Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2014) **23**, 780–788

A Journal of Macroecology

Global Ecology and Biogeography

RESEARCH PAPER

Asynchrony of taxonomic, functional and phylogenetic diversity in birds

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ABSTRACT

Aim We assessed the temporal trends of taxonomic, functional and phylogenetic diversities in the French avifauna over the last two decades. Additionally, we investigated whether and how this multifaceted approach to biodiversity dynamics can reveal an increasing similarity of local assemblages in terms of species, traits and/or lineages.

Location France.

Methods We analysed a large-scale dataset that recorded annual changes in the abundance of 116 breeding birds in France between 1989 and 2012. We decomposed and analysed the spatio-temporal dynamics of taxonomic, phylogenetic and functional diversities and each of their α-, β- and γ-components. We also calculated the trend in the mean specialization of bird communities to track the relative success of specialist versus generalist species within communities during the same period.

Results We found large variation within and among the temporal trends of each biodiversity facet. On average, we found a marked increase in species and phylogenetic diversity over the period considered, but no particular trend was found for functional diversity. Conversely, changes in β-diversities for the three facets were characterized by independent and nonlinear trends. We also found a general increase in the local occurrence and abundance of generalist species within local communities.

Main conclusions These results highlight a relative asynchrony of the different biodiversity facets occurring at large spatial scales. We show why a multifaceted approach to biodiversity dynamics is needed to better describe and understand changes in community composition in macroecology and conservation biogeography.

Keywords

Beta diversity, breeding bird survey, functional traits, homogenization, Rao, species turnover, temporal dynamics.

INTRODUCTION

Past as well as recent rapid global change has already triggered community reshuffling and important species range shifts across the globe (Parmesan, 2006). An increasing number of studies have also quantified the potential future impacts of global change on the composition of local communities over large areas by sorting particular species, functional traits or lineages (Thuiller *et al.*, 2011; Le Viol *et al.*, 2012; Buisson *et al.*, 2013). In this context, it is now widely acknowledged that strategies for conserving biodiversity should no longer focus solely on species richness, but also on the ecological functions performed by species and on the evolutionary history supported by lineages (Diniz-Filho *et al.*, 2013). Functional diversity allows us to account for the differences among species in their ecological traits, and is a key factor in understanding ecosystem

DOI: 10.1111/geb.12179

functioning (Naeem *et al.*, 2012). For instance, the disappearance of species that represent unique functional traits may have drastically different consequences from the disappearance of the same number of species having common functional traits (Mouillot *et al.*, 2012). Phylogenetic diversity, on the other hand, can represent a proxy for functional diversity (i.e. more lineages represent more functions; Cadotte *et al.*, 2009) or be considered as an important aspect of evolutionary history of conservation interest (Winter *et al.*, 2013).

Taken together, the use of a multifaceted approach to describe the spatial distribution of biodiversity has recently proved to be useful for describing how biodiversity covaries in space, unravelling assembly mechanisms (Cadotte *et al.*, 2013) and understanding the drivers explaining community composition (e.g. Pavoine *et al.*, 2009 for rockfish; Graham *et al.*, 2012 for hummingbirds; Huang *et al.*, 2012 for mammals; or Bernard-Verdier *et al.*, 2013 for plants).

Future scenarios of change in biodiversity have been recently extended to include phylogenetic diversity (Thuiller *et al.*, 2011); changes in the functional composition of communities have also been documented (Villéger *et al.*, 2010). However, whether these different facets of biodiversity change show similar temporal trends remains largely unexplored (Magurran *et al.*, 2010). For example, a net increase in regional species richness may be accompanied by a decrease in functional diversity (Villéger *et al.*, 2010; Baiser & Lockwood, 2011). Metrics other than traditional diversity indices may thus be necessary to picture the actual trends.

