and the range of habitat diversity decreased with increasing altitude (Table S2). The average number of habitat diversity per cell declined from 6.97 in the hilly belt to 5.24 in the subalpine belt, with a range narrowing from [4; 10] to [3; 8]. Habitat evenness and forest cover showed similar patterns: habitat evenness was highest in the mountain belt (0.77 ± 0.11) and slightly lower in the subalpine (0.72 ± 0.11) and hilly (0.71 ± 0.14) belts. Cells with low habitat evenness (< 0.5) were mostly found at low altitudes. Forest cover was most extensive in the mountain belt (47.6% on average, with values ranging from 15.9% to 77.3%), where highly forested cells (≥ 90%) occurred. In contrast, such cells were absent in the subalpine belt, consistent with the treeline around 2000 m in the region (Pecher et al. 2011). Finally, total bird species richness showed a slight decrease with altitude, from an average of 84.07 species in the hilly belt to 80.0 species in the subalpine belt (Table S2). This decrease mostly reflected the absence of highly rich communities (i.e., cells with > 117 species) in the subalpine zone.

3.2 | The Extent of Variation of the Migratory: Sedentary Ratio in Breeding Avian Communities

The migratory–sedentary ratio R_{ms} averaged −0.92 ± 0.24 (95% CI: [−0.94; −0.91]; $N_c = 1109$; Figure 1a). Breeding avian communities were overall more biased towards sedentary species (average percentage of sedentary species: 70.7%) compared to the expected proportion of sedentary species in the regional pool (66.2%). We did not detect any community hosting more migratory than sedentary species ($R_{ms} < 0$ in all cases). Yet, R_{ms} was not homogeneously spread across the region (Figure 1b): R_{ms} was higher than average in the wetlands of the Camargue (south-western end of the region), but also along the Mediterranean coast and in the central part. In contrast, lower values for R_{ms} were recorded in the north-eastern part (Alps mountains).

3.3 | Interacting Effects of Landscape Structure and Altitude on the Migratory: Sedentary Ratio

We found interacting effects between altitude and the landscape structure (habitat diversity and evenness, forest cover) on R_{ms} (Nagelkerke pseudo-$R^2 = 0.562$; Table 2 and Figure 2). R_{ms} exhibited either a quadratic response (habitat diversity: −0.029 ± 0.007, $p < 0.001$; quadratic term = 0.013 ± 0.004, $p = 0.001$) or a linear decrease with other landscape heterogeneity variables (habitat evenness: −0.016 ± 0.006, $p = 0.009$; and

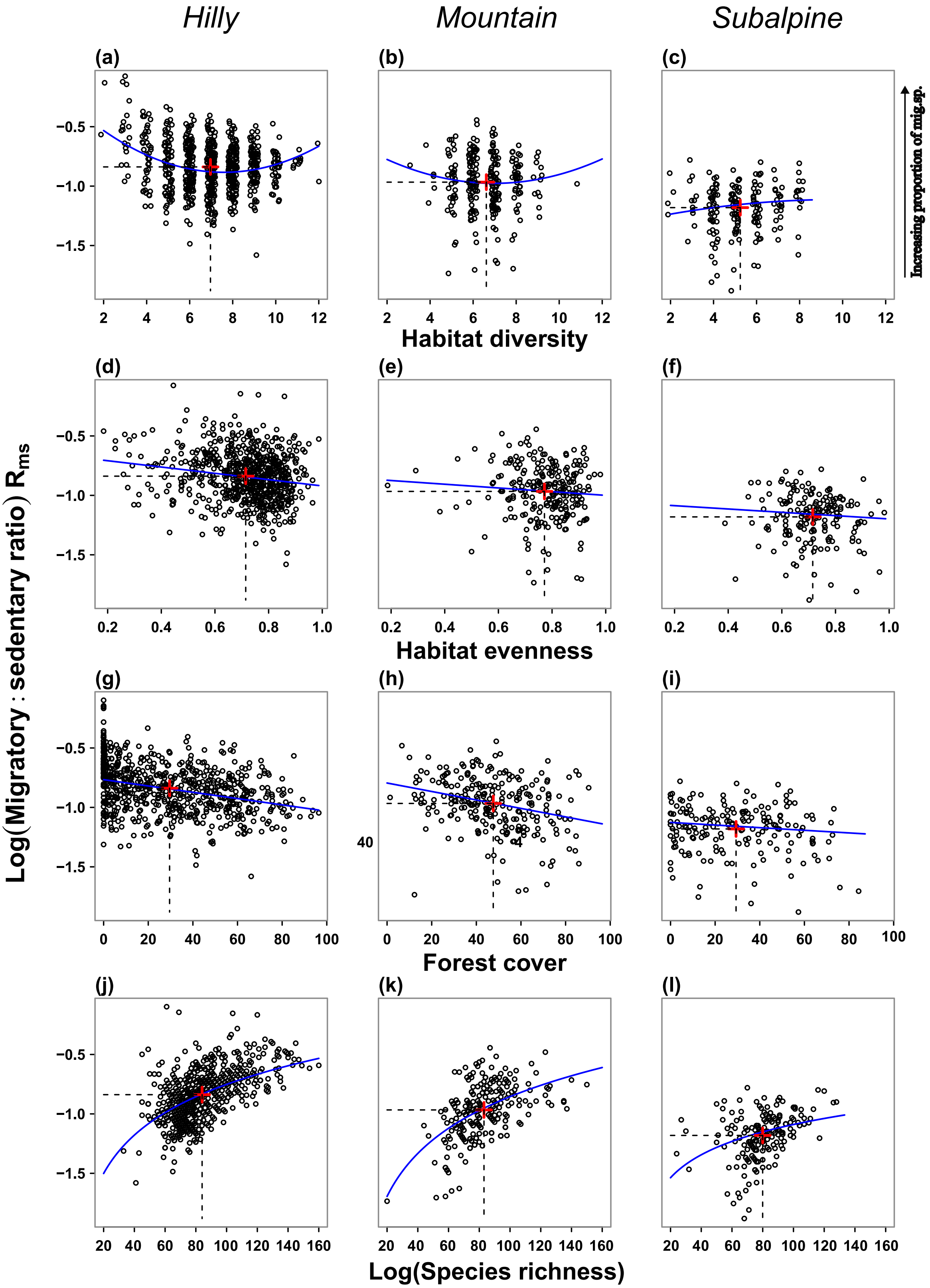

FIGURE 2 | Variations in the migratory: Sedentary ratio R_{ms} along habitat diversity (a–c), habitat evenness (d–f), forest cover (g–i) and species richness (j–l) gradients observed, at three altitudinal belts (hilly < 900 m, mountain < 1600 m and subalpine belts). The red crosses indicate the means of both variables. Grey dots represent the avian communities assessed in 5 × 5 km cells ($N = 1109$). The blue lines show predicted values from the selected SAR model (see Table 2 for details). The proportion of migratory species increases as the ratio tends towards zero (all communities showed a higher number of sedentary species compared to migratory ones and then negative R_{ms}).

forest cover: -0.016 ± 0.008, $p = 0.049$), but this trend was dampened as altitude increased (Figure 2a–i). In the subalpine belt, it can vanish (for forest cover and habitat evenness; Figure 2f,i) or even be reversed (for habitat diversity $= 0.061 \pm 0.022$, $p = 0.005$; Figure 2c). The specific responses of migratory ($R^2 = 0.913$; Figure 3a–i; Table S4) and sedentary (Nagelkerke pseudo-$R^2 = 0.955$; Figure 4a–i; Table S5) species richness helped clarify these results.

