Title: Rapid structural network changes in bird communities

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Abstract

As biodiversity is declining, the dynamics of species interactions is a growing conservation concern. However, estimating and monitoring species interactions across large spatial and temporal scales remain challenging, and thus changes in species interactions and the subsequent networks of interactions remain relatively unexplored. Here, we assess changes in the network structure of common bird communities from France. We estimate associated species pairs using spatial and temporal information for 109 species monitored across 1,969 sites during 17 years. We validate the ecological significance of associated species pairs by testing the relationship between the propensity to be associated and species functional proximity or shared habitat preference. We reconstruct association networks for these intra-guild bird communities and track temporal changes in network layout in terms of size, density of links, modularity and degree distribution. We show that, beyond species change, birds' local association networks become smaller with a similar relative number of associations that becomes unevenly distributed. These structural changes vary among types of bird communities and may impact community functioning and how communities can cope with global change.

Keywords: biotic homogenisation, connectance, CCM, co-occurrence, evenness, modularity, network, interactions.

1. Introduction

Changes in species numbers, abundances, or distributions are among the most common evidence that anthropogenic global change rapidly and profoundly modifies natural communities (Kampichler et al. 2012, Koerner et al. 2017). Less perceptible, however, are changes in the number and type of species interactions even though the negative effect of interaction loss on species co-extinctions has been documented for decades (Janzen 1971, Dunne et al. 2002). Any change in sign, strength or number of interactions has an effect on the network structure of a community and can strongly affect community dynamics (Lyons et al. 2016) and functioning (e.g. productivity, efficiency of resource use) (Fontaine and Thébault 2015, Besson et al. 2019). Although the consequences of such modifications for plant-pollinator or predator-prey network conservation have been emphasized (Tylianakis et al. 2010), they have not been documented for many groups, including non-trophic networks between species from similar guilds such as birds (but see Goodale et al. (2015) for mixed-species flocks). Focusing on species loss in conservation issues related biotic communities issues comes to assuming that loss of interactions is just a side-effect of species turnover. However, species roles in community network may vary (e.g. between connector and peripheral species (Soulé et al. 2003, Palacio et al. 2016)). Species loss could therefore be decoupled from interaction loss as the extinction of interactions may occur at a different rate than species extinction (Valiente-Banuet et al. 2015), meaning that the change in interactions can be a major but neglected form of biodiversity loss. Yet, relatively little is known of how species interaction networks change across time and space (CaraDonna et al. 2020).

This is particularly striking for networks from the same trophic level, i.e. intra-guild networks. Beyond food-webs and plant-pollinator networks, research on intra-guild networks is limited to local case studies (Orchan et al. 2013) or mixed-species flocks, a specific types of bird community, particularly

important during the non-breeding season in temperate areas and mostly composed of insectivorous species (Goodale et al. 2015). These specific communities have been shown to be highly sensitive to anthropogenic disturbance, which might affect the rest of birds species (Zou et al. 2018). Yet, changes in networks structuring bird communities mostly remain inferred from a space-for-time substitution hypothesis (Damgaard 2019), whereby temporal changes are extrapolated from comparisons between communities spatially distributed in different environments (Lane et al. 2014, Mokross et al. 2014). As shown by studies focusing on species composition, bird communities are profoundly modified by global change (Kampichler et al. 2012, Gaüzère et al. 2015). It is therefore likely that underlying networks in common bird communities are impacted as well, especially in communities that are the most affected in terms of species loss, such as farmland and urban bird communities (Rigal et al. 2022). Studying internal changes in networks of common bird communities may constitute a step forward for conservation, using the appropriate network metrics (Tylianakis et al. 2010, Harvey et al. 2017). However, analysing the fate of bird community networks has so far been challenged by two limitations: 1) the estimation of ecologically relevant associations at large scale (Vallé et al. 2024) and 2) the temporal analysis of the reconstructed networks (Olesen et al. 2011).

The main reason behind the limited studies on changes in networks of species interactions is that measuring species interactions is particularly challenging. The appropriate method (*e.g.* field observation, experiment) depends both on the type of interaction (*e.g.* mutualism, competition) and on the spatial scale considered (*e.g.* from microbial networks to biogeographic studies) (Morales-Castilla et al. 2015, Delmas et al. 2019). In local plant-pollinator or host-parasite networks, for instance, interactions are relatively straightforward to define. Nevertheless, as the number of species pairs grows in proportion to the square of the species number in a community, so grows the number of interactions to determine. Moreover, defining the nature of interaction net effect that emerge as the result of several

interacting processes between species is more challenging (Barner et al. 2016). Hence, the possibility to empirically estimate interactions in large communities and track changes over time in the underlying network is often out of reach. However, the growing number of community data with large spatial and temporal resolutions has motivated the emergence of alternative approaches for estimating proxies of species interactions in large-scale analyses.

One such alternative approach relies on coexistence theory and community assembly rules using spatial co-occurrences of species (HilleRisLambers et al. 2012, Letten et al. 2017), while disentangling the effect of the biotic filter (*i.e.* interactions) from other filters (*e.g*. habitat filtering) on co-occurrence patterns (Morueta-Holme et al. 2016, Elo et al. 2021). The relevance of obtained associations as meaningful proxies of ecological interactions has been criticised, because numerous unchecked non-biotic processes can still influence species co-occurrences (*e.g.* dispersal capacity, habitat, phylogeography) (Sander et al. 2017, Freilich et al. 2018, Dallas et al. 2019, Blanchet et al. 2020, Cordero and Jackson 2021). However, spatial co-occurrence methods are based on the hypothesis that community composition corresponds to an apparent equilibrium resulting from large-scale processes (i.e. biotic and abiotic filters) and can therefore provide a first estimate of potentially interacting species pairs by removing the effects of a given number of non-interaction filters.

