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Research Article

Spatial distribution of acoustic traits in bird assemblages along regional bioclimatic gradients

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Environmental variation shapes acoustic interactions among birds, creating spatial structures in the sonic signature of local species assemblages. Exploring these patterns at regional scales can reveal processes that segregate acoustic strategies along environmental gradients. Here, we examined how the acoustic trait composition of bird assemblages varies at a regional extent in relation to landscape resolution environmental variation. We used data on 2427 bird assemblages and 15 acoustic traits, quantifying the frequency, complexity, rhythm, and duration of vocalisations for 117 species. We used multivariate ordinations to investigate the distribution of species' acoustic traits along climatic and landscape gradients while accounting for spatial and phylogenetic dependencies. We then assessed whether these relationships resulted in directional shifts in the acoustic trait composition of bird assemblages for three key acoustic traits. Our results show that acoustic traits were phylogenetically and spatially clustered and correlated with regional climatic conditions (e.g. lower complexity and isochronous rhythms under higher precipitation and temperature seasonality). Conversely, we found mixed support for the hypothesis that the acoustic signature of species assemblages is shaped by habitat composition within landscapes. For instance, we found urbanisation to be associated with vocalisations featuring broader spectral

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bandwidths, likely facilitating their propagation under noise pollution, but also greater complexity, which may hinder transmission in urban landscapes. These regional patterns may reflect differences in the structure of acoustic networks within and among species assemblages. Our results thus form a first step towards a regional-level assessment of the environmental and anthropogenic factors that structure or disrupt acoustic connectivity in landscapes.

Keywords: acoustic traits, bird communities, common European birds, land use, song frequency and rhythm, urbanisation

Introduction

Species assemblages are distributed along regional environmental gradients by biogeographic history, topoclimatic variation, and the availability of habitats and resources (Massol et al. 2011, Cadotte et al. 2015). Previous research has examined how these patterns emerge from species' functional traits and how these traits shape local and regional assemblages (Ackerly and Cornwell 2007, Xu et al. 2017, Mittelbach and McGill 2019). In contrast, social traits that mediate communication among individuals have received comparatively less attention in this context. For instance, the role of acoustic communication in structuring assemblages of soniferous species has been well documented from proximal and evolutionary processes (Brumm 2009, Garcia et al. 2020), as well as the impact of environmental variation on evolutionary adaptations that favour signal propagation (Boncoraglio and Saino 2007). Nevertheless, how these processes are organised *regionally* along the broad environmental gradients that induce turnover in the composition of species assemblages deserves further characterisation (Morrison et al. 2021).

Across a range of taxa, including birds and insects, vocalisations are used at various stages of the life cycle for territorial defence, mating, and other social interactions (Penar et al. 2020, Erbe and Thomas 2022). The propagation of acoustic signals exchanged between conspecific or heterospecific individuals is affected by several factors including attenuation (e.g. atmospheric absorption, wind), reverberation (e.g. ground topology, tree density), and masking (e.g. ambient noise levels) – all of which vary across different habitat types, times of day, and seasons (Richards and Wiley 1980, Brumm and Naguib 2009, Hauptert et al. 2023). Habitat structure and composition integrate many of these factors and can therefore be considered to directly influence acoustic communication (Azar and Bell 2016, Rossetto and Laiolo 2024). For instance, dense vegetation attenuates high-frequency sounds and rapid tempos, making vocalisations with lower frequencies, narrower bandwidths, and slower tempos more suited for communication in forests compared to grasslands (Boncoraglio and Saino 2007, Darras et al. 2016). Vocalisations can be characterised through their spectro-temporal modulations; key features such as frequency (pitch), amplitude (loudness), complexity, and rhythmic structure carry biologically relevant information (Hopp et al. 2012) and are differentially impacted by environmental factors. We refer to these features as *acoustic traits*, a class of functional traits that influence species' roles and interactions within ecosystems (Violle et al. 2007, Volaire et al. 2020, Rossetto et al. 2025).

The properties of sound propagation in the environment thus impose evolutionary pressures on the communication strategies of soniferous species, altering both the spectral and temporal characteristics of vocal signals (Boncoraglio and Saino 2007). Accordingly, environmental variation is expected to filter acoustic traits in a similar way to other functional traits (McGill et al. 2006, Violle et al. 2007). Under this hypothesis, spatial patterns in the composition and diversity of a soniferous species assemblage are predicted to reflect the acoustic strategies that co-occurring species employ in response to habitat-specific acoustic constraints. However, at broad spatial scales, acoustic traits may also be spatially structured by processes other than environmental adaptation. In particular, bioclimatic and historical processes shaping regional species pools can produce non-random distributions of acoustic traits across local assemblages. This is expected if acoustic traits covary with other functional traits that are structured by climate, topography, and habitat, such as morphology or diet, or if they are imprinted by strong phylogenetic inertia (e.g. morphological constraint hypothesis; Bennet-Clark 1998, Friedman et al. 2019, Hay et al. 2024). Such indirect processes may obscure the direct effects of adaptations to the acoustic environment as environmental turnover and spatial scale increase. Climate may further influence assemblage-level acoustic patterns by structuring species pools, altering habitat structure, or covarying with morphological traits that constrain vocal performance. In regions where climate-driven species turnover is limited, however, such influences likely manifest as shifts in assemblage structure and acoustic trait distributions within a largely stable species pool, rather than reflecting climate-driven species replacement. Beyond clarifying the joint roles of regional and local processes in shaping acoustic traits (Ricklefs 1987), examining these patterns is essential for understanding how soniferous species respond to sensory pollution, such as artificial light and anthropogenic noise, and how these pressures may alter the regional dynamics of animal diversity under human land use (Luther et al. 2016, Derryberry et al. 2020).

Consistent with the role of environmental filtering on communication strategies, the acoustic traits of co-occurring species within a habitat influence how effectively their vocalisations propagate, leading to convergent or divergent trait patterns within assemblages (Goutte et al. 2018). The degree to which acoustic traits cluster or disperse locally may reflect the saturation of available acoustic space and the local diversity of acoustic niches (Pigot et al. 2016, Pellissier et al. 2018, Oliveira et al. 2025). Consequently, habitats often exhibit characteristic acoustic signatures that emerge from the composition of soniferous species and their

associated trait suites (Grinfeder et al. 2022a, Farina et al. 2024). Landscape modification, including changes in habitat structure, configuration, or regional topoclimatic gradients, can shift the acoustic composition of assemblages by altering these filtering mechanisms. Recent evidence suggests that habitat fragmentation, in particular, can promote acoustic divergence among bird assemblages (Han et al. 2025). At broader scales, increasing human land-use intensity tends to homogenise species assemblages due to declining habitat and resource availability (Devictor et al. 2008a). In urban environments, chronic traffic noise can further constrain vocal communication essential for territory defence and mating, thereby limiting species' ability to persist (Luther et al. 2016, Derryberry et al. 2020). Depending on their acoustic traits, species thriving in urban contexts may or may not cope with this sensory pollution, leading to acoustic homogenisation along the land-use intensity gradient (Morrison et al. 2021).

