Linking biotic homogenisation with large-scale changes of species associations

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Abstract:

Aim: The impact of global change on biodiversity is commonly assessed in terms of changes in species distributions, species richness and species composition across communities. Whether and how much interactions between species are also changing is much less documented and mostly limited to local studies of ecological networks. Moreover, we largely ignore how biotic homogenisation (*i.e.* the replacement of a set of diverse and mainly specialist species by a few generalists) is affecting or being affected by changes in the structure of species interactions. Here, we approximate species interactions with species associations based on the correlation in species spatial co-occurrence to understand the spatio-temporal changes of species interactions and their relationship to biotic homogenisation.

Location: France.

Time period: 2001-2017.

Major taxa studied: Common breeding birds.

Methods: We use network approaches to build three community-aggregated indices to characterise species associations and we compare them to changes in species composition in communities. We evaluate the spatial distribution and temporal dynamics of these indices in a dataset of bird co-abundances of more than 100 species monitored for 17 years (2001-2017) from 1,969 sites across France. We finally test whether spatial and temporal changes of species associations are related to species homogenisation estimated as the spatio-temporal dynamics of β-diversity.

Results: We document a non-random spatial distribution of both structure and temporal changes in species association networks. We also report a directional change in species associations linked to β-diversity modifications in space and time, suggesting that biotic homogenisation affects not only species composition but also species associations.

Main Conclusions: Our study highlights the importance of evaluating changes of species association networks, in addition to species turnover when studying biodiversity responses to global change.

Keywords: Avifauna, β-diversity, homogenisation, community, interaction network, species association.

1. Introduction

Among the major effects of global change on biological diversity, the modification or even the extinction of species interactions has early on been identified as being pervasive, but is still poorly understood (Janzen, 1974; Diamond, 1989). Because there are many more interactions than species, a change in species interactions may be decoupled from changes in species richness or community composition (Poisot et al., 2017; Gravel et al., 2019). In particular, modifications on species

interactions can be stronger (Valiente-Banuet et al., 2015) or weaker (Li et al., 2018) than on species richness. The structure and dynamics of species interactions are among the main drivers of community dynamics (Davis et al., 1998; Barabás et al., 2016), and therefore represent a critical subject of study for ecology and biodiversity conservation (García-Girón et al., 2020). Despite the importance of integrating species interactions into conservation biology, we still have a limited understanding of the drivers and consequences of changes in the strength and the structure of species interactions.

In the last decades, there has been an increasing use of network approaches to study species interactions in empirical and theoretical communities (Bascompte et al., 2003; Ings et al., 2009; Kéfi et al., 2015; Trøjelsgaard & Olesen, 2016). The mathematical language of graph theory allows describing the topological features of any set of nodes and links that connect these nodes (Newman et al., 2006). Ecological communities can thus be depicted as interaction networks by defining nodes as individuals or species, and links between the nodes as species interactions. That is, networks enable to represent the complexity of ecological communities by jointly displaying species and their interactions. The estimation of species interactions is however subject to 1) a conceptual question (*what is actually estimated? E.g.* trophic interactions correspond to well defined processes whereas net effect interactions represent effects of aggregated processes) and 2) a technical challenge (*how to estimate an interaction?* Which, in turn, depends on the type of interaction to estimate). In some cases, like small range studies with few taxa, observations or experiments can address both issues as the existence and type of species interactions are clearly identified. However, these studies provide limited inference of species interactions as the scale and context dependency of interactions prevents the possibility to derive general rules for interactions in larger communities (Whittaker et al., 2005; Denny & Benedetti-Cecchi, 2012). The empirical identification and measure of interactions in species-rich communities is also challenged by the

number of potential interactions to be estimated (proportional to the square of species number) (Barner et al., 2018). One alternative approach to overcome the above challenges is to study communities using species “associations” inferred from species spatial aggregation (Morueta-Holme et al., 2016). While observed ecological interactions represent evidence of ecological relationships (*e.g.* predation or mutualism), species associations are based on inference from spatial co-occurrence.

The ability of spatial co-occurrence patterns to infer pairwise species interactions is still controversial (Blanchet et al., 2020). Nonetheless, co-occurrences might be an information-rich proxy of the outcome of direct and indirect biotic interactions in communities (Freilich et al., 2018; Delalandre & Montesinos-Navarro, 2018). The composition of a local community results from interspecific interactions as well as multiple intertwined processes generating specific patterns of spatial aggregation between species (Fig. 1). These factors include neutral processes (regional dispersion and local stochasticity), historical processes (phylogeography) and niche processes (Hubbell, 2001; Kraft et al., 2007; HilleRisLambers et al., 2012; Letten et al., 2017). Niche processes combine what is sometimes referred to as Grinnellian and Eltonian processes (Chase & Leibold, 2003; Devictor, Clavel et al., 2010). Grinnellian processes (Grinnell, 1917; later extended by Hutchinson, 1957) consider the niche as the species response to environmental conditions acting as an environmental filter for the community. Eltonian processes (Elton, 1927) consider the niche as the species impact on its environment and refers to the mutual dependency of species with each other, including limiting similarity hypothesis (*i.e.* niche overlap between two species that limits their coexistence) (MacArthur & Levins, 1967; Abrams, 1975; Martin & Bonier, 2018) and facilitation between species (*e.g.* cooperation, social information (Seppänen et al., 2007; Tu et al., 2019)).

While associations and interactions are difficult to disentangle in species surveys data, several methods can help refining species associations to approach the Eltonian component of the spatial co-abundances of species (*i.e.* the part of the co-abundances due to the biotic filter). A common approach is to examine whether species are found together more or less frequently than expected by chance based on null models. That requires controlling for the associations that are simply expected by chance rather than grounded in ecological processes (Gotelli, 2000; Ulrich & Gotelli, 2010; Kohli et al., 2018). Indirect effects between species (*i.e.* the effect of a third species on the association between two other species) have been evaluated using partial correlations (Faust & Raes, 2012; Harris, 2016). Recent progress with Joint Species Distribution Models has also provided ecologists with new tools for estimating species associations by studying residual co-occurrence patterns after accounting for environmental niches from large datasets (Tikhonov et al., 2017; Zurell et al., 2018). Overall, recent methods removing non-Eltonian components from co-occurrences (Azaele et al., 2010; Faisal et al., 2010; Ovaskainen et al., 2010; Lindenmayer et al., 2015) are promising for uncovering species association networks (Araújo et al., 2011; Morueta-Holme et al., 2016). In particular, if interaction networks remain out of reach (Sander et al., 2017, Freilich et al., 2018; Thurman et al., 2019), association networks may be relevant to capture community organisation through aggregated community indices, *i.e.* statistics summarising an aspect of the network at the community level (Barner et al., 2018).