A different approach relies on relationships between species temporal dynamics to determine the effect of one species on another. Applying direct correlations between species time-series to estimate species interaction is prone to spurious correlations due to, for instance, a common environmental forcing (*e.g.* Moran effect (Moran 1953)). To tackle these limitations, methods based on dynamical system analyses have been recently applied to detect species interactions from species time-series (Barraquand et al. 2021). These methods include Convergent Cross-Mapping (CCM) (Sugihara et al. 2012) which infer,

for dynamic deterministic systems, whether one time-series is likely to be predicted by another (Ushio et al. 2018). The application of this method can be challenged by the need of long temporal time-series, and the obtained interactions may be questioned depending on the degree of noise in time-series or the influence of external drivers (Cobey and Baskerville 2016). However, in this method, the effect of a shared environmental forcing can be corrected by the use of surrogate time-series (Barraquand et al. 2021). Therefore, once the effect of large-scale processes on the apparent equilibrium of community composition is removed (*e.g.* using spatial information in the co-occurrence approach mentioned above), temporal-based methods, being based on the non-equilibrium inside community composition, may be relevant complementary tools to identify species associations independently of the effects of other locals processes (Ushio et al. 2018).

The species associations provided by the above large-scale approaches remain estimates of the effect of one species on another (Barner et al. 2016), subject to several biases (Barner et al. 2018), and their validity must therefore be tested before any network reconstruction. A possibility to investigate the estimated species associations is to analyse the ecological relevance of associated species pairs. Biotic community assembly processes enable hypotheses on the relationship between niche overlap or functional distance and species interactions in the community: species with similar functional traits or habitats may either tend to repulse (or even exclude) each other because of resource competition, under the limiting similarity hypothesis (MacArthur and Levins 1967, Abrams 1975, Martin and Bonier 2018) or attract each other through social information exchange and facilitation processes (Gil et al. 2017, Schmidt et al. 2010, Seppänen et al. 2007). Depending on trait conservatism of the species considered, a similar pattern is expected for phylogenetic distances among species: closely related species should on average interact more positively or negatively than distantly related species (Kraft et al. 2007). Overall, species functionally close to each other (or closely related along the phylogeny) or dwelling in

similar habitats are therefore expected to interact more strongly either by attraction or repulsion (Stouffer et al. 2012, Mönkkönen et al. 2017).

Once species associations are available, comprehensive and meaningful metrics of network properties remain to be estimated. The ecological association networks may be studied using a set of relevant metrics (Kaiser-Bunbury and Blüthgen 2015, Lau et al. 2017) in terms of network structure and consequences of structural changes for the community functioning (Tylianakis et al. 2010). In particular, an ecological network, constituted of species as nodes and association as edges between nodes, can be analysed as a whole (i.e. network level), at an intermediate level (i.e. by sub-groups) or at the node level (Lau et al. 2017, Delmas et al. 2019). For instance, at the network level, the network structure will be defined by the number of nodes, the number of edges and the connectance (i.e. density of edges). The network structure can be analysed at the intermediate level, e.g. by motifs (i.e. recurrent patterns), average length path (i.e. average number of steps between all possible pairs of nodes) and modularity (i.e. intensity of network division into sub-groups). At the node or species level, the network structure can be studied using, for instance, the degree distribution (i.e. probability distribution of the number of edges by nodes), the centrality (i.e. how influential is a node) or the partnership diversity (i.e. preference for nodes in a network to attach to other similar nodes). The available metrics depend on the network type, which can be either directed (i.e. edges are directed from one node to another) or indirected (i.e. edges are present or not), bipartite (i.e. nodes are divided into two distinct sets as in plant-pollinators networks), multiplex (i.e. a pair of nodes can be related by multiple types of edges) or simple (i.e. one type of nodes and one possible edge by pair of nodes) (Barabási 2003). As the associations that can be obtained from large-scale data are only estimates of species relationships, a conservative approach is to use them to reconstruct undirected simple networks. The interpretation of each metric on its own is neither relevant nor generalisable, since a change in the index may be due to

the size of the network (Heleno et al. 2012), be correlated with the other indicators (Delmas et al. 2019) and depend on the type of interaction studied (Tylianakis et al. 2010). To follows the changes in community structure and its potential consequences for conservation, we focus on the number of species (i.e. network size), the number of associations (Heleno et al. 2012, Kaiser-Bunbury and Blüthgen 2015) and a set of relevant metrics for undirected simple networks. At the network level, we use connectance, a standard metric whose mathematical relationship with other network metrics is well known and which is therefore important for analysing these other metrics. The relationship between connectance and perturbations is not consistent, but independently of the type of interactions, connectance increase has been linked to greater species generalism (Tylianakis et al. 2010). At the intermediate level, we use modularity which has been shown as a suitable metric for conservation questions: high modularity contains perturbations and local extinction within a module and thus prevent the likelihood of secondary extinctions in the rest of the network (Stouffer and Bascompte 2011). At the node levels, we use evenness of degree distribution that has been related to higher robustness as it decreases the consequences of a local extinction for the remaining species and tend to be lower in the context of degraded habitats (Kaiser-Bunbury and Blüthgen 2015, Fisogni et al. 2021).

In this paper, we assess temporal changes of reconstructed networks in French bird communities over the last two decades. Using the French Breeding Bird Survey from 2001 to 2017, we first estimate potential associated species pairs using spatial co-occurrences to account for large-scale community composition filters (Fig. 1a), and we refine the selection of associated species pairs using the dynamical system CCM approach to control for the effect of local processes (Fig. 1b). We then test the ecological relevance of the associated species pairs using species ecological traits (Fig. 1c). Lastly, we use species associations to reconstruct the network structures of bird communities and track the temporal changes

of static network metrics used in conservation (Fig. 1d) to analyse the consequences, for the conservation of bird communities, of network changes that accompany changes in species composition.