The quadratic response of R_{ms} to increasing habitat diversity arose from the quadratic response of both the migratory (linear term: -0.512 ± 0.113, $p < 0.001$; quadratic term: 0.153 ± 0.064, $p = 0.017$; Figure 3a–c) and the sedentary species richness (linear term: 0.516 ± 0.112, $p < 0.001$; quadratic term: -0.153 ± 0.064, $p = 0.017$; Figure 4a–c). Intermediate values of habitat diversity seemed to have a negative effect on the number of migratory and sedentary species in the hilly belt (more pronounced for migratory ones; Figures 3a and 4a); this effect tended to diminish in the mountain belt (Figures 3b and 4b) and to be reversed for both groups in the subalpine belt (migratory: 1.036 ± 0.358, $p = 0.004$; sedentary: -1.033 ± 0.357, $p = 0.004$; Figures 3c and 4c), where the increase in habitat diversity is favourable to both groups. The negative effect of habitat evenness indicated that higher evenness (i.e., lower landscape heterogeneity) in habitat distribution reduced R_{ms}. In contrast to the habitat diversity one, this effect appeared more consistent across the three altitudinal belts, with an overall negative effect on R_{ms} (with no significant interactions; Figure 2d–f). Finally, a higher proportion of forest cover significantly reduced R_{ms} in the hilly and mountain belts, whereas this negative effect was weaker in the subalpine belt (interaction with subalpine: -0.044 ± 0.019, $p = 0.020$; Table 2 and Figure 2g–i). In the study area, increased forest cover reduced the number of migratory and sedentary species in the hilly and mountain belts (Figures 3g,h and 4g,h). However, more forested areas tended to host more sedentary and migratory species in subalpine belts (Figures 3i and 4i).

3.4 | Interacting Effects of Species Richness and Altitude on the Migratory: Sedentary Ratio

Our results showed that species richness significantly affected the R_{ms}, by increasing the proportion of migratory to sedentary species (Figure 2j–l). While species richness varied little across the three altitudinal belts (with a mean of 84.1 in Hilly to 83.1 in Mountain and 80 in the Subalpine; Table S2), the mean R_{ms} decreased with altitude (Figure 2j–l; Table S3). At low altitude (hilly belt), the numbers of migratory and sedentary species were close to the expected value from the observed proportion of migratory species in the regional pool (34%; Figures 3j and 4j). On the contrary, at higher altitudes, the number of migratory species was far below this expected value (Figure 3k,l), while the number of sedentary species was slightly above (Figure 4k,l). The relationships between species richness and the number of both migratory and sedentary species were slightly non-linear (quadratic U-shaped: 0.137 ± 0.052, $p = 0.009$, and bell-shaped: -0.134 ± 0.052, $p = 0.010$, respectively) and especially so at hilly and subalpine belts. For the hilly belt (62% of the total number of cells; Table S2), it is interesting to note that the mean predicted number of migratory species crossed the line drawn from the observed proportion of migratory species in the regional pool. Indeed, in species-rich communities (> 117 species), the increase in species richness was mainly achieved through the addition of migratory species (Figure 3j).

4 | Discussion

Our study aimed to investigate how the migratory: sedentary ratio responds to environmental variation to infer about the equilibrium between migratory and sedentary species in breeding avian communities, revealing that species composition is strongly shaped by the interaction between environmental conditions and species' migratory behaviour.

4.1 | Altitude as a Context-Dependent Driver

Overall, we found that the total bird species richness is only slightly affected by altitude (with a loss of 3.9% between hilly and subalpine belts). While species richness has been previously found to decrease progressively with altitude (McCain 2007; Rohde 1992; Stevens 1992) according to the environmental filtering concept (Grime 2006; Keddy 1992), our results confirm that effect of the altitudinal gradient on avian diversity can be highly variable or even unpredictable (McCain 2009; McCain and Grytnes 2010). Although we initially expected a migratory-biased equilibrium at higher altitudes, assuming that migratory species benefit from short-term resource peaks and avoid harsh winter conditions (Boyle and Martin 2015; Kim et al. 2022), our results rather support the hypothesis that sedentary species, by their year-round presence (despite the inclusion of short-distance migratory species in this category), may be better adapted to the strong environmental constraints encountered at high altitudes (Kim et al. 2018, 2022; Lemoine, Schaefer, et al. 2007). As the altitudinal gradient was closely associated with both climatic and human impact gradients (Figure S1), this dual association suggests that variations in avian diversity along altitudinal gradients may result from the combined effects of changing climatic conditions and varying degrees of anthropogenic influence (Gaüzère et al. 2020; Jetz et al. 2007; Titeux et al. 2017; noting that our models did not directly test the effects of urbanisation or seasonal resource availability). In particular, the negative relationship between urbanisation and the abundance of migratory birds (Evans et al. 2018; Husté and Boulinier 2011; Loss et al. 2009) is reinforced by the effects of climate change, where milder winters on breeding grounds increase the density of sedentary species, thus intensifying competition for food and nesting sites when migratory species come back from their wintering grounds (Berthold et al. 1998; Lemoine and Böhning-Gaese 2003).

Beyond this general pattern, we also found significant interactions between altitude and both landscape structure and species richness, shaping the migratory: sedentary ratio, the number of migratory species and the number of sedentary species within communities. Our results highlight the complex response of avian communities to both regional (i.e., altitude) and local-scale (abiotic and biotic) factors. This complexity likely contributes to the observe inconsistencies in bird diversity patterns along