Understanding how species associations are changing in space and time can have several implications for conservation biogeography. First, it is likely that the temporal rate with which species associations respond to environmental changes is not the same as the rate of the response of species composition itself (Valiente-Banuet et al., 2015). If species association responses to environmental changes are faster than species composition responses, monitoring their dynamics becomes crucial for implementing conservation policies early enough. Second, the magnitude of

structural changes which could affect a community is not directly reducible or accessible through modifications only in species composition, *e.g.* through the change in species diversity within local communities or, at a larger scale, between communities (β-diversity) (Poisot et al., 2017). While communities are getting more and more similar in species composition (Clavel et al., 2011; Newbold et al., 2018), it remains unclear how species association are changing (Li et al., 2018) as this depends on the initial association structure, and on whether remaining species can be associated with incoming species. Assessing changes in species associations and understanding the relationship between species homogenisation and species associations can help to better estimate the modifications experienced by community composition and structure. This is particularly important as ecological processes are ultimately influenced by which and how species interact (Cardinale et al., 2002; Goudard & Loreau, 2008).

In this study, our aim is to explore: 1) whether we can estimate species interactions from monitoring data available over large spatial and temporal scales, 2) what are the spatial and temporal patterns of such estimates, and 3) how such patterns are related to the biotic homogenisation process, *i.e.* the replacement of a set of diverse and mainly specialist species by a few generalists (McKinney & Lockwood, 1999; Olden et al., 2004)? To answer the three above questions we conduct a spatio-temporal analysis of bird species association networks where:

1. *we reconstruct species association networks in communities from co-abundance data*. We first infer species associations from the French Breeding Bird Survey co-abundance data corrected for non-Eltonian co-abundance processes. We then quantify different aspects of the species association networks using three complementary network indices: intensity, attractiveness and clique structure of the network. Intensity corresponds to the mean association strength. Attractiveness is the ratio of

positive/negative associations, and clique structure describes the structural complexity of the association network (Fig. 2).

2. *we track the spatial and temporal dynamics of species association networks* using those three community indices. We map the distribution of each network index across France and describe their temporal changes over 17 years (2001-2017).

3. *we test whether biotic homogenisation was linked to directional changes in association networks*. We analyse the relationship between the spatio-temporal dynamics in β-diversity and the spatio-temporal dynamics in bird associations measured by intensity, attractiveness and clique structure.

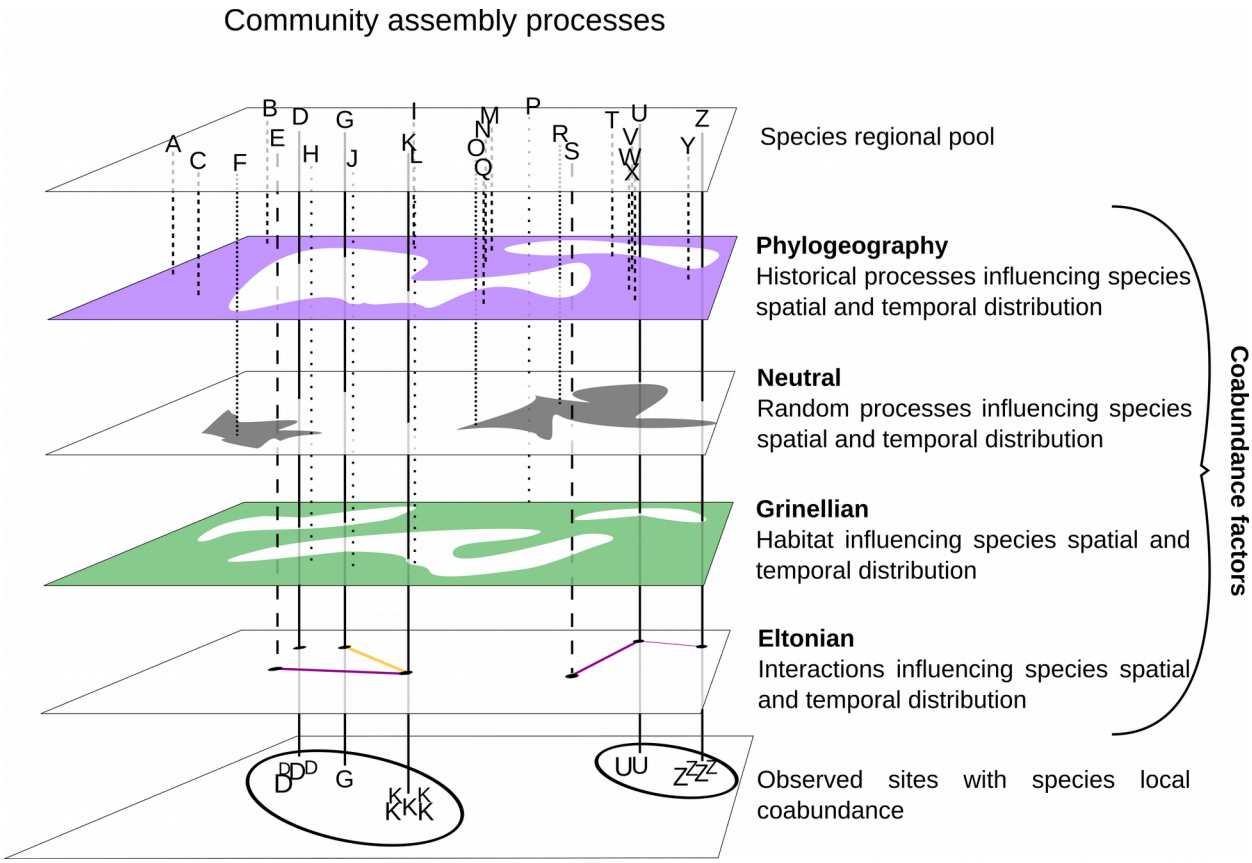

Figure 1: Community assembly processes and species co-abundance. Species' interactions that influence species spatial aggregation (or segregation) and temporal change in abundance are referred to as the Eltonian component of species co-abundance. In addition to the Eltonian

component, co-abundances are also the result of habitat filtering (Grinellian), random processes due to neutral dispersal, as well as historical processes related to the species phylogeography. The result of all these processes leads to the observed species co-abundances. Each letter stands for a different species. Species U and Z share a common biogeographic region and random processes have not prevented them from co-occurring. As they live in a similar habitat and interact in a way that enable their coexistence, they can be observed together in a same location at a same time.