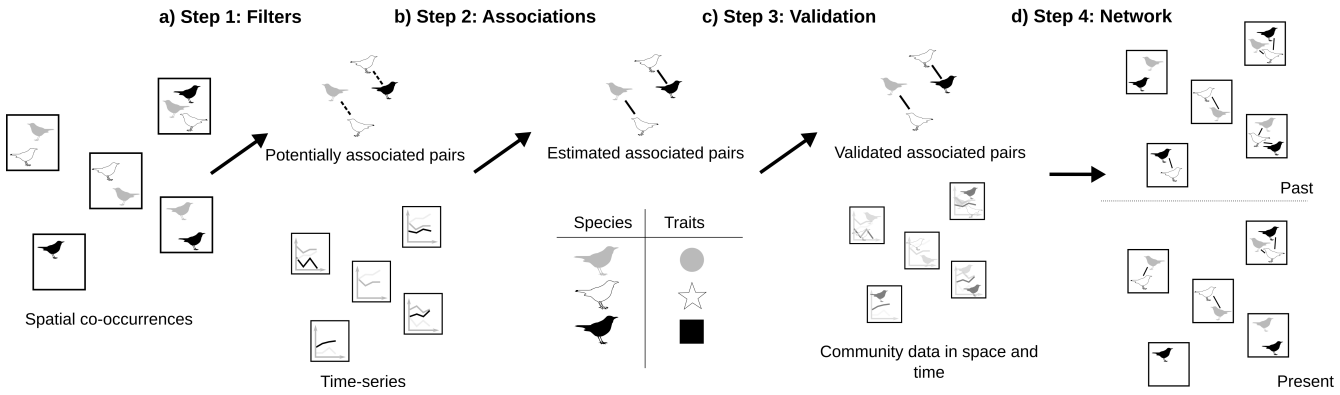

Figure 1: Framework of the network reconstruction from large-scale spatio-temporal data. a) In a first step, the effects of large-scale processes on species co-occurrences are removed using community apparent equilibrium, to estimate the potentially associated species pairs. b) In a second step, the estimation of associated species pairs is refined by removing the effects of non-biotic local processes on the non-equilibrium of community composition. c) The ecological relevance of the estimated associations is tested using the ecological hypothesis on community assembly and species traits. d) Community composition in space and time are combined with associated species pairs to reconstruct the underlying networks and track changes in network layout.

2. Material and methods

2.1 Spatial data and time-series of birds

We use the French Breeding Bird Survey (FBBS) (Jiguet et al. 2012) monitoring the abundance of common bird species in 2,514 sites in mainland France between 2001 and 2017. Sites are randomly distributed over France and correspond to 2x2 km squares in which the abundances of breeding bird species were counted on 10 sampling points (during 5 min, 1 to 4 h after sunrise) by volunteer experienced ornithologists, twice a year between 1st of April and 15th of June from 2001 to 2017. Each site represents a species assemblage changing in abundance and composition over time. Habitats are described for each sampling point in 19 types (supplementary material 1). The data made available by the MNHN provide abundances that are already corrected for the difference in species detectability. Among the 242 recorded species, we select the most abundant species representing 99% of the total abundance to avoid over-representation of rare species for which the FBBS is not well designed. After removing rare species and sites only monitored once, our dataset is composed of 1,969 sites and 109 species.

2.2 Potentially associated species pairs

We use spatial co-occurrence to estimate the species pairs potentially associated (Fig. 1a) by removing large-scale non-interaction filters (historical dispersal, neutral dispersal and habitat filtering) following Rigal et al. (2022). To do so, we measure the partial correlations between species pairs using their co-occurrence profile. We account for historical and habitat filtering by estimating potentially associated pairs for each type of habitat and each biogeographic region. We limit the influence of random processes and uncontrolled habitat filtering using a null model by resampling species in a site. This provides 1000 random co-occurrence datasets obtained by keeping constant the total number of individuals in a given sampling point, and assuming that the probability for a species to occur in a given sampling point was proportional to its frequency in the dataset. We calculate the standardised

effect size (SES) of the observed partial correlations compared to the partial correlations from the random datasets. Significant associated pairs are based on p-values (<0.05) obtained from the rank of the observed partial correlations in the distribution of random partial correlations (Morueta-Holme et al. 2016). Among the 292,796 combinations of species pairs (5886 species pairs of 109 different species), habitats (19) and biogeographic regions (4) (not all species pairs were present in each habitat and each biogeographic region), this first step highlights 89,270 potentially associated species pairs in a given habitat and a given biogeographic region.

2.3 Species associations

For each potentially associated species pair in a given habitat and a given biogeographic region, we determine which species pairs were significantly associated (Fig. 1b) based on the relationship between species time-series estimated by Convergent Cross-Mapping (CCM) (Sugihara et al. 2012). In CCM, the time-series of two species are linked if we can predict the dynamics of species X using the time-series of species Y, *i.e.* if the attractor of X (defined as the set of states reconstructed from the original and lagged time-series of X) can be estimated from the attractor of Y. If so, species X has a signature into the dynamics of species Y, meaning that species X is affecting species Y (see detailed in supplementary material 2 and in Tsonis et al. (2018)). CCM results in a correlation value ρ, depicting the correlation between the two attractors, associated to a p-value for significance.

Because of the limited times-series length in the dataset, we use the multispatial CCM method (R package *multispatialCCM*) (Clark et al. 2015), an extension of CCM for short times-series that uses data from multiple sites and a bootstrap routine to determine ρ. We select sites monitored during at least six consecutive years. This represents the best compromise to combine a high number of sites

(766 sites) and long enough time-series from a given site to enable the assessment of significant associations between two species. For each species, we reconstruct its time-series at a given site using its recorded abundance, set to zero when the species was not recorded during a monitoring session of the site. Obtaining pseudo-time-series (*i.e.* the times-series reconstructed by placing side by side data from multiple sites) longer than 500 time steps (following the empirical example from Clark et al. (2015)) requires to select the 32,491 combinations of species pairs, habitats and biogeographic regions that match this criteria among the 89,270 potentially associated species pairs in given habitat and biogeographic region obtained from spatial co-occurrences.

To apply the multispatial CCM for each of the 32,491 combinations, we use 300 replicates for the bootstrap routine due to computational time. The multispatial CCM provides species pairs for which the time-series of one species was causally related to the time-series of the other. Information given by CCM is directional: species X can significantly affect species Y (X → Y) and species Y can significantly affect species X (Y → X). However, the aim of our conservative approach is to reconstruct simple undirected networks. Thus, without taking direction into account, if one or both directions is significant, the pair of species is considered to be associated.