The interest in the study of these facets of biodiversity can be fostered by spatially partitioning them into α-, β- and γ-diversity (Ricotta, 2005a; Jost, 2007). The trend in γ-diversity provides information about the dynamics of the diversity in a specific area, while the trend in α-diversity reflects the trends of each local community within this area. The complementary use of β-diversity reflects the turnover (taxonomic, functional or phylogenetic) among communities (Bernard-Verdier *et al.*, 2013). This decomposition of biodiversity facets into α-, β- and γ-components was shown to be valuable in conservation or macroecological studies (Melo *et al.*, 2009; Meynard *et al.*, 2011). Nevertheless, it remains unclear whether these complementary components have similar temporal dynamics. For instance, after a decrease in taxonomic β-diversity, functional β-diversity may or may not decrease, depending on how functional traits are distributed among communities.

Apart from multifaceted approaches, community-weighted means (CWM) were specifically developed to measure the relative change in abundances (or occurrences) of species with specific traits (or any characteristics) within communities (Ricotta & Moretti, 2011). These traits can be a priori selected to reflect species-specific sensitivities to a given pressure. For instance, following habitat or climate changes, individuals (or species) sensitive to those changes should be replaced locally by other individuals (or species) that benefit from the same changes. This approach has been successfully used to show that, following habitat disturbance, species dependent on a few habitat types (specialist species) tend to be replaced by generalist species (Kampichler *et al.*, 2012; Le Viol *et al.*, 2012), a process interpreted as a specific form of biotic homogenization (Clavel *et al.*, 2010). While the complementarity between CWM and other diversity metrics has been proposed to better describe community reshuffling (Ricotta & Moretti, 2011), the relevance of these two alternative approaches has never been supported by empirical data at large temporal and spatial scales.

Here, we conducted a temporal analysis of biodiversity dynamics (i.e. taxonomic, functional and phylogenetic diversities and their respective spatial turnover) and of a CWM measuring the average community specialization of bird communities. We analysed data from a high-resolution survey of birds conducted over two decades in France (1989–2012), a time period during which large climate (Jiguet *et al.*, 2010) and land-use changes (Antrop, 2004) have taken place in Europe. More specifically, we: (1) assessed whether taxonomic, functional and phylogenetic diversities (and their respective spatial turnover) had different temporal trends over the same period; and (2) investigated the complementarity of multifaceted approaches and CWM to reveal potential change in the similarity of local assemblages in terms of species, traits and/or lineages.

METHODS

Bird data

We analysed data from the French breeding bird survey (FBBS), which provided the abundances of French avifauna over a 24-year period on an annual basis (from 1989 to 2012) (Jiguet *et al.*, 2012). The monitoring programme used two schemes. These two schemes both used standardized protocols and followed the same basic principles ensuring the possibility of comparing the yearly changes in the relative abundances of species from year to year. During the first scheme (corresponding to the period 1989–2001), survey routes were freely chosen by observers (note, however, that these routes were located in various habitats including farmlands, forests and urban areas) and the same observer monitored the same route from year to year. Along each route, the observer had to monitor from 10 to 15 point counts evenly distributed within the habitats along the route. The same observer monitored exactly the same point counts in the same order over 5 min. Population trends obtained from this first scheme were comparable to those obtained in other European countries with a random sampling of surveyed sites (Julliard *et al.*, 2004). From 2001, a new scheme was launched, in which the same protocol was used, but instead of being freely chosen by the observers, 2 km × 2 km plots were randomly selected among 80 possible plots around the locality proposed by the observer (Jiguet *et al.*, 2012). As in the former protocol, the same observer monitored the same 10 point counts evenly distributed within the plot from year to year.

In both schemes, point counts were monitored on approximately the same day of the year (± 7 days), at the same time of the day (± 15 min, within 1–4 h after sunrise), for 10 min. Sampling sessions were repeated twice a year during the breeding period, once before and once after the pivotal date of 8 May (4–6