Methodologically, assessing acoustic diversity at regional scales requires extensive acoustic datasets and is constrained by the considerable logistical challenges of conducting regional-scale field surveys (Gibb et al. 2019). An alternative approach involves exploring how acoustic traits are distributed among species assemblages using methodologies from functional ecology (Gasc et al. 2013, Chakravarty et al. 2021). For instance, macroevolutionary research has examined the phylogenetic conservatism and spatial distribution of song frequencies in regional or global species assemblages (Pearse et al. 2018, Mikula et al. 2021). This approach entails defining a set of acoustic traits that can be consistently measured across a wide range of species' vocalisations, and which are relevant indicators of environmental filtering processes. Understanding the distribution of these traits across landscapes therefore offers a valuable framework for linking bioacoustics with functional ecology.

In this study, we integrate theoretical frameworks from bioacoustics and functional biogeography to investigate the distribution of acoustic traits in bird assemblages at a landscape scale across a regional extent. To achieve this, we paired a comprehensive dataset of bird counts with data on species-specific acoustic traits extracted from reference field recordings. We hypothesised that acoustic traits are spatially distributed among species assemblages by a combination of regional species sorting along environmental gradients, phylogenetic conservatism in communication strategies, and local filtering consistent with the acoustic properties of the environments species occupy. Specifically, we predicted that the acoustic trait composition of species assemblages is explained by: 1) regional bioclimatic gradients structuring species distributions, 2) acoustic niche conservatism, and 3) species turnover along landscape composition and heterogeneity gradients.

Material and methods

Overview

The composition of 2427 bird assemblages was derived from a long-term breeding season survey of bird counts covering

continental France. Acoustic traits for each species were then extracted from field recordings and used as a reference for species' songs and/or calls (Roché 1993). We selected 11 acoustic traits to describe species vocalisation frequency, complexity, rhythm, and duration (Table 1), and matched them with a published phylogeny to account for species relatedness (Thuiller et al. 2011). Finally, data on spatial variation in environmental and climatic factors were sourced from public repositories. These included 15 environmental variables describing the land cover, topography, and climate, with their potential associations with bird distributions and vocal signal transmission outlined in Table 2. From these data, we examined regional patterns of acoustic trait distributions along environmental gradients at both the species and assemblage levels (Supporting information) using an ordination approach (ESLTP) and regressions on community weighted means (CWM). While the ESLTP analysis identifies how species-level acoustic traits are associated with environmental gradients through their abundance-weighted distributions (Pavoine et al. 2011), CWMs summarise how these traits are expressed at the assemblage level through shifts in species dominance.

Bird assemblages

The composition of avian assemblages in France from 2006 to 2021 was inferred from the French Breeding Bird Survey (Suivi Temporel des Oiseaux Communs, STOC EPS; Jiguet et al. 2012). This standardised long-term survey of the spatio-temporal dynamics of breeding songbirds is conducted by volunteer ornithologists yearly. Counts of each species heard or seen are made in 4 km² plots randomly selected in continental France during the breeding season (from March to June; for further details on the protocol see Jiguet et al. 2012). Climate-driven constraints on species distributions in the STOC EPS have limited impacts on our dataset, being largely limited to the separation between the medio-European region and the Mediterranean biome at the southern edge of the study region, mountain ranges, and the northernmost and northeasternmost areas.

A mean of 848.8 plots (± 127.1 , uncertainty stated in SD units for descriptive statistics) was monitored each year during, on average, 8.7 years (± 4.4) per plot. We averaged species counts across the 15 years for each plot to study spatial patterns of assemblage composition without focusing on the effects of temporal fluctuations, capping counts above ten to buffer the effect of gregariousness and coloniality. At 4 km² resolution, direct acoustic responses to habitat are averaged out, but this scale allows us to capture broader regional variation in acoustic trait composition stemming from the imprint of landscape composition and configuration on avian assemblages. Averaging bird data across 15 years also provides a more stable estimate of species' typical presence and abundance, smoothing over short-term fluctuations; capping maximum abundance at 10 reduces the disproportionate influence of highly dominant species on community-weighted trait calculations. However, both decisions may also dampen signals of recent ecological change or the impact of locally abundant species (details available in the Supporting information).

Table 1. Acoustic features included in the analyses. Each feature quantifies an aspect of the core acoustic traits – frequency modulation, vocalisation complexity, rhythmicity, and time duration. For each feature, we provide a short definition and justification (relevance) for its inclusion in the analyses, as well as references. Further details, such as value ranges and software implementations, are provided in the Supporting information.

Trait	Feature	Definition	Relevance	References
Frequency	Spectral bandwidth (of the power spectrum)	Bandwidth of the power spectrum	Large bandwidth sounds are attractive to potential mates but energetically costly. In dense environments and in the presence of noise (natural or urban), smaller bandwidths are more optimal	Vallet and Kreutzer 1995, Drăgănoiu et al. 2002, Luther et al. 2016
Frequency	Peak frequency	Pitch of the loudest note	High frequencies do not carry well through dense environments but are less masked by low frequency noise (traffic/rivers/wind)	Morton 1975, Boncoraglio and Saino 2007, Pearse et al. 2018; but see Wiley 1991 on frequency and bird body size
Complexity	Temporal entropy (Ht)	Energy dispersion in the audiogram	Complexity evolved to differentiate from other species in the same area and to optimise transmission in the local vegetation types. Transmission of complex sounds can be hampered by thick vegetation or urban noise	Sueur et al. 2008, Montague et al. 2013, McLaughlin and Kunc 2013, Pearse et al. 2018
Complexity	Spectral entropy (Hf)	Energy dispersion in the power spectrum	Same as above, but focuses on the frequency domain	Tchernichovski et al. 2000, Sueur 2018
Complexity	Num(ber of) frequency peaks	Number of prominent peaks in frequency	Higher values have higher energy expenditure and transmit best in open habitats with no noise	Gasc et al. 2013
Rhythm	Ugof (universal goodness of fit)	Isochronicity of a sequence	Trait socially inherited in oscines and under selection. Not yet studied at the community level	Burchardt et al. 2021
Rhythm	Tempo (or number of syllables per time unit)	Tempo	Faster tempos are more costly. Slower tempos are typical of forest species. Faster tempos have been observed under urban noise	Richards and Wiley 1980, Briefer et al. 2008, Nemeth and Brumm 2009
Rhythm	nPVI (pairwise variability index on inter-offset intervals)	Temporal regularity of a sequence	Trait socially inherited in oscines and under selection. Not yet studied at the community level	Grabe and Low 2002, Ravnani and Norton 2017, Ravnani et al. 2017
Time	Duration	Total length	Longer vocalisations have higher energy costs and contain more information than shorter vocalisations. Longer songs are best transmitted in open habitats	Van Dongen and Mulder 2006, Briefer et al. 2008, Geberzahn and Aubin 2014a
Time	IOI (inter-offset interval) duration	Median inter-offset interval length	There is often a trade-off between syllable and IOI duration because it is very costly to produce long notes with short gaps in between	Ravnani and de Reus 2019
Time	Syllable duration	Median syllable length	Same as for total vocalisation duration	Podos 2001, Briefer et al. 2008, Geberzahn and Aubin 2014b

We only included bird orders captured by the STOC protocol (Supporting information; Bucerotiformes, Caprimulgiformes, Columbiformes, Coraciiformes, Cuculiformes, Passeriformes, and Piciformes). The final dataset included 117 species (Supporting information) and 2427 plots, each representing an assemblage of soniferous birds. We further collated information about each species' habitat preference (open, semi-open, or closed) from Tobias et al. (2022).