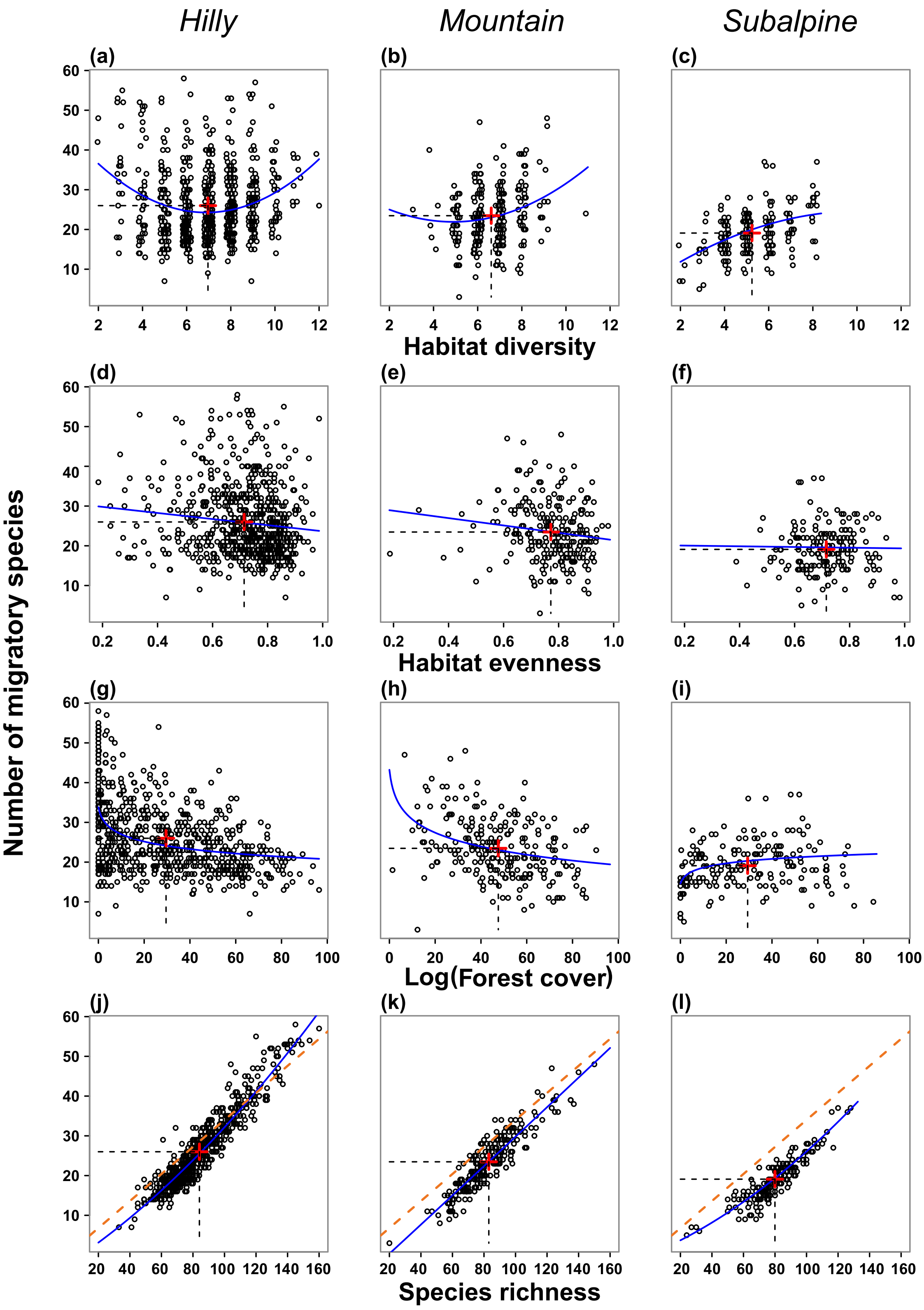

FIGURE 3 | Variations in the number of migratory species along habitat diversity (a–c), habitat evenness (d–f), forest cover (g–i) and species richness (j–l) gradients observed, at three altitudinal belts (hilly < 900 m, mountain < 1600 m and subalpine belts). The red crosses indicate the means of both variables. Grey dots represent the avian communities assessed in 5 × 5 km cells ($N = 1109$). The blue lines show predicted values from the selected SAR model (see Table S4 for details). In panels j–l, orange lines represent the expected number of migratory species assuming that each community reflects the regional proportion of migratory species (34%)—providing a baseline for comparison in the absence of environmental filtering.

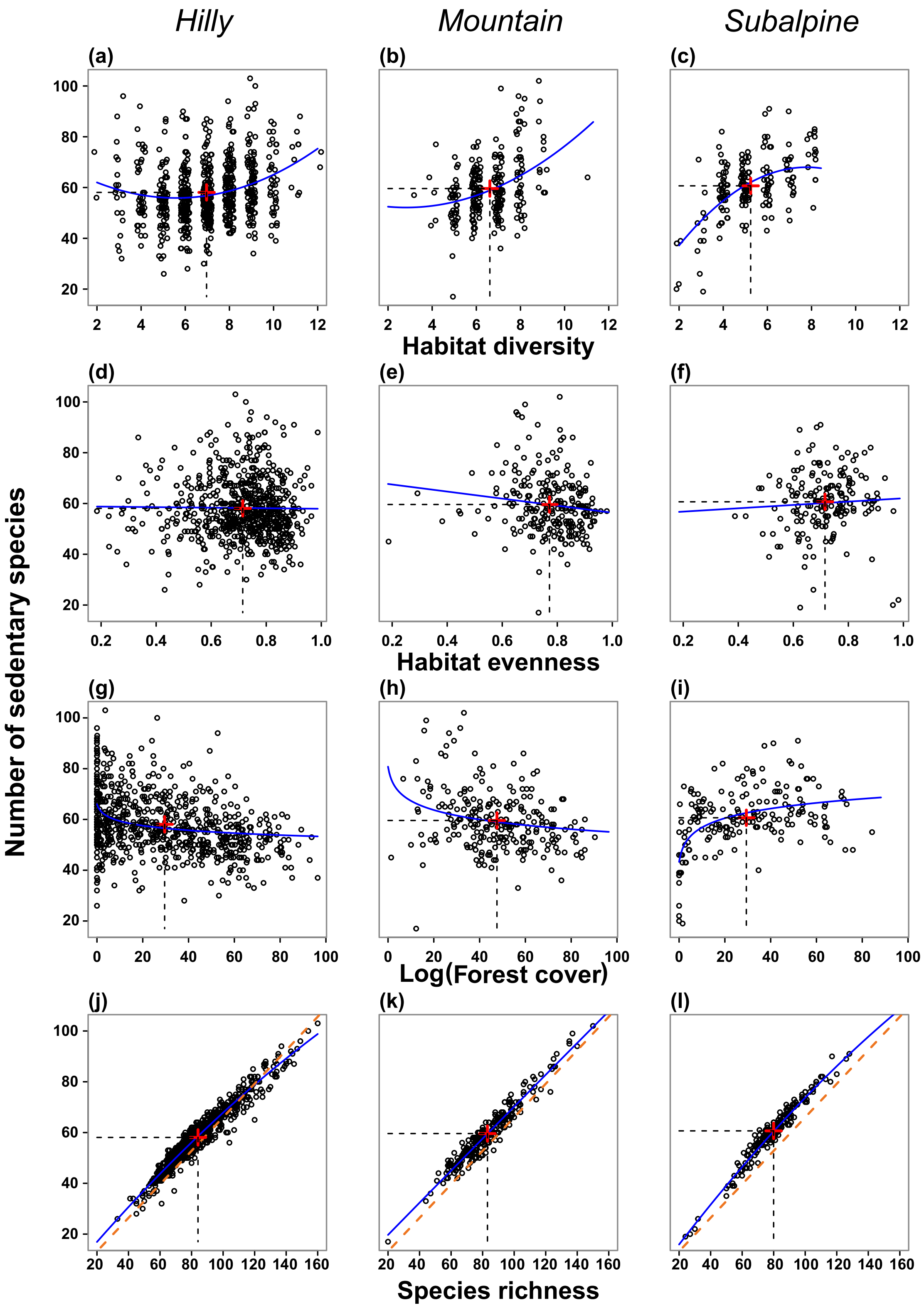

FIGURE 4 | Variations in the number of sedentary species along habitat diversity (a–c), habitat evenness (d–f), forest cover (g–i) and species richness (j–l) gradients observed, at three altitudinal belts (hilly < 900 m, mountain < 1600 m and subalpine belts). The red crosses indicate the means of both variables. Grey dots represent the avian communities assessed in 5 × 5 km cells (N = 1109). The blue lines show predicted values from the selected SAR model (see Table S5 for details). In panels j–l, orange lines represent the expected number of sedentary species assuming that each community reflects the regional proportion of migratory species (66%), providing a baseline for comparison in the absence of environmental filtering.

altitudinal gradients. Since the altitudinal gradient in the PACA region (ca. 4000 m) correlated with climatic drivers such as mean annual temperature and precipitation (Figure S1), our study aligns with recent research in plant community ecology emphasising the importance of multiple, interacting abiotic stressors in shaping biodiversity (e.g., Butterfield and Suding 2012; Le Bagousse-Pinguet et al. 2017; Oliver and Morecroft 2014). In the same vein, our results show that neither altitude nor individual environmental drivers alone suffice to explain patterns in avian richness or migratory strategies. Instead, our study highlights the importance of considering the interplay between climate and land-use changes, two processes increasingly recognised to interact in shaping future biodiversity dynamics (Maestre et al. 2022; Peñuelas et al. 2013; Rillig et al. 2019; Stocker and Qin 2013).

4.2 | Landscape Heterogeneity Biased the Equilibrium Towards Sedentary Species, but Altitude Dampens This Effect

In the hilly and mountain belts, we found that the cells with fewer than seven habitat types and a low habitat evenness promoted the occurrence of migratory species within the breeding community. Our study thus identifies the set of environmental conditions under which the equilibrium of avian communities is more biased towards migratory species than expected from the regional species pool. This result also aligns with the view that landscape structure is a key driver shaping the intrinsic structure of avian communities by modulating resource availability and providing varied breeding opportunities for migratory and sedentary species (Elsen et al. 2021; Kim et al. 2022). Landscapes dominated by a limited number of habitat types tend to reduce resource diversity and nesting niches. This simplification acts as an environmental filter, favouring species adapted to exploit seasonal resource availability, such as migratory birds, in line with the environmental filtering hypothesis (Grime 2006; Keddy 1992). Large-scale wetlands provide such highly productive conditions with for example in our study area, the Camargue wetland (Rhône River delta) in the south-western part of the region, hosting a hotspot for both breeding and staging long-distance migratory species.