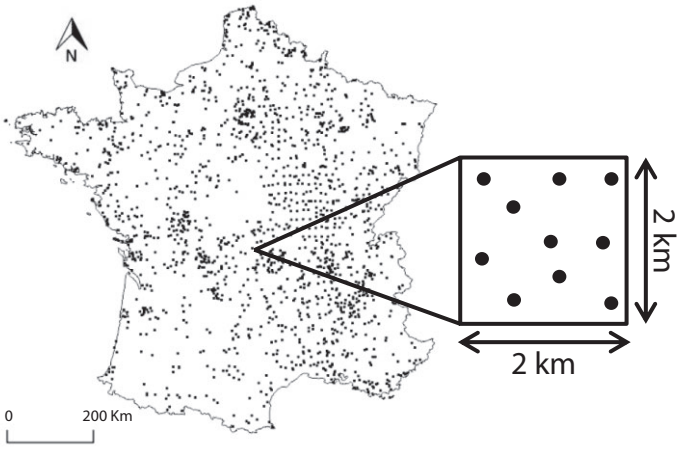

Figure 1 Spatial distribution of sites from the French breeding bird survey. Example of the distribution of 10 point counts (black filled circles) within a plot (a 2 km × 2 km square). Each black circle within the plot corresponds to a local community.

weeks apart). This allowed a sampling of early singing species and late migrants. For each point count, in each monitored site (routes or plots), each year, we took the maximum abundance of each species recorded during the two sessions as a measure of the relative abundance of the species. To ensure that each site included the same number of point counts over the 24-year period, we selected 10 point counts per site. Among the 1818 sites retained, each site was monitored at least twice and on average 5.7 ± 2.8 years (mean ± SD; Fig. 1).

The FBBS focused on common birds that regularly breed in France (about 300). Among those, we selected species that have been monitored at least twice at two different sites. To avoid the influence of rare species not correctly monitored by the protocol (e.g. wetland species) we only retained the most common species, i.e. we retained species with individuals representing 99% of all individuals monitored in the database; which correspond to 116 breeding species.

Measuring taxonomic, functional and phylogenetic diversity

We adapted the method developed by Devictor *et al.* (2010) to describe the taxonomic, functional and phylogenetic diversity of bird communities. Here, a community was considered as a pool of species that co-occur in a given point count in a given year. In brief, we used the Rao (1982) quadratic entropy index, which offers the same mathematical framework for all three facets of diversity, allowing straightforward comparisons between their trends (de Bello *et al.*, 2010). The Rao index is given by the formula $Q = \sum_{i=1}^{S}\sum_{j=1}^{S} p_i p_j d_{ij}$, where d_{ij} is the distance between species i and j, p_i and p_j are their relative abundances and S is the total number of species in the community. The Rao index integrates the abundance of species and a measure of distance between species (d_{ij}) which can be either functional or phylogenetic. Taxonomic diversity was estimated with the same index, except that $d_{ij} = 1$ was used between each pair of species (in this case, the Rao index was thus reduced to the Gini–Simpson diversity index; Ricotta, 2005a).

Matrices of pairwise functional and phylogenetic distances were both required to estimate functional and phylogenetic diversity. We obtained pairwise functional distances among the 116 species from a set of 22 functional traits. These traits embraced major life-history traits, feeding habits and morphological characteristics of birds (Petchey *et al.*, 2007; Devictor *et al.*, 2010). From these traits (see Appendix S1 in Supporting Information for a detailed description of each trait), we calculated pairwise distances between species using the Gower distance, and then we produced a dendrogram (UPGMA clustering, selected from the consensus method of Mouchet *et al.*, 2008) to ensure that distances between species pairs were ultrametric. Note that in measuring functional diversity (whatever the metric considered), the included traits and their specific categorization may rely on arbitrary decisions. In our case, we used major ecological traits described in birds as being sensitive to large-scale environmental filters (Petchey *et al.*, 2007; Meynard *et al.*, 2011). Most of these traits are also directly or indirectly involved in ecosystem functioning (Şekercioğlu, 2006). However, other trait selections would also have been possible to test more specific variation in community composition.

Ultrametric phylogenetic distances between the 116 species were directly extracted from a dated, calibrated molecular phylogenetic tree assembled by Thuiller *et al.* (2011) (see Appendix S2). For this phylogeny, consistent estimates of branch lengths were available. Maximum distances in both the phylogenetic and functional matrices were standardized to a maximum value of 1 before further analysis.