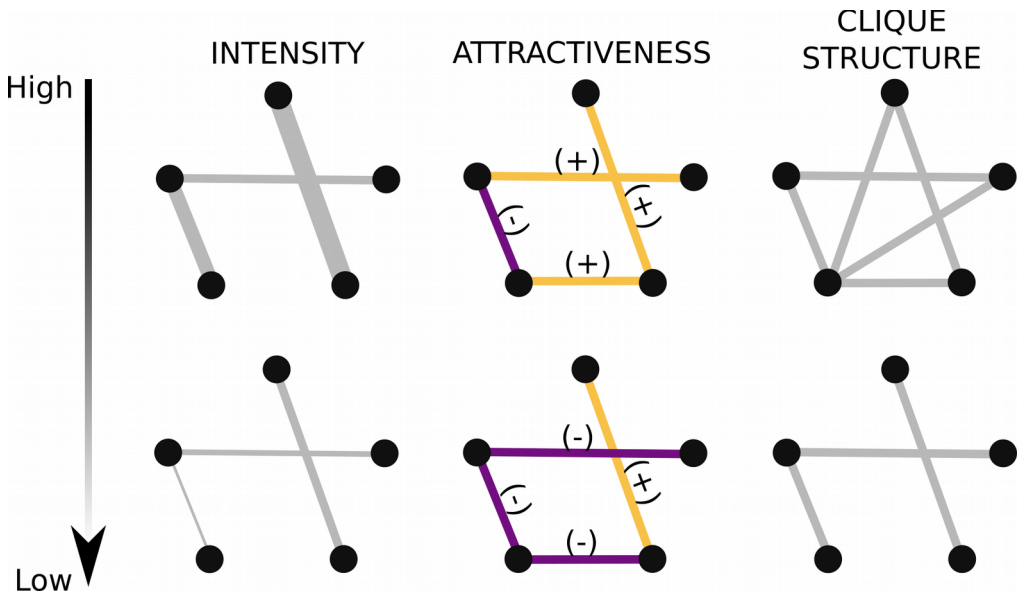

Figure 2: Association network indices: intensity (i.e. mean strength of species associations), attractiveness (predominance of positive (light orange) or negative (dark purple) species associations) and clique structure (level of structuration of the species association network). Dots represent species and lines stand for species' associations. For each index, examples corresponding to high and low values are displayed on the top and bottom rows, respectively. For intensity, the thicker the line, the higher the absolute value of the association. For attractiveness, the high value example is 0.5 (three positive associations and one negative association out of 4 existing associations) and the low value is -0.5. For clique structure, the high value is 0.125 (two realised cliques out of 16 possible cliques) and the low value is 0.

2. Materials and methods

2.1 Bird data

Bird data were extracted from the French Breeding Bird Survey (FBBS) (Jiguet et al., 2012). In this scheme, volunteer ornithologists monitored common bird species on 2,514 sites (Fig. 3) from 2001 to 2017, following a standardised protocol. Sites are 2x2 km squares in which breeding bird species and abundances were monitored on 10 homogeneously distributed sampling points across habitats in the landscape. In order to avoid habitat classes with too few observations, we grouped the 37 main types of habitat described in the field in 19 classes (see Appendix S1 in Supporting Information). Among the 242 species recorded in the dataset, we selected the 109 most abundant species (representing 99% of the total abundance) to avoid an over-representation of rare species (that are therefore more difficult to monitor). After removing rare species and the sites only monitored once, our dataset comprised 19,580 sampling points in 1,969 sites and 109 species (species list in Appendix S2).

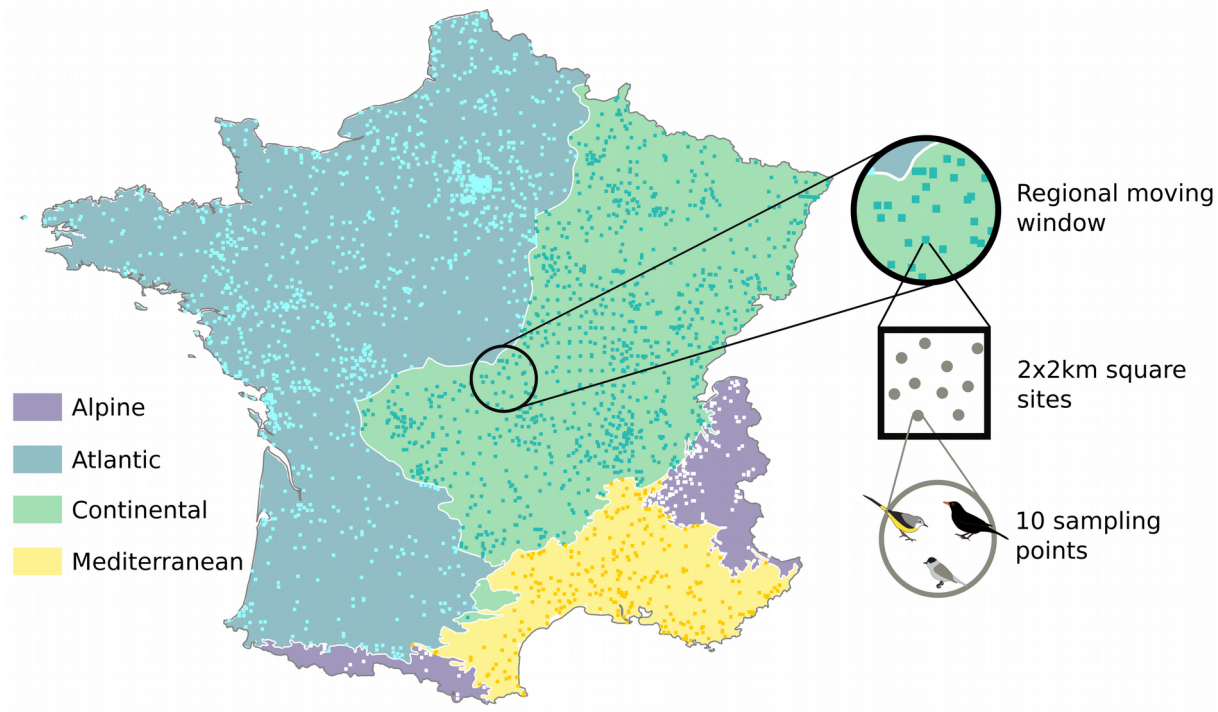

Figure 3: Spatial distribution of the 1,969 selected (out of 2,514) sites from the 2001 to 2017 FBBS (STOC-EPS). On each site (2x2 km square), bird observations were recorded on 10 sampling points. Geographically Weighted Regression using data from moving windows were used to assess metric values (see methods). Mainland France was split in 4 biogeographic regions (Alpine, Atlantic, Continental and Mediterranean).