Acoustic traits

We selected 11 acoustic traits to capture interspecific variations in the frequency and temporal domains of bird vocalisations,

including rhythmicity and vocalisation complexity (Supporting information). In non-oscines, calls may serve the same functions as songs in oscines, whereas in oscines, calls and songs often have distinct functions (Supporting information). We thus measured acoustic traits on songs for most oscine passerines, and included calls for some oscines (e.g. Corvidae) and non-oscines (e.g. Piciformes) when they represent the most frequent and species-informative vocalisations in these groups.

Vocalisations for each of the 117 species were obtained from recordings published in field audio guides used as a reference by European ornithologists (Roché 1993, Supporting information). We preferred this source over recordings from

Table 2. Environmental layers included in the analyses. We describe their type, relevance for sound transmission, and potential effects on bird counts. Further details, including value ranges, are provided in the Supporting information.

Type	Description	Relevance for acoustic transmission	Relevance for bird counts
Landcover	Imperviousness (cover of soil sealing)	Imperviousness is highly correlated with human presence and thus with urban noise	Fragmentation and habitat degradation impact species abundance
Landcover	Imperviousness in the 9 neighbouring cells	Same as above, but effect from neighbouring areas	Same as above but effect from neighbouring areas
Landcover	Tree cover density	Trees interfere with sound propagation (e.g. high reverberation and fast attenuation)	Major habitat for many species
Landcover	(Cover of) broad-leaf forest	Higher sound absorption in broad-leaved forests than in coniferous forests	Different species compositions in coniferous forests versus broad-leaf forests
Landcover	(Cover of) coniferous forest	Same as above but differently distributed	Same as above but differently distributed
Landcover	(Cover of) grassland	Slow attenuation and small reverberation in grasslands (in the absence of wind)	Habitat type for many species
Landcover	(Cover of) crops	Similar to grasslands	Negative effect of agriculture on bird richness and abundance
Landcover	(Cover of) small woody features (i.e. herbaceous features such as hedgerows and shrubs)	Can act as windbreaks and noise barrier	Important habitats for many species
Landcover	Freshwater (cover)	Small attenuation over freshwater, but currents in steep rivers produce low-frequency noise	Riparian species abundances depend on freshwater availability and size
Landcover	Freshwater cover in the nine neighbouring cells	Same as above but effect from neighbouring areas	Same as above but effect from neighbouring areas
Topology	(Mean) elevation	Sound moves more slowly at high elevations	Species are constrained to their elevation limits
Climate	(Annual) temperature mean	Sound travels faster at higher temperatures	Species are constrained by their tolerances to climatic conditions
Climate	(Annual) temperature seasonality	Sound travels faster at higher temperatures	Same as above
Climate	Isothermality (oscillation in day-to-night temperature relative to summer-winter)	Sound travels faster at higher temperatures	Same as above
Climate	Annual precipitation	Heavy rain produces low-frequency noise	Same as above

citizen science repositories because recording quality and processing are more standardised across species, allowing for comparisons between species (similar to pattern traits defined in [Volaire et al. 2020](#)). Audio guides were designed for species-level identification and thus included only one representative track per species, selected by an expert to minimise reliance on unusual vocalisations. Each track consisted of recordings from an unknown number of individuals (often just one). This impairs our ability to assess intraspecific variability, which can be high in certain species ([Borror 1961](#), [Briefer et al. 2011](#)) and may influence assemblage-level compositional indicators ([Fu et al. 2020](#), [Brandl et al. 2023](#)). Nevertheless, we had strong a priori expectations regarding the key role of the acoustic traits retained in our analyses in facilitating conspecific recognition during critical life stages, such as mating (see [Table 1](#) for a description and rationale for the inclusion of each acoustic trait, and the Supporting information for a summary of existing research linking these traits to fitness components). It is therefore reasonable to assume that these traits are sufficiently stable within species and show a high degree of conservatism within genera to ensure that

our results remain robust despite any unmeasured intraspecific variation.

Start and end times of each vocalisation within a track were labelled using Audacity ([Audacity-Team 2024](#)). Vocalisations within each track were extracted for separate analysis (8.3 ± 6.9 vocalisations per track). A combination of time and frequency domain analyses were carried out (Python ver. 3.11.4; package ‘scikit-maad’ ver. 1.4.0; [Ulloa et al. 2021](#)). Temporal features were computed directly on the time series. Spectral features were computed from a spectrogram (created by applying a short-time Fourier transform, STFT with a window size of 1024 and an overlap of 870 windows). Rhythmic patterns were identified by integrating information derived from both time and frequency domain analyses (package ‘thebear’ ver. 1; [Werff et al. 2024](#)). To remove background noise, the frequencies below the minimum and above the maximum possible range on each species’ frequency bandwidth, as assessed by experts, were filtered out (Supporting information). To distinguish syllables from gaps of silence with low energy, we segmented each vocalisation into regions of interest (ROI) (length of 0.05 s and energy level threshold of 1×10^{-6} in the

rois module in ‘scikit-maad’; technical details are available at Ulloa et al. 2021). From this segmentation, we extracted the 11 acoustic traits and averaged them to obtain a single value per trait and per species (Table 1, Supporting information). We did not quantify amplitude because the recordings were not calibrated.

To assess within-track variability in vocalisations, we calculated four additional traits: the coefficient of quartile variation for the peak frequency, number of frequency peaks, normalised pairwise variability index (nPVI), and syllable duration (to make a total of 15 acoustic traits). The only missing values were the duration of the songs of *Alauda arvensis* and *Locustella naevia*, two species that produce long songs that exceed some track lengths. These missing values were replaced with the maximum duration observed in the other species.

We quantified the phylogenetic signal in acoustic traits with Abouheif’s C_{mean} and Pagel’s λ (Münkemüller et al. 2012), based on the bird phylogeny by Thuiller et al. (2011) (Supporting information). For both indices, higher values indicate a stronger phylogenetic signal. In particular, Pagel’s λ values close to 1 indicate trait evolution consistent with a Brownian motion model along the phylogeny, whereas values closer to 0 indicate weaker phylogenetic structure.

Environmental conditions

To estimate environmental variation among the STOC EPS plots, we collated several environmental layers (Table 2) available from public archives (the European Space Agency, Fendrich et al. 2023, WorldClim, Fick and Hijmans 2017) (Supporting information) and matched each plot with the corresponding terrestrial ecoregion (Olson et al. 2001). We tested spatial autocorrelation in these data using Moran’s I test (Dormann et al. 2007, Dray and Dufour 2007).