2.4 Testing ecological relevance of species associations

We then investigate whether the associated species pairs are ecologically meaningful (Fig. 1c) according to trait-based assembly theory and specific expected interactions. According to trait-based assembly theory, species that share similar functional traits, are phylogenetically clustered or with significant habitat overlap, are expected to interact more strongly (Fontaine and Thébault 2015, Mönkkönen et al. 2017). This stronger interaction may be either positive through social information

exchange and facilitation processes (Gil et al. 2017), or negative because of resource competition under the limiting similarity hypothesis (Abrams 1983), which should result in a funnel pattern when species interactions are combined with trait-related distances (Mönkkönen et al. 2017). We test whether the associations obtained from previous steps are in line with these expectations using two approaches. In a first test based on distances between species characteristics, we compute functional, phylogenetic and niche overlap distances (see relationship and complementarity between distances in supplementary material 3) and relate them to the probability of a species pair to be associated. In a second test that is specifically focused on expected interactions, we analyse whether species pairs with a similar diet or nest requirement are more prone to be associated, while controlling for their preferred habitat.

2.4.1 Functional distance

Functional distance is estimated using a life-history trait dataset for the birds of the Palaearctic (Storchová and Hořák 2018). We compute the Generalized Functional Diversity (GFD) following Mouchet et al. (2008) to generate a pairwise functional distance between all pairs of species (Mouchet et al. 2010). This method computes all the combinations of the clustering algorithms from a functional distance matrix and provides the best consensus tree, *i.e.* the one for which the dissimilarity with the original distance matrix is the lowest according to the 2-norm goodness-of-fit index (Mérigot et al. 2010). We construct the initial functional distance matrix using the Gower's distance as the trait matrix contained both qualitative and quantitative data (Gower 1971). The best consensus dendrogram is built using the Unweighted Pair Group Method using arithmetic Average algorithm (UPGMA) (2-norm=0.03, threshold=3.49). From this dendrogram, we compute the cophenetic functional distance (Sokal and Rohlf 1962) between species.

2.4.2 Phylogenetic distance

Phylogenetic trees of the 242 bird species are assessed from **birdtree.org** (Jetz et al. 2014). We estimate the consensus tree from 10,000 trees using the *ape* R package (Paradis et al. 2019). We calculate the phylogenetic distance as the cophenetic distance between each pair of species in the consensus tree.

2.4.3 Niche overlap distance

We compute niche overlap for each species pair as the overlap between the frequency distribution of each species within the 19 classes of habitat. To do so, we use the habitat information for each sampling point and we calculate the frequency distribution of each species over the 19 classes of habitats in the whole dataset. We then compute the χ^2-distance, widely used to compare ecological assemblages (Ben-Shahar and Skinner 1988, Flower et al. 1997), to estimate the distance between each species habitat profile. The χ^2-distance characterises the proximity in habitat distribution profiles independently of species abundance. We define the habitat niche overlap distance (*NOD*) using the similarity between habitat profiles as follows (Eq. 1 and see details on NOD in supplementary material 3):

$$NOD_{a,b} = 1 - \chi^2_{dist\,a,b} = \sqrt{\sum_{j=1}^{H} \frac{y_t}{y_h}\left(\frac{y_{ah}}{y_a} - \frac{y_{hb}}{y_b}\right)} \qquad \text{(Eq. 1)}$$

with $NOD_{a,b}$ the niche overlap distance between species *a* and *b*, $\chi^2_{dist\,a,b}$ the χ^2-distance between habitat profiles of species *a* and *b*, *H* the number of habitats, y_t the total abundance of species *a* and *b* in all the

habitats, y_h the abundance of species *a* and *b* in habitat *h*, y_{ah} the abundance of species *a* in *h*, y_a the total abundance of species *a*, y_{hb} the abundance of species *b* in *h* and y_b the total abundance of species *b*.

2.4.4 Test with functional, phylogenetic and niche overlap distances

To test the ecological relevance of the associated species pair, we perform a binary logistic regression using Generalised Linear Models (GLM). The response variable (*A*) is the presence or absence of association for each species pair (a species pair is considered to be associated if this has been the case in at least one habitat and one biogeographic region), with a binomial distribution with parameter *p* and a logit link function *g*. The explanatory variables are scaled functional distance (*FD*), phylogenetic distance (*PD*) and niche overlap distance (*NOD*) (FD and PD being slightly correlated but not with NOD, see supplementary material 3) for species pair *i* (Eq. 2):

$$\begin{aligned} A_i &\sim Binomial(p) \\ g(p) &= \beta_0 + \beta_1 FD_i + \beta_2 PD_i + \beta_3 NOD_i \\ g(x) &= \log\left(\frac{x}{x-1}\right) \end{aligned} \qquad \text{(Eq. 2)}$$

2.4.5 Test with expected interactions for food and nest location

Using the life-history trait dataset for the birds of the Palaearctic (Storchová and Hořák 2018), we compute for each species pair if the two species used the same nest type among the five recorded types (*closed arboreal; on ground directly; in tussock very close to ground but not directly on ground; hole in*

tree, bank, ground, crevice; open arboreal cup in bush, tree, on cliff ledge) and have the same diet pattern during breeding season using nine diet descriptors (*at least 10% of diet composed of small plants; fruits; grains and seeds; arthropods; other invertebrates; fish; other vertebrates; carrions; diet composed of similar amount of plants and animals*). To assess the effect of these share traits while controlling for the habitat requirement of the species pair, we record whether the two species of the pair prefer the same habitat among the 19 classes, according to their occurrence frequency in each habitat class.

A second GLM is performed in which the binomial response variable (*A*) is the presence or absence of association for each species pair and the explanatory variables are the presence or absence of a share diet (*Diet*), the presence or absence of a share nest type (*Nest*) and the presence or absence of a similar preferred habitat (*Habitat*) for species pair *i* (Eq. 3).

$$g(p)=\beta_0+\beta_1 Diet_i+\beta_2 Nest_i+\beta_3 Habitat_i \qquad \text{(Eq. 3)}$$