Higher habitat diversity (i.e., above seven habitats in the hilly and mountain belts, for which the average is 6.97 and 6.61 respectively) and evenness had consistent, but opposite effects across altitudinal belts. Increasing the diversity of habitats promoted both sedentary and migratory species, as a result of the greater number of available niches or combinations of niches, increasing the number of species that can coexist at equilibrium (Hutchinson and MacArthur 1959; Kisel et al. 2011). Yet, we still found that high habitat diversity tended to favour migratory species, notably because the number of sedentary species reached a plateau above six habitats in the subalpine belt. This plateau may reflect specific ecological traits of sedentary species, which tend to be more habitat-specific with narrower ecological niches and lower tolerance to environmental variability compared to migratory species (e.g., niche breadth hypothesis; Devictor et al. 2010). As a result, in highly stressful environments like in the subalpine belt, increasing habitat diversity may no longer benefit sedentary species, whose persistence depends on specific stable conditions. Instead, it promotes niches availability for migratory species, which often exhibit broader habitat tolerance and flexibility in exploiting temporal and spatial resource heterogeneity (Barbosa et al. 2020). This pattern partly confirms our hypothesis that higher habitat diversity favours a higher proportion of migratory species, highlighting that while a wider range of habitats is beneficial, the spatial configuration and environmental context remain key factors influencing the overall impact across different altitudinal belts. In contrast to habitat diversity, cells with a highly even proportion of habitats hosted avian communities more biased towards sedentary bird species. This bias may result from both the reduction of available specific niches essential to migratory birds or from the increased competition with sedentary species that benefit from resources available all year long (Lemoine and Böhning-Gaese 2003).

We found that increasing forest cover promoted both the richness of sedentary and migratory species in the subalpine belt, but decreased them at lower altitudes. At high altitudes, forests are typically scarcer (upper limit of the timberline in the PACA region at ca. 2200 m, F. Guibal, *pers. comm.*), with a shift towards more patchy and cold-adapted coniferous tree species (Ozenda 1981). These forests are particularly crucial for both species group in the subalpine belt, as they are even more dependent on forest habitats and habitat connectivity for survival. While increasing forest cover has been recently found to promote bird species richness (particularly in tropical regions, Carrara et al. 2015; Vargas-Cárdenas et al. 2022), our results indicated that the direction and strength of the relationship between forest cover and the equilibrium between migratory and sedentary species can change along altitudinal gradients, and is therefore highly dependent upon the environmental context. We observed a sharp increase in migratory species, which are specialists of open habitats (Böhning-Gaese and Oberrath 2003), below ~10% of forest cover. This result highlights the high sensitivity of migratory species to landscape structure, as even a small amount of forest can drastically reduce their richness (Barbosa et al. 2020; Böhning-Gaese and Oberrath 2003; Mönkkönen and Helle 1989). We observed a similar, but less pronounced pattern for sedentary bird species. One explanation, supported by previous studies, is that sedentary and short-distance migrants arrive earlier in the breeding season and may secure more suitable forest habitats, whereas long-distance migrants arriving later are constrained to less optimal nesting sites (not directly test in our study; Böhning-Gaese and Oberrath 2003).

4.3 | Migratory Species Contribute More to Richest Avian Communities

We found a positive effect of total bird species richness on the proportion of migratory species within the breeding avian community. Increasing bird species richness within communities has been suggested to alter the equilibrium between sedentary and migratory species through increased competition, and potentially favouring species such as migratory species whose temporary presence and specialisation on seasonal resources reduce competition (Pigot and Tobias 2013; Wiens 2011). The increasing proportion of migratory species with increasing total bird richness was more pronounced at lower altitudes, and indicated that relaxing the altitudinal constraints (and associated low temperatures and short growing season of the vegetation) could have promoted the presence of migratory species, instead of locally adapted sedentary species (Kim et al. 2018, 2022; Lemoine, Schaefer, et al. 2007). We even found that the richest avian communities in the hilly belt (i.e., those above ~117 bird species) hosted a number of migratory species higher than expected from the ratio observed in the regional pool (Figure 3a). Favouring the addition of migratory species in the richest communities—instead of sedentary species that are present all year round—may reduce competitive interactions for available resources and limit niche saturation (Hutchinson 1957; Macarthur and Levins 1967; Pianka 1974). This pattern is also consistent with the heterospecific attraction hypothesis, according to which migrants use sedentary species as indicators of high-quality breeding sites, with sedentary species generally occupying better-quality habitats (Mönkkönen et al. 1997; Mönkkönen and Forsman 2002). Although we acknowledge that our design does not provide a formal test of this hypothesis, it provides an empirical assessment of this hypothesis at the community level (the original hypothesis has been proposed considering the abundance of a few species [typically < 10]). Our study also identifies under which environmental conditions heterospecific attraction may prevail. Indeed, we observed that avian communities exhibited a lower richness of migratory species (and a higher richness of sedentary species) than expected from the regional pool, with deviation increasing with altitude. While our analysis focused on species richness rather than abundances (not available at the spatial scale of the study), future studies incorporating abundance data could reveal whether shifts in migratory equilibrium are primarily driven by a few dominant species or, alternatively, result from an even contribution across the community. Similarly, our study was limited to the breeding season only and patterns involving wintering communities could differ and merit further investigation. Moreover, the slightly lower contribution of migratory species in some communities may partly reflect the under-representation of rare migratory species, potentially linked to environmental filtering or competitive exclusion. Such a pattern aligns with previous findings that migratory species are more vulnerable to habitat degradation and phenological mismatches (Both et al. 2006; Gilroy et al. 2016), suggesting that observed assemblages result from both ecological processes and species-specific sensitivities.

5 | Conclusion

Our study examined the equilibrium between migratory and sedentary bird species across environmental gradients. By considering interactions among multiple environmental drivers, we revealed the complex effects of environmental filtering on avian community composition. Future studies could gain further mechanistic insight by considering functional traits (food- and habitat-related) and their variability that can strongly impact community assembly (e.g., Le Bagousse-Pinguet et al. 2014, 2015; Siefert et al. 2015). Notably, we showed that interactions between altitude and landscape structure and altitude and species richness are fundamental to understand avian diversity patterns, highlighting the importance of environmental filtering. Finally, our study can help to identify the combinations of environmental factors favouring (or threatening) migratory and sedentary bird species richness, a pre-requisite to any attempt for mitigating the effects of environmental change on avian communities.

Author Contributions

C.R., Y.L.B.-P., A.L. and A.M. developed the conceptual and methodological foundation of this study. C.R. and A.L. conducted statistical analyses. A.F. and C.G. designed the field study and coordinated field data acquisition. C.R. wrote the first draft, and all authors substantially contributed to the subsequent drafts.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data file and script necessary to replicate the analyses of this article can be found at: http://datadryad.org/share/eWeORTz-Deh_qQogc5L-na4WEIZvVr20Ry3eSbImGPI.

References

Ahola, M. P., T. Laaksonen, T. Eeva, and E. Lehikoinen. 2007. "Climate Change Can Alter Competitive Relationships Between Resident and Migratory Birds." *Journal of Animal Ecology* 76, no. 6: 1045–1052. https://doi.org/10.1111/j.1365-2656.2007.01294.x.

Akhrorov, D., T. Cai, G. Song, et al. 2022. "Ecological Constraints on Elevational Gradients of Bird Species Richness in Tajikistan." *Avian Research* 13: 100026. https://doi.org/10.1016/j.avrs.2022.100026.

Andersen, A. H., K. K. Clausen, S. Normand, T. Vikstrøm, and J. E. Moeslund. 2023. "The Influence of Landscape Characteristics on Breeding Bird Dark Diversity." *Oecologia* 201, no. 4: 1039–1052. https://doi.org/10.1007/s00442-023-05351-8.

Barbosa, K., A. Rodewald, M. Ribeiro, and A. Jahn. 2020. "Noise Level and Water Distance Drive Resident and Migratory Bird Species Richness Within a Neotropical Megacity." *Landscape and Urban Planning* 197: 103769. https://doi.org/10.1016/j.landurbplan.2020.103769.

Basile, M., I. Storch, and G. Mikusiński. 2021. "Abundance, Species Richness and Diversity of Forest Bird Assemblages – The Relative Importance of Habitat Structures and Landscape Context." *Ecological Indicators* 133: 108402. https://doi.org/10.1016/j.ecolind.2021.108402.