We calculated the three components for each biodiversity facet: γ-diversity (total diversity of a site), β-diversity (turnover between point counts within a site) and α-diversity (diversity in a point count). Because α-diversity can be fully determined by γ- and β-diversities, we focused only on γ- and β-diversities which were obtained from the standard decomposition of the Rao quadratic entropy: $\gamma = \beta - \alpha$ (Ricotta, 2005a). Although the division of biodiversity into α-, β- and γ-components has often been applied to a larger spatial scale/region, this landscape decomposition is meaningful and relevant for bird communities. Indeed, γ-diversity (here considered as representing the

bird diversity of a landscape) is composed of heterogeneous habitats, and thus β-diversity (turnover between point counts within a site) represents intra-landscape variability for which birds were shown to be sensitive (Devictor *et al.*, 2008). All indices were then transformed according to Jost (2007) to normalize the properties of all diversity metrics.

Measuring specialization of communities

To describe the dynamics of the relative proportion of specialized species in communities, we calculated the community specialization index (CSI) for each site in each year. CSI is a community-weighted mean representing the average of the species-specific level of habitat specialization of co-occurring species, weighted by their abundances (Julliard *et al.*, 2006). We quantified the degree of habitat specialization for a species (the species specialization index, SSI), following the approach of Julliard *et al.* (2006). SSI is calculated as the coefficient of variation (SD/mean) of species densities across habitat classes (we used the SSI values available in Devictor *et al.* (2007) based on species densities recorded in 2005 by the FBBS). This approach assumes that a given species is more specialized to certain habitat classes if its density is higher there than elsewhere. Note that SSI values were shown to be robust to the change in the habitat classification considered (Le Viol *et al.*, 2012). CSI is then given by the average of each species' SSI, weighted by the species' abundance within each site:

$$\mathrm{CSI}_j = \frac{\sum_{i=1}^{S} p_{ij} \times \mathrm{SSI}_i}{\sum_{i=1}^{S} p_{ij}}$$

where p_{ij} is the relative abundance of species i in site j and S is the total number of identified species in the site. One expects that the CSI calculated for a given site will decrease following a relative increase in generalists in that site (Julliard *et al.*, 2006).

To assess the potential contribution of generalist species to the observed changes in functional and phylogenetic diversity, we also tested the linear relationships between species specialization and their functional and phylogenetic originality, using linear regressions. Specialization (SSI) was considered as the response variable and functional (or phylogenetic) originality, measured as the average pairwise functional (or phylogenetic) distance of that species with all others, as the independent variable.

Statistical analyses

To estimate the temporal dynamics of the different community indices, we used a two-step approach. We first modelled the change in the yearly average of each diversity index. To do this we used a generalized additive mixed model (GAMM) designed as follows to meet the general structure of the framework proposed by Dornelas *et al.* (2012). The community measures (taxonomic, functional and phylogenetic diversity, or CSI) were considered as the response variables. Sites were considered as a random effect to account for variability in the level of indices among sites. We integrated geographical coordinates in isotropic smooth terms, according to the methods of Wood (2006), to account for structural spatial gradients. In this model, we also accounted for temporal autocorrelation structure by fitting an autoregressive model of order 1. Note that a more formal integration of spatial autocorrelation was not possible in these models that already accounted for temporal autocorrelation. However, the study of the semi-variograms of the residuals of that model confirmed that no spatial structure remained in the residuals after the smoothing of coordinates. In this model, time (in years) was considered as a discrete variable. As we expected that the size of the community could affect diversity indices, taxonomic diversity (TD) was also systematically included as a covariate when analysing functional diversity (FD) and phylogenetic diversity (PD) and CSI. β-TD was also systematically added for the models involving β-FD or β-PD. This first model provided us with the effect of each transition for years t to $t + 1$ on each index and its corresponding standard error. We arbitrarily fixed all community measures to 100 for the year 2001, considered as the reference year.

Then, a second GAM model was used to summarize the overall changes (and their nonlinear trends, if any) in the yearly estimates of each index over the 24-year period. To do this, we used, for each community measure, its yearly estimates (provided by the first model) as a response variable and we used a smoothing structure with a fixed degree of freedom of 4 for the smoothing function of year, considered as a continuous variable. In this second model, the sampling effort (i.e. the number of sites monitored per year) was also used as a covariate. The variance of the yearly estimates (given by the first GAMM) was also used as a weight in this second model. We tested whether this model could effectively describe a nonlinear trend in each index.