Species-level trait–environment associations

Species-level correlations between acoustic traits and environmental gradients were explored through a five-table multivariate ordination (‘ESLTP analysis’, Pavoine et al. 2011; R package ‘adiv’ ver. 2.2.1; Pavoine 2020, 2024, www.r-project.org). The ESLTP method extends the RLQ analysis, a three-table ordination framework that links environmental variables (R), species composition (L), and species traits (Q) to examine how trait variation aligns with environmental gradients (Dray and Legendre 2008, Thioulouse et al. 2018). By additionally incorporating phylogenetic similarity among species and spatial proximity among plots, the ESLTP enables a more comprehensive analysis of acoustic trait variability in local assemblages inheriting from regional species assemblages structured by environmental gradients (Pavoine et al. 2011). The data sources included in the analysis are (L) a plot-by-species matrix with counts averaged over time; (T) a species-by-acoustic traits matrix; (P) a phylogenetic dissimilarity matrix; (E) a site-by-environment matrix; and (S) a spatial dissimilarity matrix. Each matrix only included quantitative values (additional details are available in the Supporting information). All environmental variables

exhibited spatial autocorrelation. We excluded the following environmental variables: imperviousness in the nine neighbouring cells, freshwater cover in the nine neighbouring cells, and elevation because of their high correlation (> 70%) with imperviousness, freshwater, and temperature mean, respectively. Moreover, we selected only the acoustic traits that were correlated with the retained environmental variables (as per the fourth-corner algorithm with a p-value < 0.05; Dray and Legendre 2008, Pavoine et al. 2011) and showed a phylogenetic signal. These were spectral bandwidth, spectral entropy, number of frequency peaks, and nPVI. All these steps followed the methodologies outlined by Pavoine et al. (2011) and Pavoine (2020).

Community-weighted mean analysis

To investigate variations in the average acoustic trait composition of the 2427 bird assemblages we computed the CWM for four acoustic traits retained in the ESLTP analysis: spectral bandwidth, spectral entropy, number of frequency peaks, and nPVI. The CWM is the value of a given trait averaged over all species occurring on a plot, weighted by their counts (Ali et al. 2017, Guerrero et al. 2024), and denotes which traits prevail in local assemblages under specific environmental conditions. The traits analysed with CWM served as proxies for three primary dimensions of the acoustic niche: frequency (spectral bandwidth), complexity (spectral entropy and number of frequency peaks), and rhythm (nPVI). The CWMs showed correlation strengths below a 70% threshold, except for spectral entropy, which was strongly correlated with spectral bandwidth (82%) and the number of frequency peaks (79%) (Supporting information). Consequently, we excluded spectral entropy from subsequent analyses.

CWMs are arithmetic means that do not differentiate between average variation between similar species or variation driven by extreme trait values. As a result, spurious relationships between CWMs and environmental gradients may arise when CWMs are disproportionately influenced by a few dominant species (Zelený 2018, Lepš and de Bello 2023). To mitigate this potential artefact, we analysed only acoustic traits (Table 1, Supporting information) and environmental variables (Table 2) with established ecological links to signal transmission and/or species assemblages. Additionally, we repeated all analyses using community means (CMs), calculated as the average trait value within each assemblage based solely on species presence, without weighting by abundance. Unlike CWMs, CMs are less influenced by dominant species. A large CWM–CM discrepancy indicates that a few dominant species shape community-level patterns. Conversely, congruence between CWMs and CMs suggests that acoustic trait distributions are relatively homogeneous across species within the same assemblages.

Community-weighted mean models

The CWMs were treated as a Gaussian process using linear regression with the environmental variables listed in Table 2 (R package ‘spaMM’ ver. 4.5.0; Rousset and Ferdy 2014, Rousset 2023). We scaled the predictors to permit

comparisons of parameter magnitudes. Quadratic and interaction terms were excluded from the model, as our primary focus was on the magnitude of the responses rather than on exploring complex interactions or non-linearities. After excluding collinear predictors with a variance inflation factor (VIF) above 2 (R package ‘usdm’ ver. 2.1.7; Naimi et al. 2014), our models included six environmental variables: the cover of imperviousness (representing soil sealing from urbanisation), tree density, coniferous forest, grassland, small woody features, and freshwater; and three climatic variables: temperature seasonality, isothermality, and annual precipitation. These environmental variables were spatially autocorrelated. To reduce bias and error in the parameter estimates under spatial autocorrelation in the residuals (tested with Moran’s I test), we added a Cauchy correlation matrix of site \times site spatial dissimilarity to our linear models (Dormann et al. 2007, Rousset and Ferdy 2014, Rousset 2023). We assessed fit with a pseudo- R^2 for spatial models (Magee 1990, Rousset 2023). We reported errors around parameter estimates with parametric 95% confidence intervals (CI). Additional details are available in the Supporting information.

Results

Relationships between acoustic traits, phylogeny, and environment

Based on the phylogeny of the 117 species, we found that most acoustic traits exhibited a phylogenetic signal (Supporting information). The residuals from our models displayed spatial autocorrelation (Supporting information). However, in the multivariate version of the fourth-corner analysis, only four acoustic traits were correlated with the 12 environmental variables: spectral bandwidth, spectral entropy, the number of frequency peaks, and nPVI. Hence, we retained only these acoustic traits, along with the environmental gradients, for the ESLTP analysis.

We retained the two first axes of the ESLTP, which explained 94 and 5% of the total inertia, respectively (third axis: 1%, not retained; Fig. 1, Supporting information). Values in axis 1 of the ESLTP were phylogenetically clustered (Fig. 2c). A more detailed representation of the axes values in the phylogeny, distinguishing between trait-based, phylogeny-based, and global coordinates, can be found in the