2.2 Association network indices

We estimated associations between pairs of species from bird co-occurrence data (Morueta-Holme et al., 2016) for each year (2001 to 2017), for each of the four biogeographic regions and for each of the 19 habitats using the five following steps (Fig. 4).

Step 1. In order to limit the influence of phylogeography and habitat features on species associations, we first grouped the data by biogeographic region (Continental, Atlantic,

Mediterranean, Alpine), by habitat and by year to estimate an association for each pair of bird species, for each year, for each of the four biogeographic regions (EEA, 2016) and for each of the 19 habitats (19 classes inherited from the habitat described by observers, see Appendix S1).

Step 2. In each biogeographic region and habitat, we used the log-transformed co-abundance data (to obtain normally distributed data) to calculate observed associations as partial correlations between each pair of species (Schäfer and Strimmer 2005) as follows (Eq. 1):

$$Pc(O)_{i,j} = \frac{-\sum_{i,j}^{-1}(\mathrm{O})}{\sqrt{\sum_{i,i}^{-1}(\mathrm{O}).\sum_{j,j}^{-1}(\mathrm{O})}} \qquad (1)$$

with O the matrix of observed abundance (species x sites), $Pc(O)_{i,j}$ the partial correlation between species i and j, and $\Sigma_{i,j}^{-1}$ the value for species i and j of the inverse of the covariance matrix. Given that the association between two species can be influenced by the presence of another co-occurring species, this approach partially removes the indirect effects of the other co-occurring species on the estimated association between the two considered species, by focusing on the conditional association (Harris, 2016; Morueta-Holme et al., 2016).

Step 3. Partial correlations can be affected by species commonness, common species having higher probabilities to co-occur than less abundant species only because of higher representativeness in the data (Blüthgen et al., 2008). To correct this bias, we computed partial correlations on 1000 random co-abundance 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 then calculated partial correlation standardised effect size of species i and j ($SES_{i,j}$) as follows (Eq. 2):

$$SES_{i,j} = \frac{Pc(O)_{i,j} - \mu\left(Pc(N)_{i,j}\right)}{\sigma\left(Pc(N)_{i,j}\right)} \qquad (2)$$

where $Pc(O)_{i,j}$ is the observed partial correlation between species i and species j, $\mu(Pc(N))_{i,j}$ and $\sigma(Pc(N))_{i,j}$ the mean and standard deviation of partial correlations from the 1000 randomly sampled datasets.

Step 4. In order to identify "significant" associations, we calculated a two tail p-value for each pairwise association using the rank of the observed association in the Gaussian distribution of null associations. That is, we determined the number of replicates for which the absolute value of the observed partial correlation is greater than the absolute null partial correlation (p-values were corrected for multiple comparisons following Benjamini & Hochberg, 1995). Significant associations therefore corresponded to $SES_{i,j}$ for which adjusted p-values were below 0.05.

Step 5. For each species pair, for each biogeographic region and for each habitat, we averaged the significant associations over the 17 annual associations (one for each year). In the absence of any significant association across the 17 years, the association was considered null (*i.e.* equal to zero). This results in a total set of 260,191 association estimates, spread over 5,886 pairs of species, four biogeographic regions and 19 habitats (and see relationship between associations and functional dissimilarity in Appendix S3).