Berdugo, M., B. Vidiella, R. V. Solé, and F. T. Maestre. 2022. "Ecological Mechanisms Underlying Aridity Thresholds in Global Drylands." *Functional Ecology* 36, no. 1: 4–23. https://doi.org/10.1111/1365-2435.13962.

Berthold, P. 1999. "A Comprehensive Theory for the Evolution, Control and Adaptability of Avian Migration." *Ostrich* 70, no. 1: 1–11. https://doi.org/10.1080/00306525.1999.9639744.

Berthold, P. 2001. *Bird Migration: A General Survey*. Oxford University Press.

Berthold, P., W. Fiedler, R. Schlenker, and U. Querner. 1998. "25-Year Study of the Population Development of Central European Songbirds: A General Decline, Most Evident in Long-Distance Migrants." *Naturwissenschaften* 85, no. 7: 350–353. https://doi.org/10.1007/s001140050514.

Blount, J. D., J. J. Horns, K. D. Kittelberger, M. H. C. Neate-Clegg, and Ç. H. Şekercioğlu. 2021. "Avian Use of Agricultural Areas as Migration Stopover Sites: A Review of Crop Management Practices and Ecological Correlates." *Frontiers in Ecology and Evolution* 9: 650641. https://doi.org/10.3389/fevo.2021.650641.

Böhning-Gaese, K., and N. Lemoine. 2004. "Importance of Climate Change for the Ranges, Communities and Conservation of Birds." In *Advances in Ecological Research*, vol. 35, 211–236. Academic Press. https://doi.org/10.1016/S0065-2504(04)35010-5.

Böhning-Gaese, K., and R. Oberrath. 2003. "Macroecology of Habitat Choice in Long-Distance Migratory Birds." *Oecologia* 137, no. 2: 296–303. https://doi.org/10.1007/s00442-003-1346-9.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. "Climate Change and Population Declines in a Long-Distance Migratory Bird." *Nature* 441, no. 7089: 81–83. https://doi.org/10.1038/nature04539.

Boyle, W. A., and K. Martin. 2015. "The Conservation Value of High Elevation Habitats to North American Migrant Birds." *Biological Conservation* 192: 461–476. https://doi.org/10.1016/j.biocon.2015.10.008.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, et al. 2002. "Habitat Loss and Extinction in the Hotspots of Biodiversity." *Conservation Biology* 16: 4. https://doi.org/10.1046/j.1523-1739.2002.00530.x.

Burnham, K. P., and D. R. Anderson, eds. 2002. *Model Selection and Multimodel Inference*. Springer. https://doi.org/10.1007/b97636.

Butchart, S., M. Walpole, B. Collen, et al. 2010. "Global Biodiversity: Indicators of Recent Declines." *Science* 328: 1164–1168. https://doi.org/10.1126/science.1187512.

Butterfield, B. J., and K. N. Suding. 2012. "Single-Trait Functional Indices Outperform Multi-Trait Indices in Linking Environmental Gradients and Ecosystem Services in a Complex Landscape." https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12013.

Campbell, C. E., D. N. Jones, M. Awasthy, J. G. Castley, and A. L. M. Chauvenet. 2022. "Big Changes in Backyard Birds: An Analysis of Long-Term Changes in Bird Communities in Australia's Most Populous Urban Regions." *Biological Conservation* 272: 109671. https://doi.org/10.1016/j.biocon.2022.109671.

Carrara, E., V. Arroyo-Rodríguez, J. H. Vega-Rivera, J. E. Schondube, S. M. de Freitas, and L. Fahrig. 2015. "Impact of Landscape Composition and Configuration on Forest Specialist and Generalist Bird Species in the Fragmented Lacandona Rainforest, Mexico." *Biological Conservation* 184: 117–126. https://doi.org/10.1016/j.biocon.2015.01.014.

Ceresa, F., P. Kranebitter, J. S. Monrós, F. Rizzolli, and M. Brambilla. 2021. "Disentangling Direct and Indirect Effects of Local Temperature on Abundance of Mountain Birds and Implications for Understanding Global Change Impacts." *PeerJ* 9: e12560. https://doi.org/10.7717/peerj.12560.

Chao, A., N. J. Gotelli, T. C. Hsieh, et al. 2014. "Rarefaction and Extrapolation With Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." *Ecological Monographs* 84, no. 1: 45–67. https://doi.org/10.1890/13-0133.1.

Chao, A., and L. Jost. 2012. "Coverage-Based Rarefaction and Extrapolation: Standardizing Samples by Completeness Rather Than Size." *Ecology* 93, no. 12: 2533–2547. https://doi.org/10.1890/11-1952.1.

Chao, A., Y. Kubota, D. Zelený, et al. 2020. "Quantifying Sample Completeness and Comparing Diversities Among Assemblages." *Ecological Research* 35, no. 2: 292–314. https://doi.org/10.1111/1440-1703.12102.

Clavero, M., D. Villero, and L. Brotons. 2011. "Climate Change or Land Use Dynamics: Do we Know What Climate Change Indicators Indicate?" *PLoS One* 6, no. 4: e18581. https://doi.org/10.1371/journal.pone.0018581.

De Camargo, R. X. 2023. "Avian Diversity Responds Unimodally to Natural Landcover: Implications for Conservation Management." *Animals* 13, no. 16: 16. https://doi.org/10.3390/ani13162647.

Devictor, V., J. Clavel, R. Julliard, et al. 2010. "Defining and Measuring Ecological Specialization." *Journal of Applied Ecology* 47, no. 1: 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

D'Odorico, P., A. Bhattachan, K. F. Davis, S. Ravi, and C. W. Runyan. 2013. "Global Desertification: Drivers and Feedbacks." *Advances in Water Resources* 51: 326–344. https://doi.org/10.1016/j.advwatres.2012.01.013.

Eglington, S. M., and J. W. Pearce-Higgins. 2012. "Disentangling the Relative Importance of Changes in Climate and Land-Use Intensity in Driving Recent Bird Population Trends." *PLoS One* 7, no. 3: e30407. https://doi.org/10.1371/journal.pone.0030407.

Elsen, P. R., L. S. Farwell, A. M. Pidgeon, and V. C. Radeloff. 2021. "Contrasting Seasonal Patterns of Relative Temperature and Thermal Heterogeneity and Their Influence on Breeding and Winter Bird Richness Patterns Across the Conterminous United States." *Ecography* 44, no. 6: 953–965. https://doi.org/10.1111/ecog.05520.

Evans, T., A. Pigot, S. Kumschick, Ç. H. Şekercioğlu, and T. M. Blackburn. 2018. "Determinants of Data Deficiency in the Impacts of Alien Bird Species." *Ecography* 41, no. 8: 8. https://doi.org/10.1111/ecog.03232.

Fahrig, L. 2003. "Effects of Habitat Fragmentation on Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515.

Flitti, A., B. Kabouche, Y. Kayser, and G. Olioso. 2009. *Atlas des oiseaux nicheurs de Provence-Alpes-Côte d'Azur*, 543. Delachaux et Niestlé. ISBN 978-2-603-01622-0 sections 345–493.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, et al. 2009. "Loss of Functional Diversity Under Land Use Intensification Across Multiple Taxa." *Ecology Letters* 12, no. 1: 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x.

Forsman, J. T., and M. Mönkkönen. 2003. "The Role of Climate in Limiting European Resident Bird Populations." *Journal of Biogeography* 30, no. 1: 55–70. https://doi.org/10.1046/j.1365-2699.2003.00812.x.

Gaüzère, P., L. Barbaro, F. Calatayud, et al. 2020. "Long-Term Effects of Combined Land-Use and Climate Changes on Local Bird Communities in Mosaic Agricultural Landscapes." *Agriculture, Ecosystems and Environment* 289: 106722. https://doi.org/10.1016/j.agee.2019.106722.

Gaüzère, P., L. O'Connor, C. Botella, et al. 2022. "The Diversity of Biotic Interactions Complements Functional and Phylogenetic Facets of Biodiversity." *Current Biology* 32, no. 9: 2093–2100.e3. https://doi.org/10.1016/j.cub.2022.03.009.