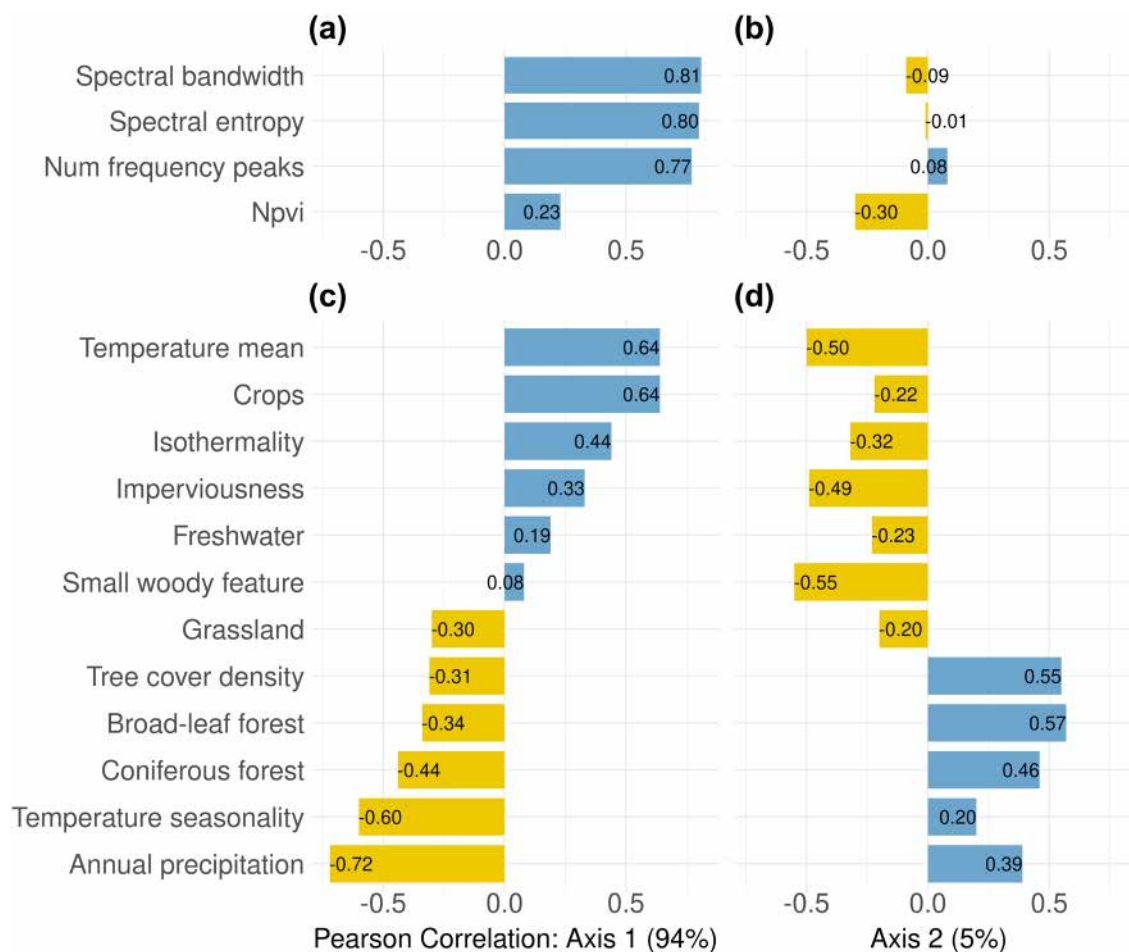


Figure 1. Pearson correlation coefficients of the axis 1 and axis 2 scores in the ESLTP ordination with acoustic traits (a)–(b) and environmental variables (c)–(d).

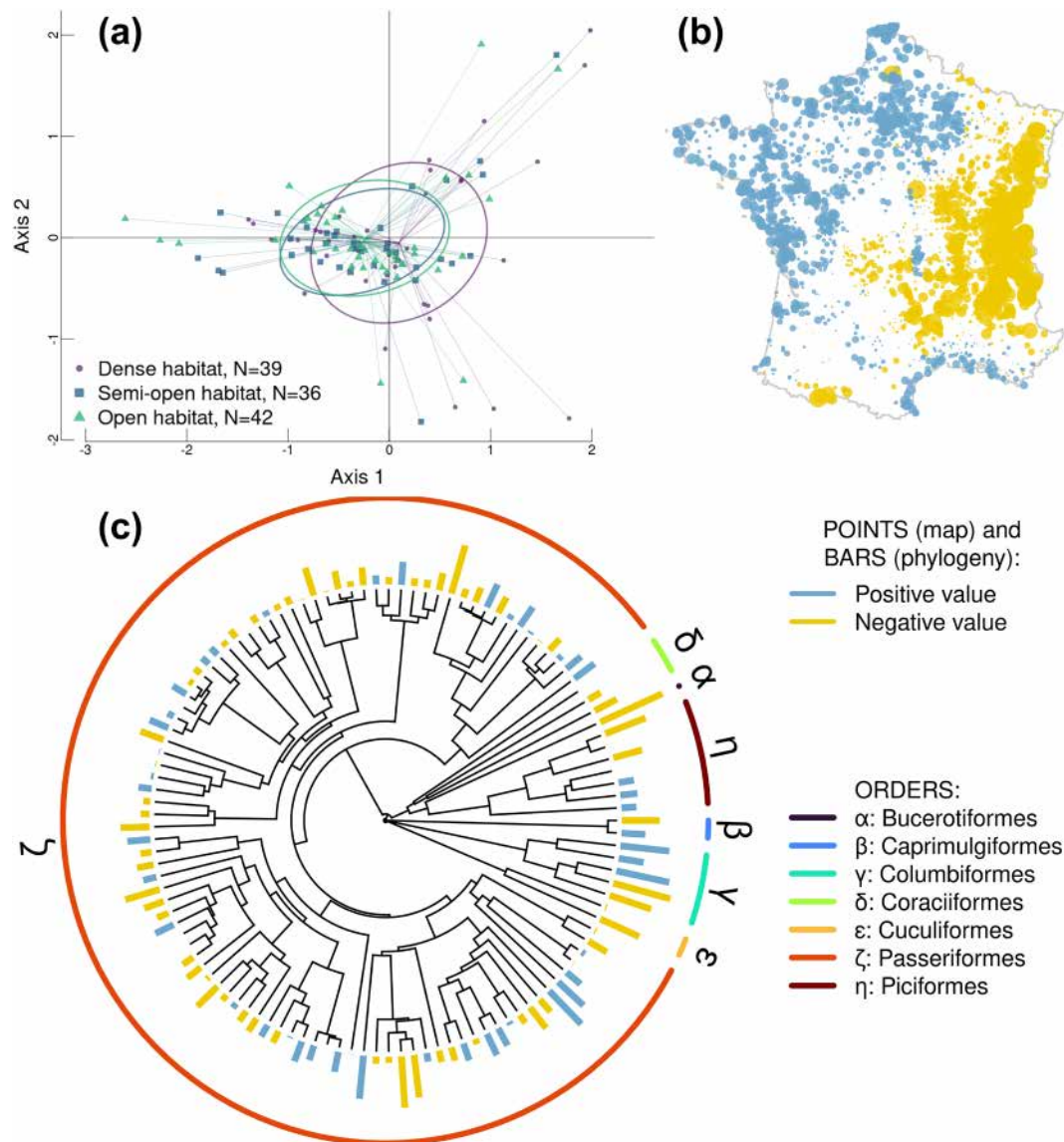


Figure 2. Results of the ESLTP. (a) Highlights the projection of species associated with open, semi-open, and closed habitats (showing both axis 1 and axis 2). In (b) we mapped the values of axis 1 (point sizes are scaled to their absolute values, the largest values capped at the 0.99 quantile and the lowest values to the 0.01 quantile) within the STOC EPS grid. (c) Displays the phylogeny alongside the axis 1 values for each species. In (b) and (c), positive values are coloured in blue, while negative values are in yellow. The outer circle around the phylogeny in (c) represents the taxonomic order of the species.

Supporting information. The spatial distribution of axes of the ESLTP within the STOC EPS grid (axis 1 in Fig. 2b) and axis 2 in the Supporting information) showed that similar values in each axis were clustered together in space. The positive side of the first ESLTP axis was associated with high values of spectral bandwidth, spectral entropy, number of frequency peaks, and nPVI (Fig. 1a). These characteristics defined the acoustic signature of bird species located in areas with low seasonality (e.g. the oceanic climate in the northwest of the country) or in regions with warmer temperatures (e.g. the Mediterranean climate in the southeast) (Fig. 1, 2b). For example, *Cettia cetti* is found both in the northwest and in the southeast of France and is characterised

by high values in all its acoustic traits, while *Phylloscopus trochilus* is typically found in the north and centre of France and is characterised by high spectral bandwidth and complexity. Conversely, species inhabiting forests with large seasonality and high precipitations (e.g. the mountainous regions of the Alps, the Cévennes, and the Pyrenees) exhibited on average lower values of spectral bandwidth, spectral entropy, number of frequency peaks, and nPVI (e.g. *Loxia curvirostra*; Fig. 1, 2b). Additional details on the distribution of different traits in the four quadrants of the ordination space can be found in the Supporting information.