2.5 Network structure analysis

2.5.1 Network reconstruction and network structural metrics

We reconstructed the species association network (Fig. 1d) at each site and for each year using the species composition (species as nodes) and the associated species pairs (associations as edges). To explore potential differences in network changes across habitats, we also conduct the analysis for the four main habitat classes (farmland, forest, urban, natural open land), obtained by grouping the 19 habitats (see supplementary material 1). We then calculate the following metrics from each network *j*:

network size *s* (i.e. number of species), number of associations *a*, connectance *c* (i.e. density of associations in the network), modularity *m* (i.e. intensity of network division into sub-groups) and evenness of degree distribution *e* (i.e. evenness of probability distribution of the number of associations by species). Connectance is the ratio between the observed number of associations *a* and the potential number of associations a_{max} (Landi et al. 2018) (directly linked to the number of species pairs $\binom{s}{2}$, Eq. 4):

$$c_j = \frac{a_j}{a_{max\,j}} = \frac{a_j}{\binom{s_j}{2}} \qquad \text{(Eq. 4)}$$

Modularity is computed using the R package *rnetcarto* (Doulcier and Stouffer 2015) which enables fast modularity computation (required for the analysis of the amount of networks in this study). It is based on the *rgraph* R package (Guimerà and Nunes Amaral 2005). The evenness of the degree distribution is calculated using the Shannon entropy of the degree distribution (Blüthgen et al. 2008) (Eq. 5):

$$e_j = \frac{-\sum_{k=1}^{s_j} p_{k\,j} \ln p_{k\,j}}{\ln s_j} \qquad \text{(Eq. 5)}$$

with p_k the frequency of degree *k*.

2.5.2 Network structural changes through time

We calculate the yearly change in network metrics by estimating the effect of years *Y* (set as an explanatory variable) on each network metric, while explicitly modelling spatial auto-correlation between sites using a Generalised Additive Mixed Model (GAMM) (Eq. 6) with a tensor product of a thin plate regression spline based on geographic coordinates of sites (longitude *lo* and latitude *la*) (Wood 2003, 2017). As the number of associated pairs and connectance are directly affected by the network size (i.e. the number of species, see correlation between network metrics in supplementary material 4) (Blüthgen et al. 2006, Besson et al. 2019), we add the number of species as a control variable for these two metrics, to estimate if the observed change is higher or lower than expected. Similarly, connectance constrains the possible values of modularity and degree distribution (Poisot and Gravel 2014, Delmas et al. 2019), and thus connectance is added as a control variable for estimating changes in modularity and evenness of degree distribution. As the number of monitored sites changes between years, site identity *z* is added as a random variable.

$$NM_j \sim \alpha_0 + \alpha_1 Y_j + \alpha_2 CV_j + f(lo_j, la_j) + \epsilon_j \qquad \text{(Eq. 6)}$$

with *NM* the network metric (number of species *s*, number of associations *a*, connectance *c*, modularity *m* and evenness *e*) and *CV* the control variable ($\varnothing$ for *s*, *s* for *a* and *c*, *c* for *m* and *e*) and $\varepsilon_j \sim N(0,\sigma)$.

3. Results

3.1 Species associations

Among the 292,796 combinations between 5,886 pairs of bird species, from four biogeographic regions and 19 habitats, we find 89,270 potential species associations (Fig. 1a). Among them, 32,491 combinations enable to reconstruct time-series with more than 500 time steps and we find 585

combinations with significantly associated species pairs (Fig. 1b). Among the 5,886 species pairs, this represents 396 (7%) associated species pairs (some species pairs are significantly associated in several habitats and biogeographic regions).

There is very strong evidence (Muff et al. 2022) of negative relationships between the propensity of a species pair to be associated (Fig. 1c) and functional (-0.22 ± 0.10, Fig. 2a) and niche overlap distances (-1.73 ± 0.17, Fig. 2a). In other words, species that are more functionally similar and with higher niche overlap are more likely associated. There is however only weak evidence of a relationships between the propensity of a species pair to be associated and phylogenetic distance (-0.09 ± 0.10, Fig. 2a and model validation in supplementary material 4) as part of the variation might be already explained by functional distance (slightly correlated with phylogenetic distance, see supplementary material 3). Concerning specific expected interactions, there is moderate evidence of a positive relationship between the propensity of a species pair to be associated and diet during breeding season (0.23 ± 0.20, Fig. 2b), very strong evidence of a positive relationship with similar preferred habitat (1.05 ± 0.19, Fig. 2b) and no evidence of a relationship with similar nest type (0.10 ± 0.18, Fig. 2b).