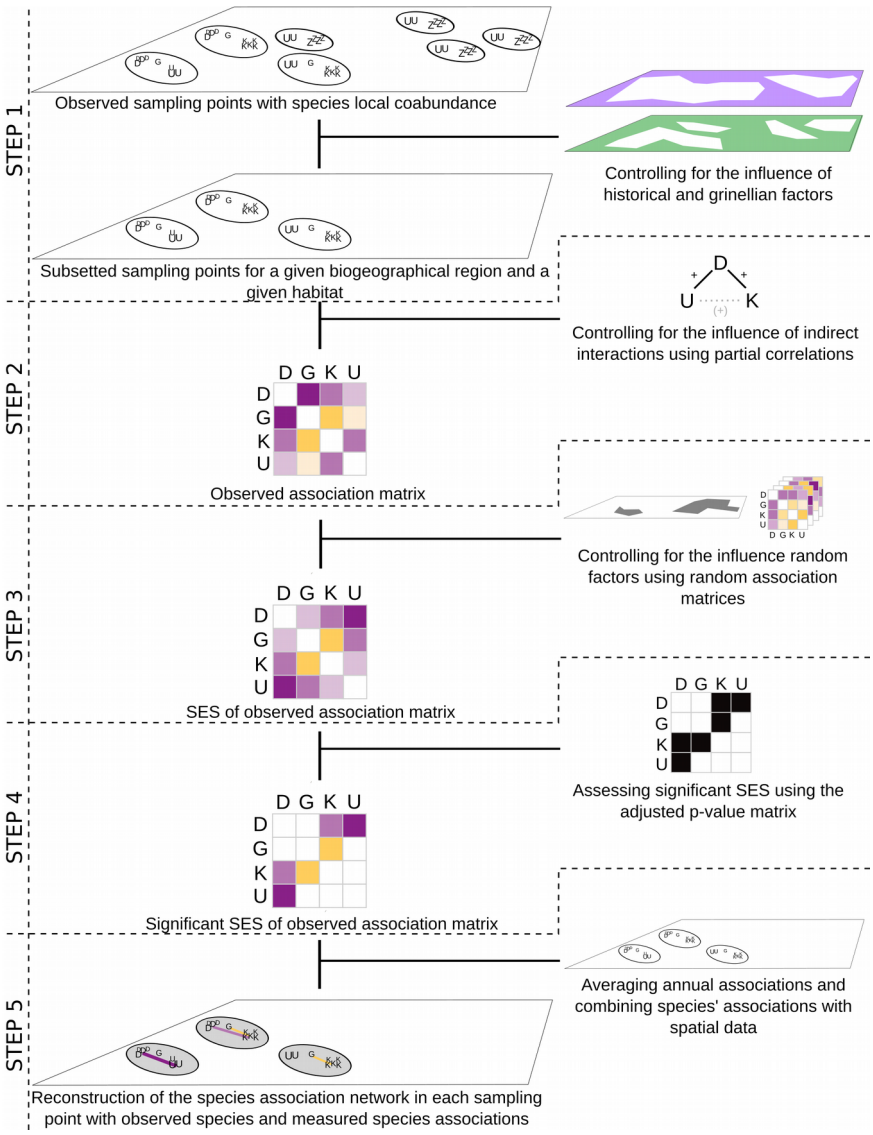

Figure 4: Workflow for estimating species association networks. For each biogeographical region and each habitat (Step 1), an observed association matrix was obtained by partial correlations (Step 2) (positive correlations in orange, negative correlations in purple, colour intensity proportional to correlation strength) from co-abundance data (species D, K, G, U as an example). Random association matrices were calculated using partial correlations on permuted datasets (1000 times) and were used to calculate standard effect sizes (Step 3) of observed associations as well as their adjusted p-values to obtain significant SES of the observed association matrix (Step 4). Steps 1 to 4 were repeated for each year providing annual associations, which were then averaged over years for each species pair. Species' associations were finally added to the spatial co-abundance data to obtain a species' association network for each of the sampling points (Step 5).

2.3 Community-wide association indices

We joined association estimates obtained from section 2.2 with annual species presence and abundance to describe species association networks with three mathematically independent indices that describe different aspects of the network (Fig. 2) (examples in Appendix S4). The three indices were calculated for 121, 172 networks corresponding to the communities monitored in the 19,580 sampling points between 2001 and 2017.

Intensity *I* quantifies the strength of associations in the species association network of a community. It reflects the average intensity of the associations in the network. It is weighted to account for the differences between species abundances (Eq. 3).

$$I = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} n'_{ij} \cdot |\alpha_{ij}|}{\sum_{i=1}^{n} \sum_{j=1}^{n} n'_{ij}} \qquad (3)$$

with n the number of species, n'_{ij} the number of pairs of species i and j in the community pool, and α_{ij} the association (as defined in step 5) between species i and j (with $i \neq j$; when $i=j$, $\alpha_{ij}=0$). I varies between 0 and $|\alpha|_{max}$. High values of I are reached in communities including mainly strong associations.

Attractiveness *A* quantifies the prevalent sign of the associations as the number of positive associations minus the number of negative associations standardised by the total number of associations (Eq. 4). Attractiveness is analogous to the *association ratio* in plant networks (Saiz et

al., 2014). However we choose not to use *association ratio* because it also stands for methods estimating associations (Chiyo et al., 2011).

$$A = \frac{\pi^{+} - \pi^{-}}{\pi^{+} + \pi^{-}} \tag{4}$$

with π^{+} the number of positive associations and π^{-} the number of negative associations. It varies between -1 (if all the associations are negative) and 1 (if all the associations are positive).

Clique structure *C* quantifies the level of structuring of the species association network. It is calculated using the number of existing cliques (*i.e.* fully connected groups of species, Luce and Perry 1949) with three or more nodes, standardised by the number of potential cliques in a given network (Eq. 5).

$$\begin{aligned} C &= \frac{c_{obs}}{c_{max}} \\ &= \frac{c_{obs}}{\sum_{i=3}^{n} \binom{n}{i}} \\ &= \frac{c_{obs}}{\sum_{i=0}^{n} \binom{n}{i} - \sum_{i=0}^{2} \binom{n}{i}} \\ &= \frac{c_{obs}}{2^{n} - \frac{n(n+1)}{2} - 1} \end{aligned} \tag{5}$$

with c_{max} the maximum possible number of 3- to *n*-cliques, c_{obs} the observed number of 3- to *n*-cliques, *n* the number of species in the network.

C quantifies the complexity of the network architecture resulting from the interweaving of associated species (see Appendix S4). Networks with higher *C* values have more complex structure, with multiple imbricated groups of interconnected species. Networks with low *C* only have a few small sized interconnected groups of species.

We controlled the intensity, attractiveness and clique structure values for differences in species abundance and network size (see Appendix S4) for each of the 121, 172 species association networks.

2.4 Spatial averages and temporal trends in association network indices

2.4.1 Spatial averages of association network indices

For spatial analyses, we averaged the annual values of each index (*I*, *A* and *C*) for each sampling point, resulting in one value for each index for each sampling point. We then computed "spatial window values" of each association network index, for each site and for each year, using an 80-km radius window. We determined the window size as a compromise between a large spatial coverage and a fine spatial resolution and we conducted all subsequent analyses for various radii to assess the robustness of our results to changes in the window size (see Appendix S5). Spatial window values were computed to analyse, on a similar spatial scale, the relationships between community indices and β-diversity which is an inter-site measure based on species data from multiple sites (see below part 2.5). It also provided more complete data when sampling points or sites were not monitored every year, in particular for calculating temporal trends (see below part 2.4.2). We estimated spatial window values using Geographically Weighted Regression (GWR) (Gollini et al., 2015). In this approach, the centre of each site was consecutively considered as the centre of a fixed radius window. Each index was calculated using data from all sampling points encapsulated within the spatial window. A weight was attributed to each sampling point, which decreased with the distance to the central selected site following a bisquare kernel function.

2.4.2 Temporal trends of association network indices

We estimated the “spatial window trends” as the temporal trend of each association network index (*I*, *A* and *C*) following the same framework as for spatial window values (see above 2.4.1). The trend of each index corresponds to the coefficient of a linear regression calculated using annual index values in the selected sampling points, weighted according to their proximity to the central site. Only significant trends were used for subsequent analyses.

2.5 Spatial and temporal variation of β-diversity

We assessed the spatial and temporal variation of β-diversity following the same framework as for spatial window values (see paragraph 2.4.1). β-diversity corresponds to species diversity between a set of sites. It results here from the conversion of the bias-corrected β-entropy into β-diversity (*entropart* R package, Marcon et al., 2014). We first aggregated species data from sampling point level to site level to obtain species data for each site. We then randomly selected 10 sites in each spatial window (see 2.4.1) (Devictor, Mouillot et al., 2010) and computed β-diversity of the set of sites in that window. We repeated 10 times this selection step, and we took the mean of β-diversity.