In parallel, we repeated the whole analysis presented above, but with presence/absence data rather than abundances. We conducted this analysis to assess the importance of including abundance in estimating the facets of biodiversity (Newbold *et al.*, 2012).

All calculations of indices, randomizations for the null model and statistical analyses were performed with R, version 3.0.1 (R Core Team, 2013).

RESULTS

Although there is no accepted way to formally estimate model fit for the first GAMMs (Wood, 2006; Zuur *et al.*, 2009), each index shows very important variation for a given year and among years (Fig. 2). Beyond these variations, the yearly changes in all diversity metrics could also be described by nonlinear trends from 1989 to 2012 with one or two specific inversions in their direction (Fig. 2). For instance, the general trend in species diversity corresponded to a nonlinear curve, with three successive periods ($F_{3,24} = 4.8$, $P = 0.01$, $R^2 = 0.87$): a relatively stable period of 7 years (1989–95), followed by a consistent increase over 13 years (1996–2008) and a new stable (or even slightly decreasing) period of 5 years (2008–12). The trends of local species richness

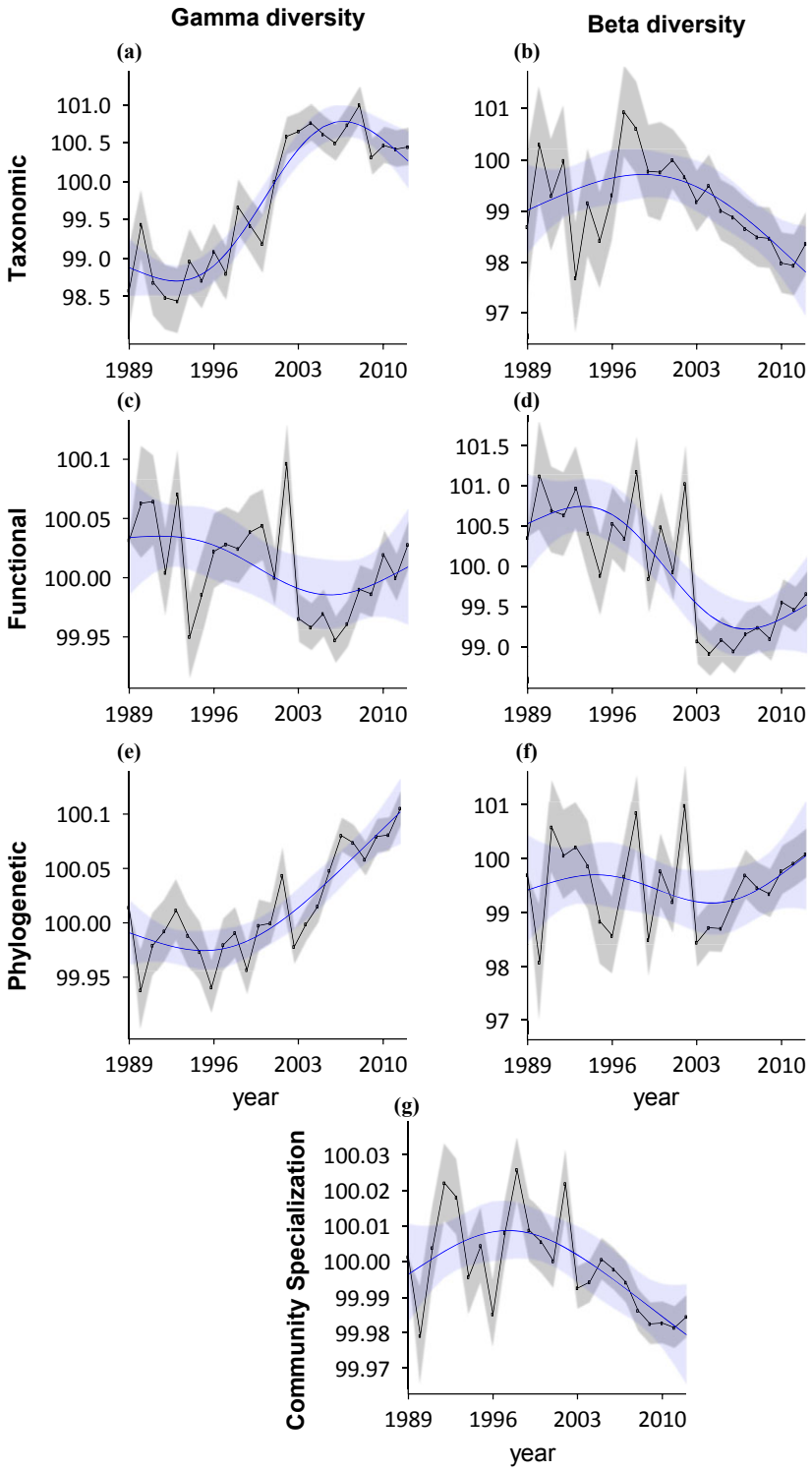

Figure 2 Temporal trends of diversity facets over 1989–2012. Taxonomic (a) γ-diversity and (b) β-diversity. Functional (c) γ-diversity and (d) β-diversity. Phylogenetic (e) γ-diversity and (f) β-diversity. (g) Community specialization index (CSI). Yearly changes in diversity indices (and their standard error, in the grey band) were obtained from a model accounting for spatial gradients and temporal autocorrelation. Variations in (γ or β) functional and phylogenetic diversities and in CSI were adjusted to variations in (γ or β) taxonomic diversity. The *y*-axis represents the relative variation of the facet considered compared with its value in 2001 set to 100 as a reference. We also added a nonlinear regression (smoothed line) to describe the major temporal trajectory of each index during the period.