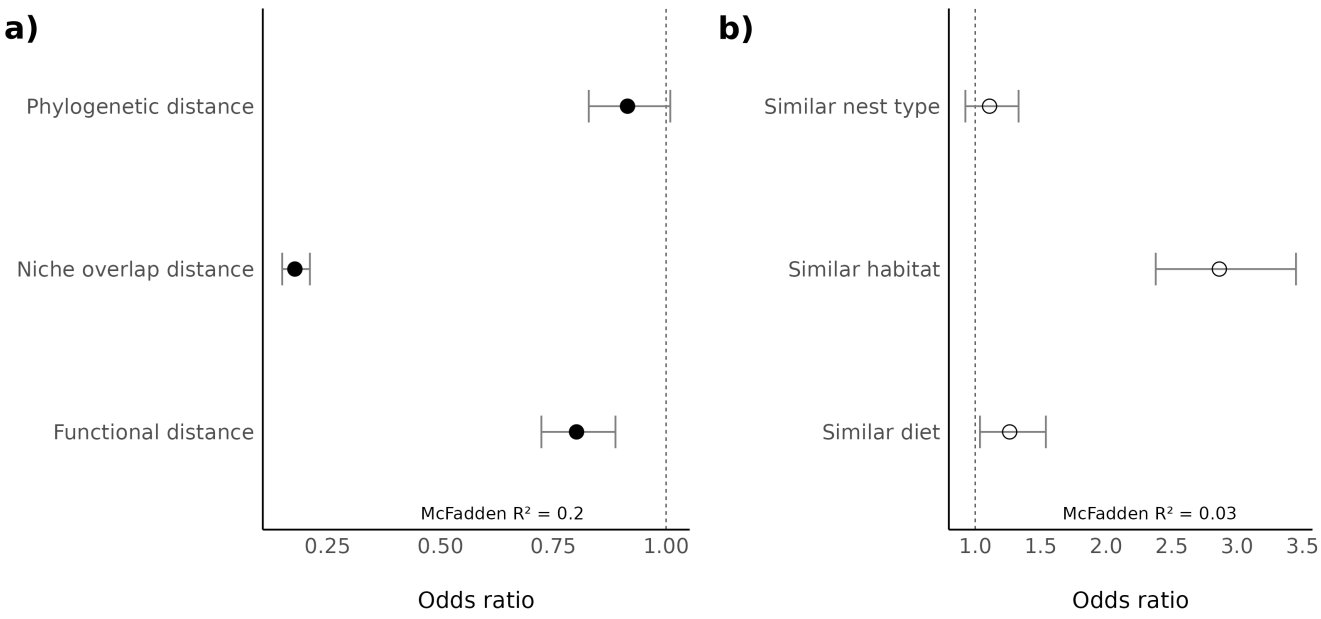

Figure 2: Odd ratios of GLM between propensity of a species pair to be associated and a) in black, the ecological distances (phylogenetic, niche overlap and functional distances), b) in white, specific expected interactions (similar nest, similar preferred habitat and similar diet in breeding season). 95% CI are displayed with grey bars. McFadden R^2 corresponds to the pseudo-R^2 for logistic regression models (McFadden 1974).

3.2 Temporal change in species association networks

Networks in breeding bird communities tend to decrease in size ($s.year^{-1}$ = -0.15 ± 0.02, Fig. 3a), increase in connectance ($c.year^{-1}$ = $5.6.10^{-4}$ ± $2.3.10^{-4}$, Fig. 3c) and decrease in evenness of the degree distribution ($e.year^{-1}$ = $-1.1.10^{-4}$ ± $0.5.10^{-4}$, Fig. 3d) over the studied period (2001-2017). This is verified for farmland and forest communities that represent the majority of networks (55.3% in farmland, 29.7% in forest, 7.9% in natural open land and 7.1% in urban areas). For farmland and forest communities, the increase in connectance is related to the decline in the number of species, whereas the number of associations really increases compare to the number of species in natural open land

communities. For networks in urban communities, the only significant change is the decline of the number of species (Fig. 3a), the other metrics staying constant.

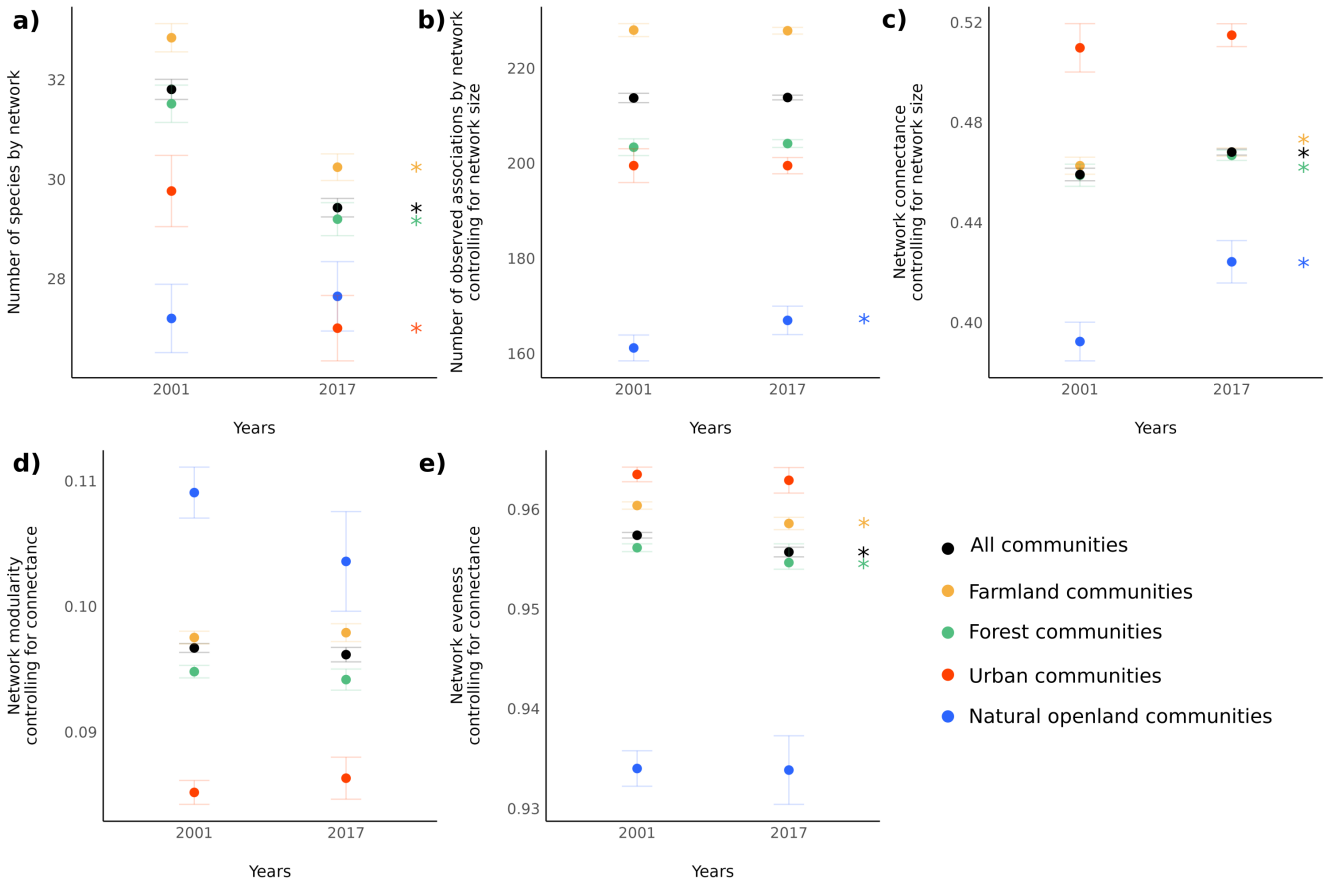

Figure 3: Temporal changes in network metrics of bird communities between 2001 and 2017 (note that only estimates for 2001 and 2017 of the linear model are presented for clarity). a) Temporal change in the number of species *s*, b) temporal change in the number of associations *a* (while controlling for the number of species), c) temporal change in connectance *c* (while controlling for the number of species), d) temporal change in modularity *m* (while controlling for connectance), e) temporal change in evenness of the degree distribution *e* (while controlling for connectance). Black dot is for all

communities, colours for communities from each habitat: yellow for farmland, green for forest, red for urban, blue for natural open land. 95% CIs are displayed and significant changes are shown by ∗.