To facilitate the interpretation of species positions within the ordination space, we categorised species into ecologically

relevant guilds. Figure 2a and the Supporting information illustrate species variations based on their preferred habitat types. Species favouring open and semi-open habitats had overlapping ellipses clustered toward negative values on axis 1. For instance, open-habitat species like *Corvus monedula* and semi-open-habitat species such as *Emberiza cirius* were characterised by low spectral bandwidth and moderate complexity. Species preferring dense habitats, while overlapping significantly with the other two guilds, often exhibited positive values on axis 1. For example, typical songs of *Garrulus glandarius* and *Sylvia borin* displayed higher spectral bandwidths, complexities, and non-isochronous rhythms.

Community-weighted means

The maps depicting the distribution of CWMs spectral bandwidth, number of frequency peaks, and nPVI across France revealed distinct distribution patterns (Fig. 3, Supporting information). In the Mediterranean ecoregion (Supporting information), we generally observed assemblages characterised by medium-low spectral bandwidths (< 1700 Hz; Fig. 3a), complex vocalisations (number of frequency peaks ≥ 24 ; Fig. 3b), and considerable variability in rhythmic patterns (notable variations in nPVI values across the region, Fig. 3c). In the temperate coniferous forest ecoregion, roughly corresponding to the Alps (Supporting information), acoustic bird assemblages typically exhibit medium-low spectral bandwidths (values often ranging between 1800 and 1500 Hz; Fig. 3a), high-medium complexity (number of frequency peaks often between 21 and 25; Fig. 3b), and more isochronous rhythmic patterns (nPVI values often between 15 and 18; Fig. 3c).

As the temperate broadleaf and mixed forests ecoregion spanned most of the study region, we partitioned it into three arbitrary sub-regions: the northwest, northeast, and southwest (Supporting information). In the northwest, CWM spectral bandwidth was significantly higher in Brittany (westernmost peninsula, spectral bandwidths > 2100 Hz; Fig. 3a), while species assemblages typically show high-medium complexity (number of frequency peaks > 22; Fig. 3b), and the least isochronous rhythmic patterns with significant alterations in onset timing (nPVI typically > 18; Fig. 3c). In the northeast, bird assemblages exhibited medium-low spectral bandwidths (typically 1600–1800 Hz; Fig. 3a), low complexity (number of frequency peaks typically < 23; Fig. 3b), and moderately isochronous rhythmic patterns (nPVI typically 17–18; Fig. 3c). Finally, southwest bird assemblages generally displayed medium-low spectral bandwidths (typically 1600–1800 Hz; Fig. 3a), medium complexity (number of frequency peaks often 23–25; Fig. 3b), and non-equally spaced rhythmic patterns (nPVI often 17–19), except in the Pyrenees where rhythms were more isochronous (nPVI ≤ 17 ; Fig. 3c).

The fit of spatial models explained 15–30% of the variance in CWMs (Supporting information). We found higher spectral bandwidths in assemblages associated with landscapes characterised by relatively higher cover of freshwater, small woody features, urban areas, grasslands, and forests,

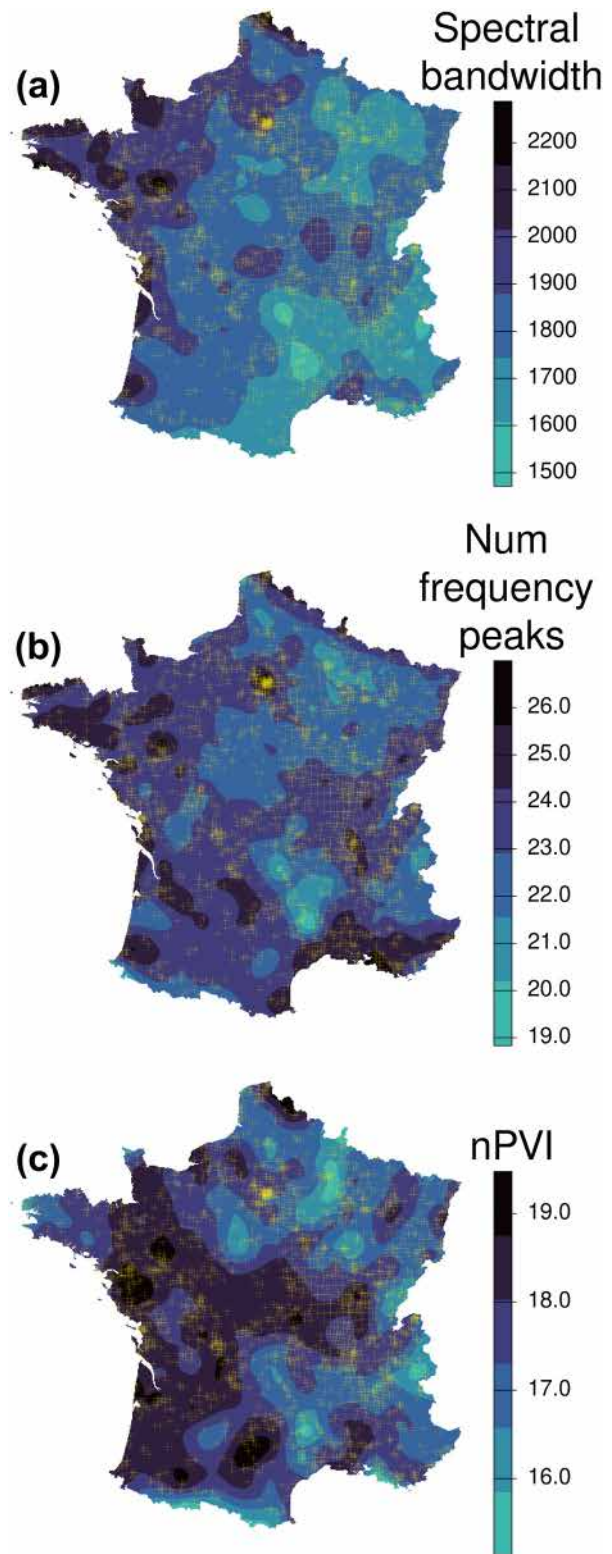


Figure 3. Map of interpolated community-weighted means of spectral bandwidth (Hz) (a), number of frequency peaks (b), and normalised pairwise variability index (nPVI) (c). Transparent yellow crosses indicate the locations of plots where bird assemblages were sampled within the STOC EPS. We interpolated community-weighted means across pixels without direct observations using a thin plate spline surface to visualise spatial trends.