Gilroy, J. J., J. A. Gill, S. H. M. Butchart, V. R. Jones, and A. M. A. Franco. 2016. "Migratory Diversity Predicts Population Declines in Birds." *Ecology Letters* 19, no. 3: 308–317. https://doi.org/10.1111/ele.12569.

Graham, C. H., J. L. Parra, C. Rahbek, and J. A. McGuire. 2009. "Phylogenetic Structure in Tropical Hummingbird Communities." *Proceedings of the National Academy of Sciences* 106, no. supplement_2: 19673–19678. https://doi.org/10.1073/pnas.0901649106.

Grime, J. P. 2006. "Trait Convergence and Trait Divergence in Herbaceous Plant Communities: Mechanisms and Consequences." *Journal of Vegetation Science* 17, no. 2: 255–260. https://doi.org/10.1111/j.1654-1103.2006.tb02444.x.

Guillaumet, A., and I. J. Russell. 2022. "Bird Communities in a Changing World: The Role of Interspecific Competition." *Diversity* 14, no. 10: 857. https://doi.org/10.3390/d14100857.

Hurlbert, A. H., and J. P. Haskell. 2003. "The Effect of Energy and Seasonality on Avian Species Richness and Community Composition." *American Naturalist* 161, no. 1: 83–97. https://doi.org/10.1086/345459.

Husté, A., and T. Boulinier. 2011. "Determinants of Bird Community Composition on Patches in the Suburbs of Paris, France." *Biological Conservation* 144, no. 1: 243–252. https://doi.org/10.1016/j.biocon.2010.08.022.

Hutchinson, G. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22, no. 0: 415–427. https://doi.org/10.1101/SQB.1957.022.01.039.

Hutchinson, G. E., and R. H. MacArthur. 1959. "A Theoretical Ecological Model of Size Distributions Among Species of Animals." *American Naturalist* 93, no. 869: 117–125. https://doi.org/10.1086/282063.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. "Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds." *PLoS Biology* 5, no. 6: e157. https://doi.org/10.1371/journal.pbio.0050157.

Karger, D. N., S. Lange, C. Hari, C. P. O. Reyer, and N. E. Zimmermann. 2021. "CHELSA-W5E5 v1.0: W5E5 v1.0 downscaled with CHELSA v2.0 (Version 1.0) [Data set]." ISIMIP Repository. https://doi.org/10.48364/ISIMIP.836809.

Karger, D. N., D. R. Schmatz, G. Dettling, and N. E. Zimmermann. 2020. "High-Resolution Monthly Precipitation and Temperature Time Series From 2006 to 2100." *Scientific Data* 7, no. 1: 1. https://doi.org/10.1038/s41597-020-00587-y.

Keddy, P. A. 1992. "Assembly and Response Rules: Two Goals for Predictive Community Ecology." *Journal of Vegetation Science* 3, no. 2: 157–164. https://doi.org/10.2307/3235676.

Kelly, J., and K. Horton. 2016. "Toward a Predictive Macrosystems Framework for Migration Ecology: Macrosystems Framework for Migration Ecology." *Global Ecology and Biogeography* 25: 1159–1160. https://doi.org/10.1111/geb.12473.

Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker. 2019. "Managing the Middle: A Shift in Conservation Priorities Based on the Global Human Modification Gradient." *Global Change Biology* 25, no. 3: 811–826. https://doi.org/10.1111/gcb.14549.

Kim, J.-Y., S. Lee, M.-S. Shin, C.-H. Lee, C. Seo, and S. H. Eo. 2018. "Altitudinal Patterns in Breeding Bird Species Richness and Density in Relation to Climate, Habitat Heterogeneity, and Migration Influence in a Temperate Montane Forest (South Korea)." *PeerJ* 6: e4857. https://doi.org/10.7717/peerj.4857.

Kim, J.-Y., J. Yoon, Y.-S. Choi, and S. H. Eo. 2022. "The Influencing Factors for Distribution Patterns of Resident and Migrant Bird Species Richness Along Elevational Gradients." *PeerJ* 10: e13258. https://doi.org/10.7717/peerj.13258.

Kisel, Y., L. McInnes, N. H. Toomey, and C. D. L. Orme. 2011. "How Diversification Rates and Diversity Limits Combine to Create Large-Scale Species–Area Relationships." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, no. 1577: 2514–2525. https://doi.org/10.1098/rstb.2011.0022.

Kissling, W. D., and G. Carl. 2008. "Spatial Autocorrelation and the Selection of Simultaneous Autoregressive Models." *Global Ecology and Biogeography* 17, no. 1: 59–71. https://doi.org/10.1111/j.1466-8238.2007.00334.x.

Kong, X., Z. Zhou, and L. Jiao. 2021. "Hotspots of Land-Use Change in Global Biodiversity Hotspots." *Resources, Conservation and Recycling* 174: 105770. https://doi.org/10.1016/j.resconrec.2021.105770.

Körner, C. 2007. "The Use of 'Altitude' in Ecological Research." *Trends in Ecology & Evolution* 22, no. 11: 569–574. https://doi.org/10.1016/j.tree.2007.09.006.

Kusumoto, B., A. Chao, W. L. Eiserhardt, J.-C. Svenning, T. Shiono, and Y. Kubota. 2023. "Occurrence-Based Diversity Estimation Reveals Macroecological and Conservation Knowledge Gaps for Global Woody Plants." *Science Advances* 9, no. 40: eadh9719. https://doi.org/10.1126/sciadv.adh9719.

La Sorte, F. A., W. M. Hochachka, A. Farnsworth, et al. 2015. "Seasonal Changes in the Altitudinal Distribution of Nocturnally Migrating Birds During Autumn Migration." *Royal Society Open Science* 2, no. 12: 150347. https://doi.org/10.1098/rsos.150347.

Le Bagousse-Pinguet, Y., L. Börger, J. Quero, et al. 2015. "Traits of Neighbouring Plants and Space Limitation Determine Intraspecific Trait Variability in Semi-Arid Shrublands." *Journal of Ecology* 103, no. 6: 1647–1657. https://doi.org/10.1111/1365-2745.12480.

Le Bagousse-Pinguet, Y., F. De Bello, M. Vandewalle, J. Leps, and M. T. Sykes. 2014. "Species Richness of Limestone Grasslands Increases With Trait Overlap: Evidence From Within- and Between-Species Functional Diversity Partitioning." *Journal of Ecology* 102, no. 2: 466–474. https://doi.org/10.1111/1365-2745.12201.

Le Bagousse-Pinguet, Y., N. Gross, F. T. Maestre, et al. 2017. "Testing the Environmental Filtering Concept in Global Drylands." *Journal of Ecology* 105, no. 4: 1058–1069. https://doi.org/10.1111/1365-2745.12735.

Lees, A. C., L. Haskell, T. Allinson, et al. 2022. "State of the World's Birds." *Annual Review of Environment and Resources* 47, no. 1: 231–260. https://doi.org/10.1146/annurev-environ-112420-014642.

Legendre, P. 1993. "Spatial Autocorrelation: Trouble or New Paradigm?" *Ecology* 74, no. 6: 1659–1673. https://doi.org/10.2307/1939924.

Lemoine, N., H.-G. Bauer, M. Peintinger, and K. Böhning-Gaese. 2007. "Effects of Climate and Land-Use Change on Species Abundance in a Central European Bird Community." *Conservation Biology* 21, no. 2: 495–503.

Lemoine, N., and K. Böhning-Gaese. 2003. "Potential Impact of Global Climate Change on Species Richness of Long-Distance Migrants." *Conservation Biology* 17, no. 2: 577–586. https://doi.org/10.1046/j.1523-1739.2003.01389.x.

Lemoine, N., H.-C. Schaefer, and K. Böhning-Gaese. 2007. "Species Richness of Migratory Birds Is Influenced by Global Climate Change." *Global Ecology and Biogeography* 16, no. 1: 55–64. https://doi.org/10.1111/j.1466-8238.2006.00252.x.