and local abundance were qualitatively similar, showing that the local increase in taxonomic diversity was accompanied by the local increase in both species richness and abundances from approximately 1996–2008 (Appendix S3). Trends in γ-FD and γ-PD (adjusted to variation in taxonomic diversity) had different shapes. While the general trend in γ-FD was non-significant ($F_{3,24} = 2.18$, $P = 0.12$; Fig. 2c), the trend in γ-PD followed a two-step period with a marked and consistent increase from 1995 to 2012 ($F_{3,24} = 24.9$, $P < 0.001$, $R^2 = 0.82$; Fig. 2e). Overall, each of these facets (γ-TD, γ-FD and γ-PD) had their own general trajectories.

The corresponding trends in β-diversities (β-TD, β-FD and β-PD) were also different. In particular, β-TD followed a curvilinear trend with only one turning point around 2002

($F_{3,24} = 5.51$, $P = 0.006$, $R^2 = 0.54$; Fig. 2b) and a marked decrease since 1997, while β-FD followed a general trend with three different periods ($F_{3,24} = 4.9$, $P = 0.010$, $R^2 = 0.78$; Fig. 2d) and β-PD did not show particular long-term trends ($F_{3,24} = 2.12$, $P = 0.12$; Fig. 2f). Note that these trends in β-diversities were different from each other and different from the trends in γ-diversities.

Finally, during the same period, CSI, reflecting the relative abundance of specialist species in local sites, followed a two-step period with a marked and consistent decrease from 1999 to 2012 ($F_{3,24} = 8.14$, $P < 0.001$, $R^2 = 0.61$; Fig. 2g). In other words, since 1999, local assemblages have tended to include more individuals of generalist species. We further found that, at the species level, the more specialist species are, the higher their values of functional (Student's t-test: $t = 3.98$, $P < 0.001$, $R^2 = 0.12$) and phylogenetic (Student's t-test: $t = 2.98$, $P = 0.003$, $R^2 = 0.07$) originality.

Beyond the change of the average trends over the 24-year period, this temporal analysis showed high yearly variation within and among indices. All trends described above thus mask several short-term increases or decreases of each facet. Noticeably, while some indices increased during a given time window (e.g. β-FD during 2003–12) others decreased during the same period (γ-TD). The γ-diversity of a given facet could also increase for a given time period while the corresponding β-diversity of this same facet was decreasing during the same period (e.g. γ-TD and β-TD, from 1997–2005). Note that the deviance explained by sampling effort ranged from 0.04 to 10.11% for all community measures and that the effect of this variable was never significant ($P < 0.05$ for all community measures).