2.6 β-diversity vs. association indices

We initially analysed the relationship between β-diversity and the three association network indices using their spatial window values. More particularly, we performed general additive models (GAM) to assess the linear relation between the three community indices and β-diversity while explicitly modelling the spatial autocorrelation. That is, to test the link between spatial values of community

indices and β-diversity, each association network index (*I*, *A* and *C*) was successively considered as the response variable regressed over β-diversity. We explicitly modelled the spatial autocorrelation using a two dimension isometric thin plate regression spline based on geographic coordinates of sites following Wood (2003, 2017).

Using a similar model, we finally tested the relationship between the temporal trend of β-diversity and the temporal trends of the three association network indices using their spatial window trends. Limits of relying on space-for-time substitution (*i.e.* relying only on spatial gradient to infer temporal relationships) are well known (Damgaard, 2019), this final step was therefore essential to support results from the spatial analysis.

All the analyses were made using the R software 3.4.4 (R core team, 2018).

3. Results

3.1 species associations from co-abundance

We found 8.1% positive associations, 38.3% negative associations, whereas 53.6% associations were non-significant. 71.9% of the species pairs showed qualitatively constant associations (*i.e.* significant associations that were either always positive or negative) across habitat/biogeographic region combinations. On average, each species showed between 73 and 108 associations (mean=103.9, sd=6.2) with wide variations between habitats and biogeographic regions (associations available in Appendices S6 and S7). Some individual species such as the lesser spotted woodpecker (*Dendrocopos minor*) or the common grasshopper warbler (*Locustella naevia*)

appeared more prone to be positively associated with other species. Conversely the Sardinian warbler (*Sylvia melanocephala*) was generally negatively associated with other species.

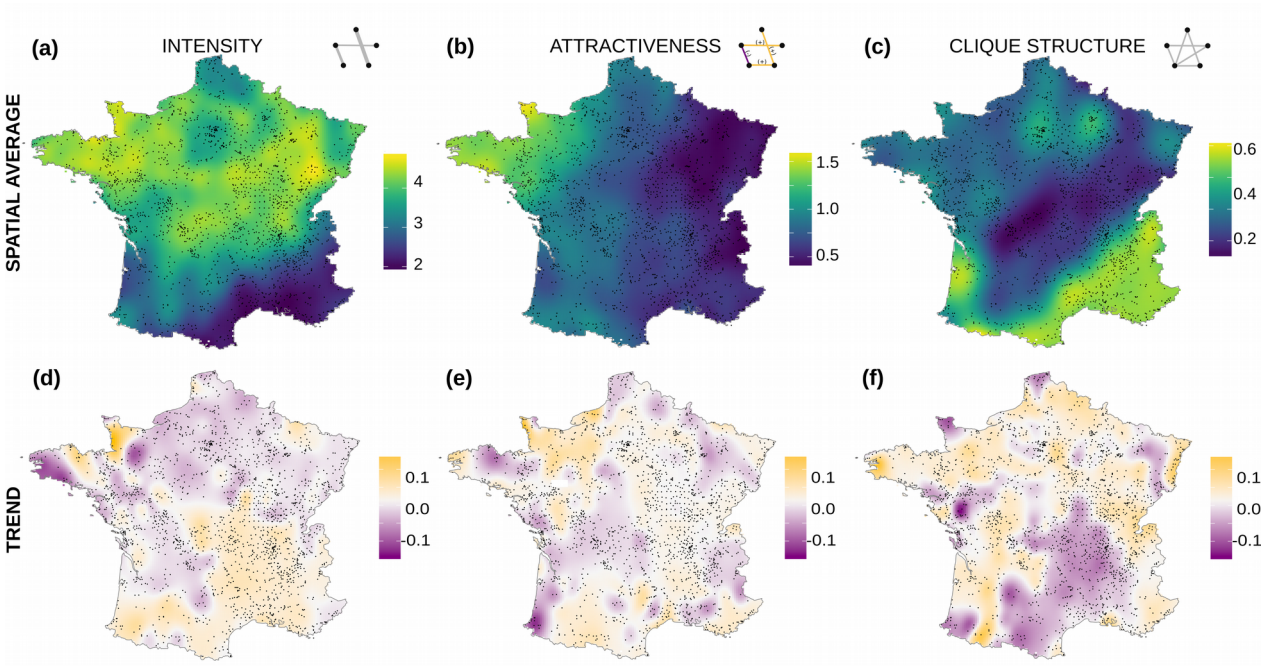

Figure 5: Spatial distribution of three indices of the association networks of bird communities. First row: Average value of (a) intensity, (b) attractiveness and (c) clique structure (average values between 2001 and 2017). Low values are represented in dark blue and high values in light yellow. Second row: spatial distribution of the temporal trends of (d) intensity, (e) attractiveness and (f) clique structure of the association networks of bird communities between 2001 and 2017. Negative values are represented in dark purple, null in grey and positive in light orange.

3.2 Spatial and temporal variation in community intensity, attractiveness and clique structure of associations

Intensity (*i.e.* the mean association strength in the network) was high in most parts of France except for the Mediterranean (south-eastern) and northern areas (Fig. 5a). Attractiveness (*i.e.* the ratio of

positive versus negative associations) was low in most parts of France except for the western and Pyrenean (south-western) areas (Fig. 5b). Clique structure (*i.e.* the ratio of existing versus possible cliques) was low in most parts of France except for the Mediterranean and Alpine (south-eastern) areas (Fig. 5c).

The temporal trend in intensity decreased in the northern areas and increased in the Mediterranean and mountainous areas (south-western and south-eastern) (Fig. 5d). Temporal changes in attractiveness were weak with only few substantial increases restricted to small areas such as the western coast (Fig. 5e). The clique structure decreased in the south-central France (Fig. 5f) (scale dependent relationships and spatial distribution of correlation between index trends in Appendix S5).

3.3 Relations between the association network and β-diversity in space and time

β-diversity clearly showed higher values in the Mediterranean region (south-eastern) than in other regions (see Appendix S8). Spatial distribution of trends in β-diversity did not exhibit any clear pattern, but small patches of alternatively positive or negative temporal trends (see Appendix S8).