Consequently, the network structure from the start of the period (Fig. 4a) is modified by a change in both the number of species (Fig. 4b) and the topology of relationships between species (Fig. 4c). At the level of network as a whole, the networks are denser in the sense that the density of associated pairs (i.e. connectance, Fig. 3c) is higher, which is mainly due to the reduction in the size of the network (Fig. 3a), not to a relative increase of the number of associated pairs (Fig. 3b). At the intermediate level, the intensity of network division into sub-groups (i.e. modularity) remains stable when accounting for the density of associations. Thus, the major change is at the node level, where the probability distribution of the number of edges by nodes (i.e. evenness) tends to become more skewed (i.e. shifting from species with a similar number of association to species with few or multiple associations). The trend over the period studied is from large networks with evenly distributed associations (Fig. 4a) to smaller networks with a similar relative number of associations but unevenly distributed (Fig. 4d), which an analysis focusing on species would not have revealed.

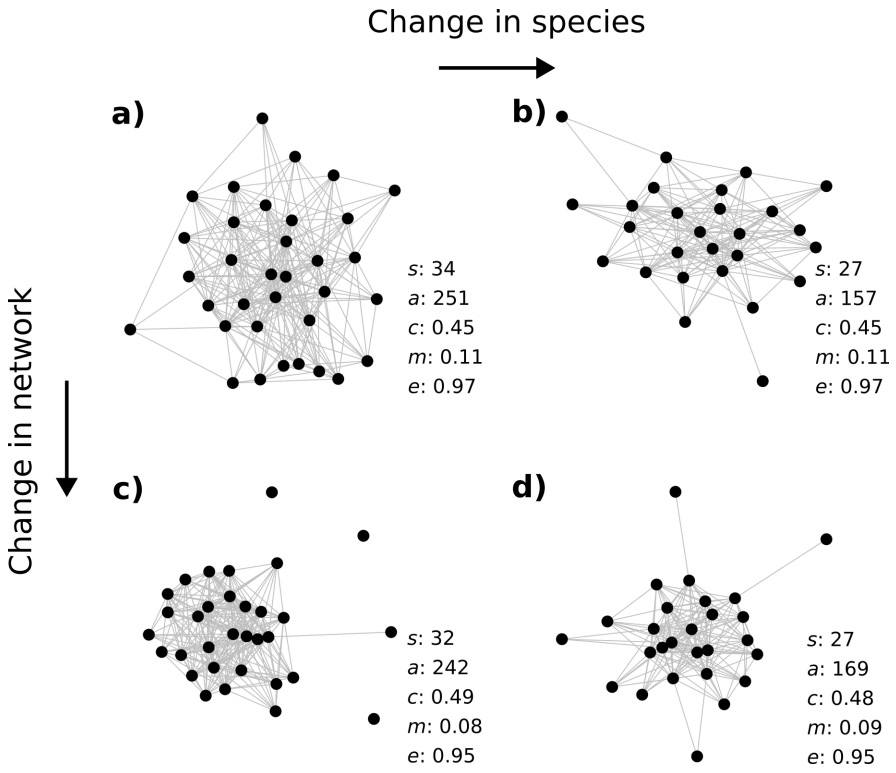

Figure 4: Examples of observed networks illustrating the topological changes between 2001 and 2017 with the values for each metrics. From a) a network with a given number of species *s* and network metrics (number of associations *a*, connectance *c*, modularity *m* and evenness *e*), b) network metrics may not be affected by a change in the number of species, c) conversely, a stable number of species may hide a change in network structure. d) On average, the observed changes in network structure show smaller networks with a similar relative number of associations but unevenly distributed at the end of the period studied.

4. Discussion

We assess temporal changes of reconstructed networks in bird communities over the last two decades in France. We document an increase in association density due to a decline in network size, not to an increase in the number of associations, and an increase in the heterogeneity in the number of associations per species (*i.e.* a decline in evenness), which can be observed in only two decades. This suggests that, as bird communities are declining in diversity, the underlying network experiences non-random changes with the replacement of moderately associated species with both highly and scarcely associated species.

4.1 Ecological relevance of associated species pairs

To analyse the ecological relevance of species pairs before reconstruction networks of bird communities, we relate associated species pair with ecological distances and observe that the species pairs are more prone to be associated when the two species share similar functional traits or habitat requirements. A part of phylogenetic diversity is encompassed by functional distance (see supplementary material 3), which could explain the absence of a significant relationship between associated species pairs and phylogenetic distance. The significant relationships with functional and niche overlap distances were in line with our hypothesis based on trait-based assembly theory and empirical results on birds (Mönkkönen et al. 2017) and suggest that our approach produced ecologically meaningful associated species pairs. Notice that despite this result and the strong filters applied in the estimation of associated pairs, some of the associated pairs can still be due to a common response to an environmental variable in space and time (Pollock et al. 2014) and that an absence of association does not imply an absence of interaction between two species (Cazelles et al. 2016). Yet, we provide an in-depth validation of the overall set of associated pairs using the ecological distances and confirm this by looking at expected interacted pairs of species based on specific interactions during the

breeding season (corresponding to the period of the survey) for food and nest location. The similarity in nest location is not significant and this may be due to the fact that competition would be the main expected interaction from this shared characteristic. On the contrary, a similar diet, that significantly increases the propensity to be associated, could induce both repulsion and attraction and thus is expected to induce interactions in a wider range of species pairs and to be more easily detected. This result supports the findings based on functional and niche overlap distances.