We found similar general trends for every diversity index when calculated from presence/absence data (Appendix S4) showing that beyond the change in the local relative abundances, changes in the identity of species recorded in local sites were also responsible for the observed changes in diversity facets.

DISCUSSION

In this paper we first assessed whether taxonomic, functional and phylogenetic diversities (and their respective spatial turnover) can have different temporal trends over the same period. Among major changes experienced by bird assemblages, a general increase in taxonomic diversity and phylogenetic diversity (since approximately 1995) as well as the overall decrease in CSI, β-TD and β-FD, can be emphasized. However, during this period, the temporal trends of each facet are best described by the succession of mid-term fluctuations than by linear trends.

These fluctuations suggest that each of these facets mirrors different and complementary aspects of community change. For instance, an increase in community taxonomic diversity and the decrease in community specialization occurred simultaneously (Fig. 2a,g). While the populations of some species may have increased recently due to favourable conservation policies (Donald *et al.*, 2007), the general increase in local species diversity coupled with the decrease in community specialization is likely to reflect the biotic homogenization of the French avifauna also described at the European level (Le Viol *et al.*, 2012).

We also found that local changes in diversity are scale dependent. In addition, the increase in species richness observed at a given spatial scale is often coupled with a decrease in diversity at a different scale (Van Turnhout *et al.*, 2007). Our results allow us to extend this conclusion to other facets of diversity. For instance, a directional change in β-TD was not necessarily coupled with a similar change in β-FD or β-PD. As also suggested by Baiser & Lockwood (2011), these results show that the biotic homogenization of a given component of biodiversity (e.g. taxonomic diversity) is thus not necessarily coupled with the homogenization of other components. Thus, the local increase in traditional diversity metrics (species richness, species diversity measure, total abundance) can mask different trends in other facets (Magurran *et al.*, 2010). But our results additionally suggest that this scale dependency is also valid over time. In other words, different diversity indices may have different temporal inertias. To our knowledge, such a potential decoupling of diversity indices at large spatial and temporal scales has hardly been investigated.

Obviously, not a single metric of biological diversity can be considered as a silver bullet. In particular, all metrics of species diversity (e.g. the Gini–Simpson index) derived from information theory have their intrinsic drawbacks (e.g. being bounded within a given range of values, having non-uniform properties across this range, or representing rare or common species differently). The Rao quadratic entropy used in this study also has its strengths and weaknesses (Ricotta, 2005b) but has the great advantage of offering a coherent and consistent framework for measuring several facets of diversity. In particular, we can be confident that the differences in the temporal trends observed among indices (taxonomic, functional and phylogenetic diversity) were not produced by changes in the indices considered (only the pairwise distance between species differed among these indices). However, a similar analysis could benefit from calculating similar temporal trends with complementary approaches (e.g. using the functional diversity indices developed by Villéger *et al.*, 2008).

Some of the observed variation in yearly indices can be explained by the sampling design itself (Magurran *et al.*, 2010). In particular, variation in the sampling effort or in the protocol could induce uncontrolled errors in the fluctuations of species abundances. To draw general trends, we thus systematically included the number of monitored sites as a covariate to account for yearly variation in sampling effort. Note also that the same observer monitored a given site with the same protocol (either from 1989 to 2001 or from 2001 to 2012) ensuring among-year standardization of diversity measures. Moreover, while many unexplained sources of variation of the diversity indices could not be described, this variation does not necessarily represent sources of bias for our general conclusions. Indeed, we were interested in the relative change in several indices measured with the same data. Unless species representing specific lineages, traits or habitat specialization were moni-

tored differently during the period considered, one does not expect to find the asynchrony of indices observed during the same period. In particular, important short-term changes in diversity indices could be observed during periods within which the protocol and the sampling effort were similar (e.g. from 1989 to 2000 and from 2001 to 2012 steep and idiosyncratic changes in some indices can still be observed; Fig. 2).