In space, β-diversity was negatively related to intensity (slope = -0.14 ± 0.005, t-value=-26 , p-value < 2.10^{-16}, df=1943, adjusted r^2 = 0.73) (Fig. 6a). β-diversity was negatively related to attractiveness (slope = -0.25 ± 0.016, t-value=-16, p-value < 2.10^{-16}, df=1943, adjusted r^2 = 0.69) (Fig. 6b). β-diversity was positively related to clique structure (slope = 0.33 ± 0.02, t-value=17, p-value < 2.10^{-16}, df=1943, adjusted r^2 = 0.75) (Fig. 6c). Moreover, if one looks at the spatial distribution of these

relationships, they are generally uniformly distributed and consistent (at the exception of some restricted areas, see Appendix S8).

In time, temporal trends in β-diversity were negatively related to the temporal trends in intensity (slope = -0.04 ± 0.018, t-value=-2, p-value = 0.01, adjusted r^2 = 0.12) (Fig. 6d). The temporal trends in β-diversity and the trend in attractiveness were also negatively related (slope = -0.09 ± 0.03, t-value=-3, p-value = 0.003, adjusted r^2 = 0.18) (Fig. 6e). However, the trends in β-diversity and the one in clique structure were not significantly related (slope = -0.08 ± 0.11, p-value = 0.45, adjusted r^2 = 0.19) (Fig. 6f). These temporal results corroborated the relationships found above for spatial values for intensity and attractiveness but not for clique structure. Yet, if one looks at the spatial distribution of these relationships, they are generally not uniformly consistent across space (see Appendix S8).

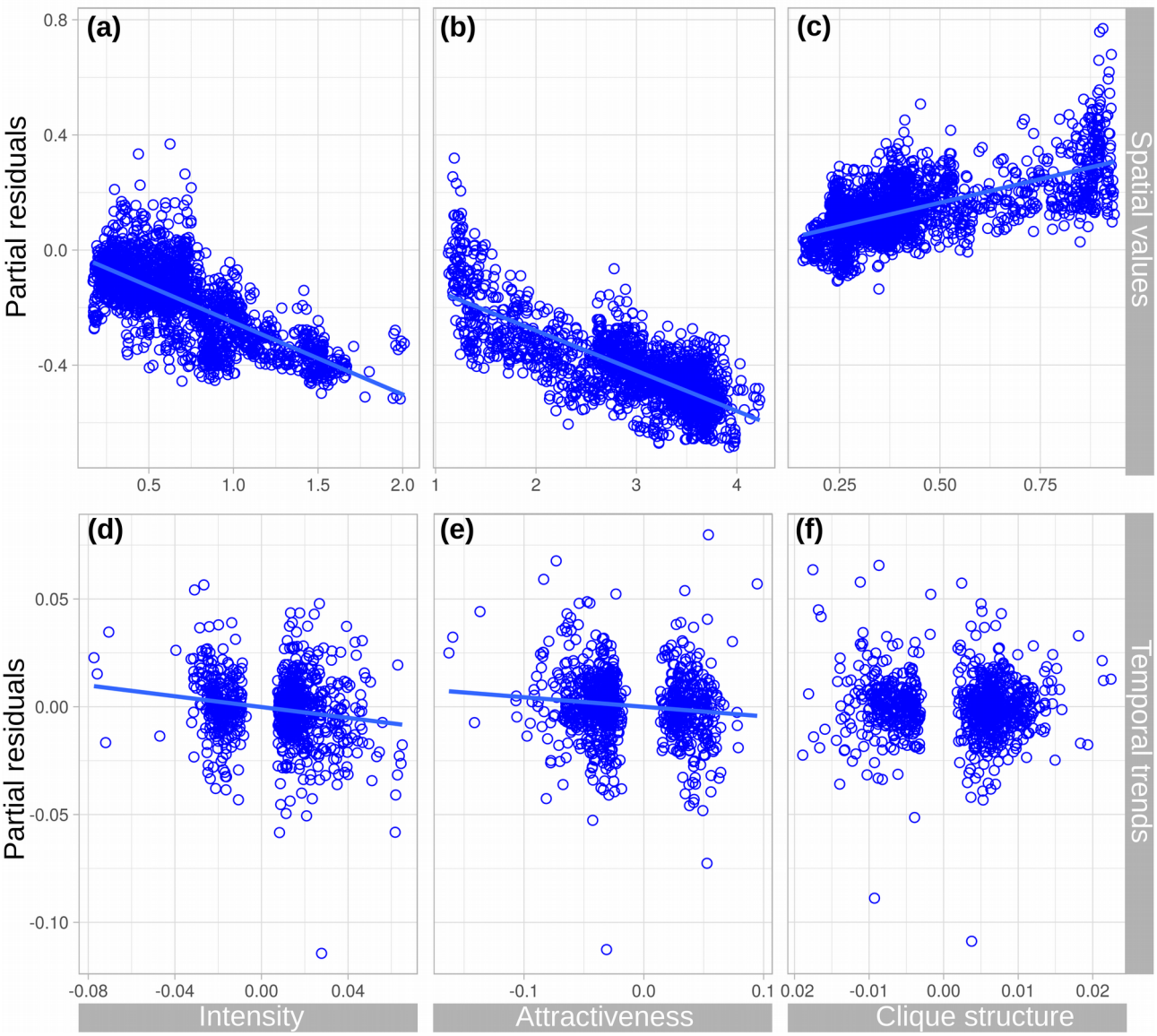

Figure 6: Effects association network indices on β-diversity display with partial residuals of the regression models regressed over predictors. First row: effects of (a) intensity, (b) attractiveness and (c) clique structure on β-diversity. Second row: effects of (d) trends in intensity, (e) trends in attractiveness and (f) trends in clique structure on trends in β-diversity. Gaps around zero are due to the removal of non-significant trends. Regression lines are shown when significant.