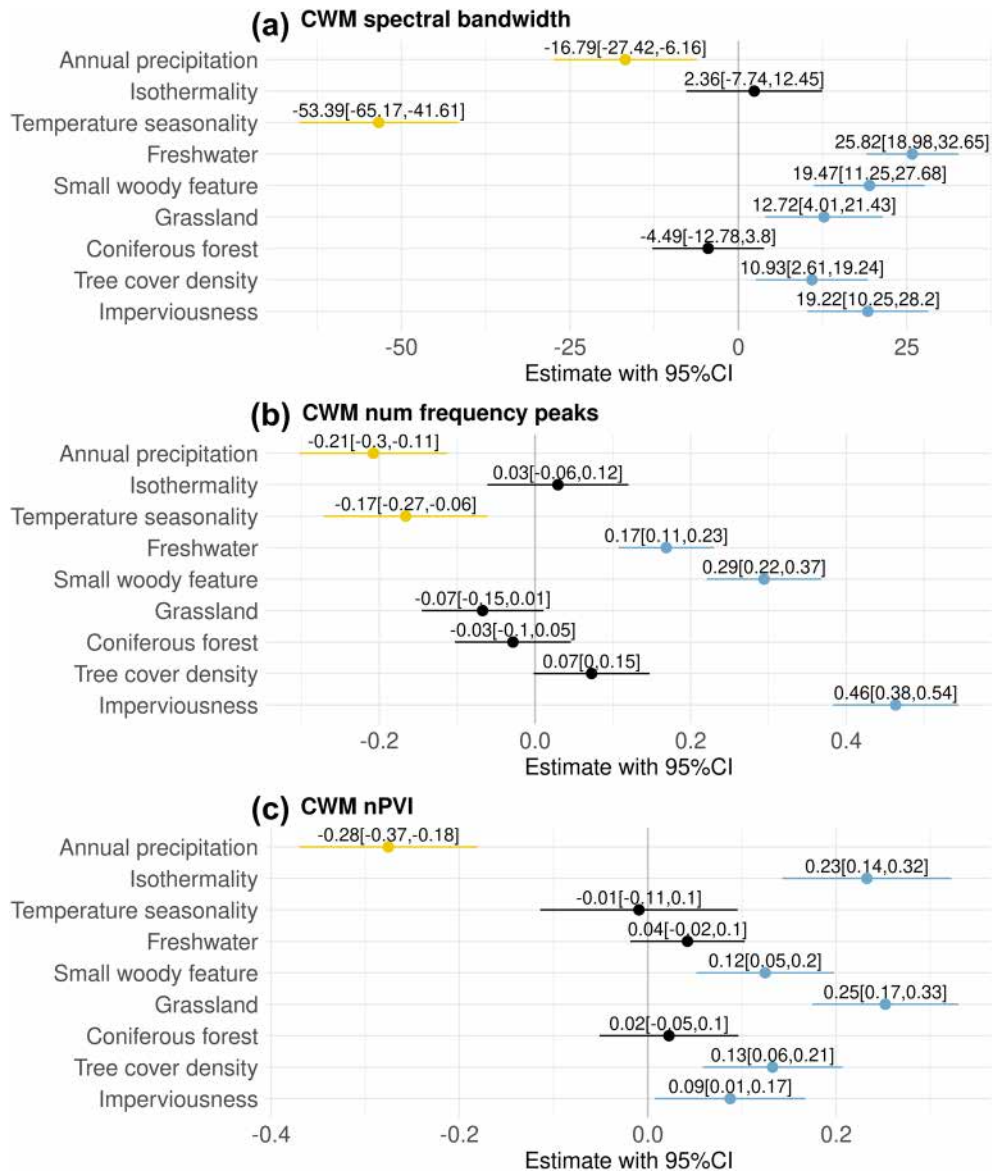


Figure 4. Parameter estimates with 95% confidence intervals (CI) of the slopes of the environmental variables predicting the community weighted means spectral bandwidth (Hz) (a), num(ber of) frequency peaks (b), and nPVI (c). Positive estimates are plotted in blue, negative in yellow. Parameter values with high uncertainty (i.e. with CI crossing 0) are plotted in black.

while spectral bandwidth was negatively correlated with temperature seasonality and annual precipitation (Fig. 4a). The vocalisation complexity, as measured by the CWM of the number of frequency peaks (Fig. 4b), was higher in urbanised areas and landscapes characterised by small woody features and freshwater. Conversely, we found low complexity in locations with high precipitations and temperature seasonality. Rhythmic patterns were less regular (i.e. higher nPVI values) in urban environments, forests, grasslands, small woody features, and pixels with high isothermality. Isochronous beats were found in pixels with high annual precipitations (Fig. 4c). Plots of the data points with lines representing the predicted relationship between the CWMs and the independent variables are available in the Supporting information.

The CM analysis (Supporting information) yielded broadly similar results to the CWMs analyses. Specifically, most environmental predictors exhibited similar signs of correlation with the dependent variables in both CMs and CWMs analyses (Supporting information). This suggested that the correlations with CWMs reflected community-level trends and were not predominantly driven by a few abundant species.

Discussion

Our analyses revealed biogeographic patterns in the acoustic trait composition of bird assemblages in continental France which were strongly associated with regional climatic and

habitat gradients. At the species level, acoustic traits varied along bioclimatic gradients and were clustered phylogenetically. These patterns are consistent with our prediction that acoustic strategies are influenced by biogeographic patterns and niche conservatism. In contrast, we found mixed support for the prediction that acoustic traits are spatially structured according to the acoustic properties of habitats in a landscape. The CWM analysis revealed that dominant acoustic traits correlated significantly with environmental variations, such as higher mean spectral bandwidths and song complexity in semi-natural habitats or urban areas, but the magnitude and direction of these variations remained relatively idiosyncratic.

Overall, the ESLTP analysis revealed that geography, phylogeny, climate, environmental variation, and acoustic traits all contributed to structuring species assemblages, with phylogeny and climate exerting the strongest effects. We found phylogenetic clustering in acoustic traits both at the regional scale and in the trait–environment correlations of local assemblages. The ESLTP analysis further showed that bioclimatic gradients are associated with biogeographic zones, each supporting distinct bird assemblages with characteristic acoustic trait suites. For example, precipitation and temperature seasonality were negatively associated with frequency traits such as spectral bandwidth and complexity in the spectral domain. These traits were also positively correlated with mean temperature. These correlations suggest that many species with similar climatic niches often converge on comparable acoustic trait profiles. For example, three species typical of the Mediterranean ecoregion – *Curruca melanocephala*, *Anthus campestris*, and *Emberiza hortulana* – share medium spectral bandwidths, complexities, and non-isochronous rhythms. The ESLTP analysis also revealed a positive correlation between all acoustic traits and cropland, suggesting that farmland-dwelling birds tend to produce vocalisations with broader spectral bandwidths, greater complexity, and non-isochronous rhythmic patterns. These traits might facilitate long-distance sound propagation over low-vegetation crops, facilitating perception by conspecifics as compared to the shorter frequency bandwidths of species found more frequently in other habitats. The correlations with other land cover types in the ESLTP were weaker and thus had less influence on the species–traits correlations.