Loss, S. R., M. O. Ruiz, and J. D. Brawn. 2009. "Relationships Between Avian Diversity, Neighborhood Age, Income, and Environmental Characteristics of an Urban Landscape." *Biological Conservation* 142, no. 11: 2578–2585. https://doi.org/10.1016/j.biocon.2009.06.004.

Macarthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *American Naturalist* 101, no. 921: 377–385.

MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Princeton University Press.

Machac, A., M. Janda, R. R. Dunn, and N. J. Sanders. 2011. "Elevational Gradients in Phylogenetic Structure of Ant Communities Reveal the Interplay of Biotic and Abiotic Constraints on Diversity." *Ecography* 34, no. 3: 364–371. https://doi.org/10.1111/j.1600-0587.2010.06629.x.

Maestre, F. T., Y. Le Bagousse-Pinguet, M. Delgado-Baquerizo, et al. 2022. "Grazing and Ecosystem Service Delivery in Global Drylands." *Science* 378, no. 6622: 915–920. https://doi.org/10.1126/science.abq4062.

McCain, C. M. 2007. "Could Temperature and Water Availability Drive Elevational Species Richness Patterns? A Global Case Study for Bats." *Global Ecology and Biogeography* 16, no. 1: 1–13. https://doi.org/10.1111/j.1466-8238.2006.00263.x.

McCain, C. M. 2009. "Global Analysis of Bird Elevational Diversity." *Global Ecology and Biogeography* 18, no. 3: 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x.

McCain, C. M., and J.-A. Grytnes. 2010. "Elevational Gradients in Species Richness." In *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0022548.

Menard, S. 2002. *Applied Logistic Regression Analysis*. SAGE Publications, Inc. https://doi.org/10.4135/9781412983433.

Mönkkönen, M., and J. T. Forsman. 2002. "Heterospecific Attraction Among Forest Birds: A Review." *Ornithological Science* 1, no. 1: 41–51. https://doi.org/10.2326/osj.1.41.

Mönkkönen, M., and P. Helle. 1989. "Migratory Habits of Birds Breeding in Different Stages of Forest Succession: A Comparison Between the Palaearctic and the Nearctic." *Annales Zoologici Fennici* 26, no. 3: 323–330.

Mönkkönen, M., P. Helle, G. J. Niemi, and K. Montgomery. 1997. "Heterospecific Attraction Affects Community Structure and Migrant Abundances in Northern Breeding Bird Communities." *Canadian Journal of Zoology* 75, no. 12: 2077–2083. https://doi.org/10.1139/z97-842.

Morelli, F., Y. Benedetti, J. D. Ibáñez-Álamo, et al. 2021. "Effects of Urbanization on Taxonomic, Functional and Phylogenetic Avian Diversity in Europe." *Science of the Total Environment* 795: 148874. https://doi.org/10.1016/j.scitotenv.2021.148874.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403, no. 6772: 853–858. https://doi.org/10.1038/35002501.

Nagelkerke, N. J. D. 1991. "A Note on a General Definition of the Coefficient of Determination." *Biometrika* 78, no. 3: 691–692. https://doi.org/10.1093/biomet/78.3.691.

Newbold, T., L. N. Hudson, S. L. L. Hill, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520, no. 7545: 45–50. https://doi.org/10.1038/nature14324.

Newton, I. 2004. "Population Limitation in Migrants." *Ibis* 146, no. 2: 197–226. https://doi.org/10.1111/j.1474-919X.2004.00293.x.

Newton, I. 2008. *The Migration Ecology of Birds*. Elsevier Academic Press.

Oliver, T., and M. Morecroft. 2014. "Interactions Between Climate Change and Land Use Change on Biodiversity: Attribution Problems, Risks, and Opportunities." *WIREs Climate Change* 5: 317–335. https://doi.org/10.1002/wcc.271.

Ozenda, P. 1981. *Végétation des Alpes sud-occidentales: Notice détaillée des feuilles 60 Gap, 61 Larche, 67 Digne, 68 Nice, 75 Antibes*. Centre National de la Recherche Scientifique.

Pearce-Higgins, J. W., S. M. Eglington, B. Martay, and D. E. Chamberlain. 2015. "Drivers of Climate Change Impacts on Bird Communities." *Journal of Animal Ecology* 84, no. 4: 943–954. https://doi.org/10.1111/1365-2656.12364.

Pecher, C., E. Tasser, and U. Tappeiner. 2011. "Definition of the Potential Treeline in the European Alps and Its Benefit for Sustainability Monitoring." *Ecological Indicators* 11, no. 2: 438–447. https://doi.org/10.1016/j.ecolind.2010.06.015.

Peñuelas, J., B. Poulter, J. Sardans, et al. 2013. "Human-Induced Nitrogen-Phosphorus Imbalances Alter Natural and Managed Ecosystems Across the Globe." *Nature Communications* 4: 2934. https://doi.org/10.1038/ncomms3934.

Pianka, E. R. 1974. "Niche Overlap and Diffuse Competition." *Proceedings of the National Academy of Sciences* 71, no. 5: 2141–2145. https://doi.org/10.1073/pnas.71.5.2141.

Pigot, A. L., and J. A. Tobias. 2013. "Species Interactions Constrain Geographic Range Expansion Over Evolutionary Time." *Ecology Letters* 16, no. 3: 330–338. https://doi.org/10.1111/ele.12043.

Pimm, S. L., C. N. Jenkins, R. Abell, et al. 2014. "The Biodiversity of Species and Their Rates of Extinction, Distribution, and Protection." *Science* 344, no. 6187: 1246752. https://doi.org/10.1126/science.1246752.

Ponti, R., A. Arcones, X. Ferrer, and D. R. Vieites. 2020. "Seasonal Climatic Niches Diverge in Migratory Birds." *Ibis* 162, no. 2: 318–330. https://doi.org/10.1111/ibi.12784.

Pörtner, H.-O., R. J. Scholes, J. Agard, et al. 2021. "IPBES-IPCC co-Sponsored Workshop Report on Biodiversity and Climate Change (Version 2)." *Zenodo*. https://doi.org/10.5281/ZENODO.4782538.

Powers, R. P., and W. Jetz. 2019. "Global Habitat Loss and Extinction Risk of Terrestrial Vertebrates Under Future Land-Use-Change Scenarios." *Nature Climate Change* 9, no. 4: 323–329. https://doi.org/10.1038/s41558-019-0406-z.

Rangel, T. F. L. V. B., J. A. Felizola Diniz-Filho, and L. M. Bini. 2006. "Towards an Integrated Computational Tool for Spatial Analysis in Macroecology and Biogeography." *Global Ecology and Biogeography* 15, no. 4: 321–327. https://doi.org/10.1111/j.1466-822x.2006.00237.x.

Ratikainen, I. I., J. A. Gill, T. G. Gunnarsson, W. J. Sutherland, and H. Kokko. 2008. "When Density Dependence Is Not Instantaneous: Theoretical Developments and Management Implications." *Ecology Letters* 11, no. 2: 184–198. https://doi.org/10.1111/j.1461-0248.2007.01122.x.

Rigal, S., V. Dakos, H. Alonso, et al. 2023. "Farmland Practices Are Driving Bird Population Decline Across Europe." *Proceedings of the National Academy of Sciences of the United States of America* 120, no. 21: e2216573120. https://doi.org/10.1073/pnas.2216573120.

Rillig, M. C., M. Ryo, A. Lehmann, et al. 2019. "The Role of Multiple Global Change Factors in Driving Soil Functions and Microbial Biodiversity." *Science* 366, no. 6467: 886–890. https://doi.org/10.1126/science.aay2832.

Riva, F., and L. Fahrig. 2023. "Landscape-Scale Habitat Fragmentation Is Positively Related to Biodiversity, Despite Patch-Scale Ecosystem Decay." *Ecology Letters* 26, no. 2: 268–277. https://doi.org/10.1111/ele.14145.

Rohde, K. 1992. "Latitudinal Gradients in Species Diversity: The Search for the Primary Cause." *Oikos* 65, no. 3: 514–527. https://doi.org/10.2307/3545569.

Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller. 2015. "Protected Areas and Global Conservation of Migratory Birds." *Science* 350, no. 6265: 1255–1258. https://doi.org/10.1126/science.aac9180.

Sherry, T. W., and R. T. Holmes. 1996. "Winter Habitat Quality, Population Limitation, and Conservation of Neotropical-Nearctic Migrant Birds." *Ecology* 77, no. 1: 36–48. https://doi.org/10.2307/2265652.

Siefert, A., C. Violle, L. Chalmandrier, et al. 2015. "A Global Meta-Analysis of the Relative Extent of Intraspecific Trait Variation in Plant Communities." *Ecology Letters* 18, no. 12: 1406–1419. https://doi.org/10.1111/ele.12508.

Somveille, M. 2016. "The Global Ecology of Bird Migration: Patterns and Processes." *Frontiers of Biogeography* 8, no. 3: e32694. https://doi.org/10.21425/F58332694.

Somveille, M., A. Rodrigues, and A. Manica. 2015. "Why Do Birds Migrate? A Macroecological Perspective." *Global Ecology and Biogeography* 24: 664–674. https://doi.org/10.1111/geb.12298.

Sreekar, R., X. Si, K. Sam, et al. 2021. “Land Use and Elevation Interact to Shape Bird Functional and Phylogenetic Diversity and Structure: Implications for Designing Optimal Agriculture Landscapes.” *Journal of Applied Ecology* 58, no. 8: 1738–1748. https://doi.org/10.1111/1365-2664.13927.

Stevens, G. C. 1992. “The Elevational Gradient in Altitudinal Range: An Extension of Rapoport's Latitudinal Rule to Altitude.” *American Naturalist* 140, no. 6: 893–911. https://doi.org/10.1086/285447.

Stocker, T., and D. Qin. 2013. *Climate Change 2013: The Physical Science Basis: Summary for Policymakers, a Report of Working Group I of the IPCC: Technical Summary, A Report Accepted by Working Group I of the IPCC But Not Approved in Detail: And Frequently Asked Questions: Part of the Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. WMO, UNEP.

Titeux, N., K. Henle, J.-B. Mihoub, et al. 2017. “Global Scenarios for Biodiversity Need to Better Integrate Climate and Land Use Change.” *Diversity and Distributions* 23, no. 11: 1231–1234. https://doi.org/10.1111/ddi.12624.

Troia, M. J., and R. A. McManamay. 2016. “Filling in the GAPS: Evaluating Completeness and Coverage of Open-Access Biodiversity Databases in the United States.” *Ecology and Evolution* 6, no. 14: 4654–4669. https://doi.org/10.1002/ece3.2225.

Troia, M. J., and R. A. McManamay. 2017. “Completeness and Coverage of Open-Access Freshwater Fish Distribution Data in the United States.” *Diversity and Distributions* 23, no. 12: 1482–1498. https://doi.org/10.1111/ddi.12637.

Underwood, E. C., J. H. Viers, K. R. Klausmeyer, R. L. Cox, and M. R. Shaw. 2009. “Threats and Biodiversity in the Mediterranean Biome.” *Diversity and Distributions* 15, no. 2: 188–197. https://doi.org/10.1111/j.1472-4642.2008.00518.x.

Vargas-Cárdenas, F., V. Arroyo-Rodríguez, J. C. Morante-Filho, J. E. Schondube, D. M. Auliz-Ortiz, and E. Ceccon. 2022. “Landscape Forest Loss Decreases Bird Diversity With Strong Negative Impacts on Forest Species in a Mountain Region.” *Perspectives in Ecology and Conservation* 20, no. 4: 386–393. https://doi.org/10.1016/j.pecon.2022.10.001.

Wang, X., Z. Yuan, A. Ali, et al. 2023. “Leaf Traits and Temperature Shape the Elevational Patterns of Phyllosphere Microbiome.” *Journal of Biogeography* 50, no. 12: 2135–2147. https://doi.org/10.1111/jbi.14719.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. “Phylogenies and Community Ecology.” *Annual Review of Ecology and Systematics* 33, no. 1: 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Wiens, J. J. 2011. “The Niche, Biogeography and Species Interactions.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, no. 1576: 2336–2350. https://doi.org/10.1098/rstb.2011.0059.

Zurell, D., C. H. Graham, L. Gallien, W. Thuiller, and N. E. Zimmermann. 2018. “Long-Distance Migratory Birds Threatened by Multiple Independent Risks From Global Change.” *Nature Climate Change* 8, no. 11: 992–996. https://doi.org/10.1038/s41558-018-0312-9.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Descriptive table of the 225 bird species breeding in the PACA region considered in the study, with their specific breeding period, indicated by the start and end of breeding date (DD/MM; NA for the three marine species considered; see section 2.2.1 Materials and Methods). The three next columns indicate whether the species is considered as strictly marine, has been introduced and is now significantly breeding into the PACA region or is considered as highly common (see section 2.2.2 Materials and Methods). The classification as long-distance migrant vs. sedentary (including short-distance migrant) is indicated in the column ‘Primary Migration Strategy’. The last column indicates whether the species crosses the Sahara during its migration. **Table S2:** Variations of environmental variables (mean ± SD [5% CI; 95% CI]) considered in our analyses for $N_c = 1109$, in the PACA region and the three altitudinal belts considered. **Table S3:** Variations of response variables (mean ± SD [5% CI; 95% CI]) considered in our analyses for $N_c = 1109$ in the PACA region and the three altitudinal belts considered. **Table S4:** Results of the spatial auto regressive (SAR) model exploring the variations in the number of migratory species in response to altitude (three altitudinal belts: Hilly, Mountain, Subalpine) and to the interactions between altitude and habitat diversity, habitat evenness, forest cover and species richness. Significant effects are shown in bold. **Table S5:** Results of the spatial auto regressive (SAR) model exploring the variations in the number of sedentary species in response to altitude (three altitudinal belts: Hilly, Mountain, Subalpine) and to the interactions between altitude and habitat diversity, habitat evenness, forest cover and species richness. Significant effects are shown in bold. **Figure S1:** (a) Map of the studied region: PACA, alongside the spatial distribution of environmental and anthropogenic variables. (b) Altitude (in meters). (c) Mean annual temperatures (in °C). (d) Human impact, i.e., median value of human-induced alteration on habitats from a cumulative measure of human modification of land around. (e) Cumulative annual precipitation (in mm). **Figure S2:** Map of the study area (PACA) showing the spatial grid (5 × 5 km cells) used for analyses. Each cell is coloured according to its sampling completeness score (sample coverage estimate, Chao and Jost 2012), reflecting the quality and thoroughness of available observation data. **Figure S3:** Frequency histograms of the 22 most common species in the PACA region and their spatial distribution. F_{140} represents, for each 5 × 5 km cell, the number of times that the given species was recorded among the 140 spatio-phenological statistical units. **Figure S4:** Spatial distribution and analysis of long-distance and sedentary species: Histogram illustrating the distribution of long-distance species (a) and sedentary species (d) across all avian communities in the dataset. Boxplots depicting the variation of long-distance species (b) and sedentary species (e) across different altitudinal belts (hilly, mountain, subalpine). Map showing the spatial distribution of the long-distance species (c) and sedentary species (f) across avian communities in the study region. The colour scale represents different values of the species richness (from blue to red), with each 5 km square corresponding to an avian community. **Figure S5:** Environmental variables collinearity evaluation: variance inflation factor values (a) of each of the 10 environmental variables considered in our study and, (b) of each 5 environmental variables selected in our study, and (c) Pearson correlation values for all pairs among the 10 environmental variables. **Figure S6:** Variation in the Moran index as a function of spatial distance (in meters), before (a) and after (b) correction for spatial autocorrelation using the spatial auto regressive model (SAR). Each point represents the Moran index calculated for a given distance class. The dotted lines delimit a zone of variation expected in the absence of spatial structure, for a 95% confidence interval. Before correction (a), there is positive spatial autocorrelation at short distances, which disappears after correction (b), indicating that the SAR model has effectively taken account of the spatial structure of the data.