4. Discussion

Deciphering the relationship between species homogenisation and structure of association networks, is an important issue for macroecology and conservation biogeography. This is all the more critical at a time when biotic homogenisation (*i.e.* the replacement of a diversity of mainly specialist species by a few generalists, McKinney & Lockwood, 1999) triggered by ongoing global change (Devictor et al., 2008; Lockwood et al., 2000; Godet et al., 2015) is considered as one of the most pervasive aspects of the biodiversity crisis (Olden et al., 2004). At the local scale, we measured the homogenisation of bird communities as a decrease of β-diversity (McGill et al., 2015) in space and time. Our study unravelled clear relationships between species homogenisation and changes affecting species associations. These relationships could be revealed thanks to the reconstruction of association networks from co-abundance data and to the ability of tracking modifications in those networks through adequate indices. We showed that homogenisation of communities was linked to stronger intensity and more positive attractiveness both in space and time, and with weaker clique structure but only in space. In other words, more similar areas in terms of species composition sheltered stronger and more positive associations but less structured association networks. Also, communities that tend to be more similar in time exhibited a temporal increase in intensity and attractiveness.

Our results emphasize that biotic homogenisation and modifications in association networks are not independent processes, which bring about a new repercussion of environmental change and species community homogenisation (see also Li et al., 2018). Concomitant analyses of species associations and species homogenisation are still scarce particularly in animal networks but some earlier empirical and theoretical studies in food-web, mutualistic-antagonistic and host-parasite systems suggest some plausible causes and implications of interdependent biotic homogenisation and association networks. Mougi & Kondoh (2012) and Kokkoris et al., (2002) found a negative relationship between species diversity and intensity of interactions similar to the one we find in our

association networks. A decrease in β-diversity is directly related to a relative increase of generalist species at the expense of specialists in communities in birds (Le Viol et al., 2012). Moreover, a few studies suggest a positive link between interaction strength and species generalism because generalists tend to have stronger interactions than specialists (Vázquez et al., 2007; Schleuning et al., 2011). Thus, the relationship between an increase in the relative abundance of generalist species and their propensity to build strong associations is likely to explain the relationships observed between variations in association network intensity and β-diversity in space and time.

The negative relationship observed between β-diversity and attractiveness was more equivocal. The prevalence of either positive or negative interactions might be mainly driven by specific pressures (*e.g.* physiological stressors) rather than species specialisation, at least in plant networks (Callaway et al., 2002; Maestre et al., 2009; He et al., 2013). However, the negative relationship between β-diversity and attractiveness was found both in space and time, suggesting that species contributing to increase the community similarity are more likely to be positively associated together. Nonetheless, the positive relationship observed between β-diversity and clique structure in space partly contradicted our expectations. Previous studies showed that specialists established fewer interactions than generalists (Bascompte et al., 2003; Ings et al., 2009) which should result in networks with an increasing clique structure along with their homogenisation. Our results showed, on the contrary, that more fully connected association networks were found in areas where species homogenisation was weak (*i.e.* still relatively numerous specialists). This result could however be partly explained by the lower abundance of weak associations in areas where β-diversity is low, which is in line with the decrease in the number of weak interactions (generally more numerous than strong ones) observed in disturbed communities (Tylianakis et al., 2010).

Our results also revealed that changes in clique structure were related to species homogenisation in space, but not in time. The spatial relationships, in turn, showed strong local variability in direction and magnitude. A possible explanation of the temporal decoupling between clique structure and β-diversity and the spatial variability of relationships observed in some areas, is that, as interactions, associations might be impacted by environmental pressures in a different way from species themselves. This is coherent with previous results on the link between species homogenisation and association homogenisation in plants (Li et al., 2018). Environmental pressures may then act as structural forces modifying association networks and species compositions at different scales of time and intensity. Fragmented or disturbed landscapes have been shown to be less favourable to specialists (Devictor et al., 2008) than to generalist species, and this resulted in partially or entirely reshaped networks even if the species turnover was restricted (Laliberté & Tylianakis, 2010; Mokross et al., 2014; Poisot et al., 2015; Burkle et al., 2016; Tylianakis & Morris, 2017). In such a case, the effect of environmental drivers on species association networks could outcompete their effect on species diversity. Concomitant and complementary analyses of the fate of species composition and structure of association networks are thus fundamental to define the impact of environmental pressures on communities.

Despite the fact that environmental pressures may influence ecological network structure, whether the responses of association networks are similar to those of interaction networks remains an open question. Several studies recurrently showed the difficulties to use species associations as evident proxies of species interactions (Sander et al., 2017; Freilich et al., 2018; Thurman et al., 2019; Blanchet et al., 2020). species associations are indeed potentially affected by non-biotic filters and some types of species interactions remain inaccessible from co-occurrence, *e.g.* amensalism (Morales-Castilla et al., 2015). While our methodology takes into account non-biotic filters, it is still subject, by construction, to the inaccessibility of some type of interactions. Another pitfall is the

difficulty to estimate temporal variation in species associations from co-occurrence data as, currently, only state-space models may allow to quantify species interrelations in varying environments (Deyle et al., 2016) and this approach requires long time-series generally not available across multiple sites and at large scales. This prevented us from estimating temporal variations in associations although species interaction are known to vary in the short (Price et al., 2005; Olesen et al., 2008) and long term (Li & Waller, 2016; Lyons et al., 2016) particularly in response to environmental changes (Rico-Gray et al., 2012; Tikhonov et al., 2017; Bimler et al., 2018; Clark et al., 2018). In spite of these limitations, coupling trait-based indices with associations suggested that species associations, if carefully estimated, could encapsulate at least some biological significance (see Appendix S3). In such a case, species associations, via aggregated indices (Barner et al., 2018) and together with changes in species, may provide a useful proxy to explore the drivers of changes in ecological networks.

Conclusion: Implication for current and future biotic homogenisation patterns and processes

We studied the species-by-species associations in the French bird communities and used them to analyse the species association network in communities focusing on the Eltonian component, *i.e.* the part of the co-abundance due to the biotic filter. We considered three aspects of community dynamics, referring to the structure and composition of the species associations within communities. These associations and their structure provided complementary information on the biotic homogenisation process estimated through changes in beta-diversity. These results imply that, in addition to abundance and taxonomic diversity (La Sorte & McKinney, 2007; Schipper et al., 2016), species associations and the topological properties of association networks should be taken into consideration to better describe and understand biotic homogenisation, beyond the uniformisation of species composition. This is particularly critical to not underestimate changes

affecting biotic communities. It is indeed likely that ongoing global change is affecting this overlooked aspect of biological diversity. Conservation biogeography efforts should therefore develop strategies towards the maintenance of complex and dynamic associations in space and time beyond the protection of individual species.

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Data Accessibility Statement:

The database and an R script will be made publicly available in the Dryad online repository.