At the assemblage level, we found that many land cover predictors showed a clear positive correlation with the CWM, but did not unambiguously match our prediction that the acoustic properties of habitats affect acoustic traits in species assemblages. For example, we found that bird assemblages in both forests and grasslands typically produced vocalisations with large spectral bandwidths and non-isochronous rhythmic patterns. The link between broader spectral bandwidths and open habitats reflects the reduced transmission constraints in these environments, which facilitates the use of strongly modulated frequencies (Barbaro et al. 2023, Hauptert et al. 2023). However, the occurrence of large spectral bandwidths in forest assemblages indicates that, even under the stronger transmission constraints typical of forest environments, broad bandwidths can still emerge, indicating

that these patterns are not mutually exclusive. This positive correlation between spectral bandwidth and forest also aligns with previous local studies reporting that species in forests often produce vocalisations with highly modulated frequencies, despite the reverberation caused by dense vegetation (reviewed by Boncoraglio and Saino 2007, Ey and Fisher 2009). Like frequency, the positive correlations between nPVI and both grasslands and forests indicate that signals with less regular rhythmic patterns tend to be favoured in these environments. Previous studies found slower tempos in forests, since their transmission among trees is more efficient than that of faster tempos (Hunter and Krebs 1979, Richards and Wiley 1980, Wiley 1991, Ey and Fisher 2009). However, nPVI and tempo were not correlated in our study (Supporting information), which could explain the difference in results. Future research could quantify the impact of reverberation on both isochronous and non-isochronous rhythmic patterns across various habitats.

The species examined in this study consisted generally of small-bodied species (e.g. the mean tarsus length was 23 mm, with only 5% of the species having tarsus lengths exceeding 40 mm. Similar patterns can be observed in the variation of body mass and beak size; Supporting information). Separating acoustic traits from morphometry was beyond the scope of our analysis, which focused on the consequences of spatial distribution in communication strategies for assemblage-level patterns, irrespective of unmeasured moderator variables. Smaller-bodied species generally produce higher-pitched sounds (Mahler and Gil 2009, Pearse et al. 2018). However, there is no direct link between frequency and habitat after controlling for body size (Wiley 1991). Thus, the covariation between body size and vocal pitch seems indirectly forced by habitat-related constraints.

Urbanisation showed a positive correlation with the CWMs of spectral bandwidth. Our interspecific analysis echoes research at the individual level showing that birds in urbanised areas often increase the frequency of their vocalisations to reduce masking from low-frequency anthropogenic noise (Rheindt 2003, Moseley et al. 2018, Derryberry et al. 2020), adjust their song amplitude (Derryberry et al. 2016), or shift the timing of songs to avoid peak traffic times (Bermúdez-Cuamatzin et al. 2020). In contrast, urbanisation also correlated positively with vocalisation complexity, contrary to the expectation that simpler songs avoid masking more easily (McMullen et al. 2014). This result was likely influenced by urban areas with large parks like Paris, where woodland-related species with complex songs persist (such as *Turdus merula* and *T. philomelos*). Acoustic masking often arises from fine-scale background noise patterns and may constrain effective signal transmission, acting as an additional filter on species occurrence. However, because masking frequently co-occurs with covariates such as impervious cover, isolating its independent influence requires sampling designs that incorporate explicit control sites and structured contrasts. At the broad spatial scale of our study, such fine-scale acoustic processes are therefore likely overshadowed by larger-scale habitat and biogeographical gradients. Hence,

acoustics may play a secondary role in shaping species distributions in urban environments, where resource availability and habitat structure are stronger limiting factors (Seress and Liker 2015). Urban assemblages were also dominated by species with non-isochronous rhythmic patterns. While we speculate that these patterns are more likely to be masked by the static and monotonous urban noise, this would need further investigation through field studies or simulations, which we suggest as future work. Overall, our results indicate that urban assemblages produce vocalisations with mixed chances of successful transmission through urban noise.

We showed that acoustic trait distributions varied independently in space. This finding emphasizes the importance of examining multiple traits simultaneously rather than relying on the spatial variations of a single proxy. While rhythmic patterns have been explored in bioacoustics (Aubin and Bremond 1983, Norton and Scharff 2016), previous interspecific studies have largely focused on frequency-related features (Pearse et al. 2018, Mikula et al. 2021, Sagar et al. 2024). Our findings suggest that results derived from single trait analyses may overlook the broad interplay between acoustic traits and environmental gradients. In particular, rhythmic patterns play a crucial role in sound and species recognition in humans (Rebuschat et al. 2011) and may hold similar significance in other taxa in interpreting conspecific vocalisations (Kotz et al. 2018, Rouse et al. 2021). Exploring how these acoustic traits interact with environmental variation and climate could deepen our understanding of interspecific differences in acoustic communication.

This study shows that the combined influence of phylogenetic constraints and environmental gradients generates distinct regional patterns in the acoustic trait diversity of bird assemblages across France. These patterns should not be interpreted as evidence of acoustic adaptation to environmental variation. Instead, they reflect the acoustic consequences of compositional turnover in species assemblages, driven by the functional traits that mediate species' responses to climate and habitat. Although local processes, such as responses to noise pollution or acoustic competition, can directly influence species distributions and shape local assemblages within landscapes, these processes are likely too spatially variable and non-stationary to generate detectable signals at a regional scale (Rossetto et al. 2025). Future research could test whether this conclusion holds in other regions and taxa. In particular, exploring further the imprint of human-induced spatial gradients on acoustic traits over large extents may impact our understanding of large-scale threats to bird communication. As habitats are transformed and climate conditions shift due to human activities, species will likely be displaced, go (locally) extinct, or adapt to new conditions, leading to shifts in assemblage compositions (Devictor et al. 2008b). These dynamics may induce multi-scale consequences, such as the disruption of acoustic connectivity within populations, a functional homogenisation of acoustic traits within meta-communities, and an impoverishment of the sounds associated with habitats exposed to varying levels of disturbance at ecosystem levels (Farina et al. 2014, Grinfeder et al. 2022b).

Human-induced changes are already resulting in a loss of acoustic diversity in North American and European soundscapes (Whitehouse 2015, Morrison et al. 2021), which could negatively affect human well-being in nature (Ratcliffe 2021, Rozario et al. 2025). Deciphering how and at what scales these trends affect the effectiveness of the acoustic communication function carried by acoustic traits is essential for a mechanistic explanation of the fate of the sonic component of ecosystems under the ongoing environmental changes. Ultimately, better understanding the drivers of acoustic traits variation across landscapes, and how humans perceive these changes, is essential for conserving nature's sensory heritage.

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and editing (supporting). **Alice Eldridge**: Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Almo Farina**: Conceptualization (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Amandine Gasc**: Conceptualization (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Charlène Gemard**: Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Sylvain Haupt**: Conceptualization (supporting); Investigation (supporting); Software (supporting); Supervision (supporting); Writing – review and editing (supporting). **Sandra Müller**: Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jean-Yves Barnagaud**: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal).

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Data availability statement

Data and scripts are available from Figshare: <https://doi.org/10.6084/m9.figshare.31446031> (Busana et al. 2026).

Supporting information

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

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