In addition to validation of theoretical expectations, several species associations found in our study were in line with current knowledge on species behaviour and interspecific relationships. For instance, the Common cuckoo (*Cuculus canorus*) was associated to the European robin (*Erithacus rubecula*), the Cirl bunting (*Emberiza cirlus*), the Common nightingale (*Luscinia megarhynchos*), and the Willow warbler (*Phylloscopus trochilus*), known to be frequent hosts of cuckoo's eggs (Davies and Brooke 1989, Moksnes and ØSkaft 1995). The Great spotted woodpecker (*Dendrocopos major*) is associated with the secondary cavity nesters, such as the Common redstart (*Phoenicurus phoenicurus*), the Great tit (*Parus major*), the Eurasian blue tit (*Cyanistes caeruleus*) and the Crested tit (*Lophophanes cristatus*) (van der Hoek et al. 2017). Therefore, if large-scale data are rarely optimal to accurately discriminate interaction type (e.g. competition or facilitation), strength and sign (Blanchet et al. 2020, Barraquand et al. 2021), highlighting sets of biologically meaningful associated species seems nevertheless within reach.

4.2 Specificity of intra-guild association networks

The analysis of network changes reconstructed from the associated species pairs shows a decrease in network size and in the evenness of the degree distribution as well as an increase in connectance. It

should be noted that changes highlighted here are based on network reconstructions that correspond to snapshots of networks, aggregating spatial and temporal data. The representativeness of these changes compared to actual changes in community structure may therefore vary according to the rate and extent of environmental change experienced by bird communities (Tylianakis and Morris 2017). In addition, the estimated links between species are coarse and static, whereas ecological interactions are known to be changing though time (i.e. in existence and strength), due in particular to changes in environmental conditions (Poisot et al. 2015). Despite the variability of interactions, species roles in network have been found to remain stable both in space and time (Baker et al. 2015, Emer et al. 2016), which support the analysis of network changes based on associated species pairs. Yet, the interpretation of network changes in intra-guild network is limited by the availability of empirical and theoretical research on this type of networks. The specificity of the interaction nature, compared to more frequently studied networks (e.g. mutualistic plant-pollinators, food-web), makes it difficult to generalise the findings based on plant-pollinator networks and food-web to intra-guild networks. In particular, the differences in the nature of links between our study and other network research might explained the relative importance of the changes observed here, while network properties are frequently reported to be stable in other network types such as frugivore-plant, pollination and foodweb networks (Petanidou et al. 2008, Kaartinen and Roslin 2012, Plein et al. 2013). Assuming an analogy where specialists species are supposed to be involved in fewer but stronger interactions, the existing literature based on plant-pollinator networks and food-web may however bring some clues, along with research on bird flocks (more closely related to intra-guild networks).

4.3 Network structural changes and consequences for conservation

If changes in connectance alone are not informative for conservation (Heleno et al. 2012), the increase in connectance is generally concomitant with a reduction of network size and might be accelerated by a relative loss of specialist species (Banašek-Richter et al. 2009). This would be consistent with the current knowledge on the decline of specialist species in bird communities (Devictor et al. 2008). Concerning the consequences for network properties, higher connectance can improve network persistence facing perturbation (Besson et al. 2019), which might be the case if all the fragile species and interactions are already wiped out while generalist involved in more associations relatively expand (Godet et al. 2015). However, if this connectance increase is at the cost of species removal, according to the biodiversity-ecosystem functioning theory (which is relevant inside a guild), this will result in a declining efficiency of resource use (Loreau 2010). According to our results, such a decline in community functioning is therefore expected for forest and farmland communities, in which the change in connectance is related to the decline in species number. Conversely, the structure and connectance of communities in natural open land are principally modified by the replacement of less associated species by more associated ones, expected to be generalists.

An increase in connectance also induces a decline in modularity (Delmas et al. 2019) which has been the case in bird communities, although modularity change is not stronger or weaker than expected (i.e. the modularity does not change through time when we control for changes in connectance Fig. 3d). A modular structure is known to reduce the impact and propagation of a perturbation throughout the network (Stouffer and Bascompte 2010). Therefore, considering consequences for networks properties, a decline in modularity might affect community network ability to cope with environmental changes and induce a higher sensitivity to cascade and secondary extinctions.

The observed decline in evenness of association degree distribution can be more directly interpreted. Low evenness in the distribution of interaction strength can be often observed in networks, due to the numerous weak interactions (Bascompte et al. 2005) known to stabilise community dynamics. However, when focusing on the presence of a link instead of its strength, the evenness of the distribution is higher in preserved or restored communities than in degraded habitats (Tylianakis et al. 2010, Fisogni et al. 2021), not only in food-webs but also in avian flocks (Mokross et al. 2014). It is therefore likely that the observed decline in evenness, which is higher than expected by the observed change in connectance, is the footprint of habitat degradation experienced by bird communities. This appears to be the case, in particular, in forest and farmland communities, which is consistent with the well-studied change on species dynamic and community composition over the past decades (Brotons and Jiguet 2010, Gaüzère et al. 2020, Rigal et al. 2023).

Although our study focuses on association networks that structure bird communities, this should not understate the importance of the marked decline observed in species numbers of those communities. A decline in species diversity and abundance is expected to affect interaction frequency as the encounter rate become lower. This could lead to the loss of some interactions while the two species are still present in the vicinity (Staniczenko et al. 2017, Tylianakis and Morris 2017). Yet, species remains a central unit for conservation purposes and our results show that change in ecological network structure should be analysed in regard with change in species number and identity (Heleno et al. 2012). This is even more important when the only observed change is the decline of network size, such as in urban communities, indicating that the stability of other network metrics is in fact due to an decline of associations density compared to what is expected. As urban communities are becoming smaller and less connected, this indicate that the remaining species are mostly disconnected specialists, filtered by the severe constraints imposed by the modern urban environment (Guetté et al. 2017, Rigal et al. 2022).

Changes in community structure and size highlighted in this study are crucial to understand how communities will be able to respond to future perturbations, in particular if community functioning is affected by changes in the network layout (Besson et al. 2019). Community responses are affected by the loss of species (Loreau and De Mazancourt 2013) which is, additionally, deepened by the rewiring (Tylianakis and Morris 2017) or the vanishing of associations (Gilljam et al. 2015). These rapid modifications of bird biodiversity, that would have been hidden by a species-centred approach, are expected to affect the stability of communities and their capacity to cope with rapid and multiple global changes.

Data availability: All the analyses are conducted using the R software v.4.2.2 (R Core Team 2018). Code and data are available on Zenodo https://zenodo.org/doi/10.5281/zenodo.12784005 (Rigal et al. 2024).

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