Even with standardized protocols and constant sampling efforts, abundances monitored from large-scale surveys should still be handled with caution. Many sources of error have been shown to influence the local abundances recorded by a given observer in a given site (e.g. variability in detectability among species, in observers' ability to detect species or even in meteorological conditions, Sauer *et al.*, 1994). However, while these sources of error can induce strong bias when true abundances are studied, they should not affect our conclusions derived from the relative changes in abundances from year to year in each local point count (Bas *et al.*, 2008). Moreover, the same analysis conducted on presence/absence data (i.e. removing variation in abundances between species) provided similar quantitative results (see Appendix S4). Newbold *et al.* (2012) have recently assessed the importance of including abundance information when mapping functional diversity and concluded that presence–absence data often already yield sensitive indices.

The causes of the observed changes in diversity facets remain to be confirmed. Ideally, to disentangle the deterministic and stochastic processes that are potentially responsible for the local changes in biodiversity, the observed trends (and their variances) should be explicitly coupled with local changes in environmental variables. In practice, however, these analyses are difficult to achieve at a large spatial scale due to the absence of land-cover surveys with sufficiently fine resolutions (e.g. the CORINE land-cover data available for France do not record landscape elements lower than 25 ha and are therefore only able to detect major changes). Using a spatial analysis of how diversity indices were related to habitat structure and compositions, Meynard *et al.* (2011) suggested that low levels of human impacts should generally favour all three facets of diversity (taxonomic, functional and phylogenetic) while higher β-diversities should be observed in heterogeneous landscapes. But whether similar relations are observed with temporal dynamics of diversity indices and temporal changes in landscape characteristics has yet to be confirmed. Our results, along with recent theoretical simulations (Münkemüller *et al.*, 2012), suggest that, following habitat or climate modifications, some indices could respond faster than others due to the specific delay with which each species can react and the inherent velocity of the dominant assembly rules.

Measuring the consequences of the observed changes is also a major challenge for macroecology and conservation biogeography. Our results reveal rather small relative changes for most facets. However, these changes result from the fluctuation of common species monitored in hundreds of sites distributed all over the country, which represent large variations in the number of species and individuals involved (on average the fluctuations of approximately two species and 40 individuals at local sites was observed during the period considered). Some of the most common species have indeed declined or increased drastically during this period (Jiguet *et al.*, 2010), potentially affecting specific functions and interactions after population depletions (Gaston & Fuller, 2008). We further showed that specialist species tend to have more original functional and phylogenetic characteristics than generalists. A more detailed species-by-species approach targeting the specific contributions of particular species (e.g. specialist versus generalist, protected versus non-protected) should help refine these findings.

Overall, our study presents the first temporal, multifaceted, multiscale analysis of change in community composition over large spatial and temporal trends. Our results emphasize that asynchrony can occur between different diversity facets so that, more than a given trend per se, it is the jointly studied trends of complementary biodiversity facets (including CWM) that provide enlightening information on major changes in the structure and composition of local communities. Beyond its ecological relevance for bird communities, our approach should provide a practical framework for evaluating temporal trends of different biodiversity facets, which can be applied to other taxonomic groups and is a step forward towards adopting more integrative approaches to the study of biodiversity on large spatial and temporal scales.

ACKNOWLEDGEMENTS

We sincerely thank the hundreds of volunteers that took part in the French breeding bird survey (STOC EPS programme). This project was supported by the 'Fondation pour la Recherche sur la Biodiversité' (FRB). W.T. received support from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Functional traits used to estimate functional diversity of bird species assemblages.

Appendix S2 Phylogenetic tree for the 116 bird species considered.

Appendix S3 General temporal trends and yearly changes in local species richness and abundance.

Appendix S4 General temporal trends and yearly changes in diversity facets estimated with presence/absence data.

BIOSKETCH

The research group combines several skills including theoretical research on community ecology, biogeography and conservation. **Anne-Christine Monnet** is doing a PhD in the impacts of global change on biodiversity using different approaches from species to communities.

Editor: José Alexandre Diniz-Filho