RESEARCH PAPER

Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices

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ABSTRACT

Aim Investigations into how different facets of biodiversity are related has become a central research agenda in ecology. Here, we use a large-scale and high-resolution data set on bird distribution to examine the robustness of the relationships between species diversity and functional or phylogenetic diversity.

Location France

Methods We measured the functional and phylogenetic diversity of 1914 bird assemblages monitored over 10 years with a standardized protocol. We investigated the consequences of incorporating abundance versus presence–absence data, changing the number and identity of traits considered, or varying the spatial scale used to estimate functional and phylogenetic diversity. We further examined the outcomes of different null model procedures that aim to reveal ecological processes influencing the distribution of each facet of diversity.

Results We found that the shape and strength of the relationship between species diversity and functional diversity are structured by several methodological choices. We show that increasing the quantity of information yielded by the indices (in particular, including abundances or increasing the number of traits considered) decreases the amount of functional redundancy estimated. Reducing the number of functional traits used to estimate functional diversity can change and even reverse the relationship of interest. Moreover, using alternative null models, we highlighted the specific role of environmental filtering and the link between species abundances and their functional originality (defined for a given species as the average of the functional distances with other species). The same tests applied to phylogenetic diversity revealed that its relationship with species diversity varies differently suggesting that this latter index cannot be used as a proxy for functional diversity.

Main conclusions Our results show that the identification of patterns and processes linking species diversity to functional or phylogenetic diversity vary with methodological choices. We further show that the study of these sources of variation via robustness tests allows ecologically meaningful information to be separated from pure artefacts.

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INTRODUCTION

One of the oldest and greatest challenges in community ecology is to elucidate the processes that shape the structure and composition of communities (Diamond, 1975; Pavoine & Bonsall, 2011). Although community ecology has long focused on species diversity (SD) there has been a more recent trend to reconsider this approach by incorporating the study of other aspects of diversity (Webb *et al.*, 2002; McGill *et al.*, 2006). Indeed, many studies have shown that species perform different functions in the ecosystem (Hooper *et al.*, 2005) and can be characterized by functional traits, i.e. the morphological, physiological or behavioural characteristics which indirectly impact their fitness via their effects on growth, reproduction and survival (Violle *et al.*, 2007).

Over the last decade, the use of functional diversity (FD), i.e. the diversity of functional traits within a community, has greatly expanded and has proven to be a useful tool in community ecology (Cadotte *et al.*, 2011; Mason & de Bello, 2013). In parallel, there has been more interest in integrating information about the phylogenetic relationships between species to study community assembly. Phylogenetic diversity (PD) is defined as the amount of evolutionary history represented in the species of a particular community (Mouquet *et al.*, 2012). It reflects the diversity of genetic and thus morphological, physiological and behavioural characteristics of species. Based on the link between evolutionary history and the traits that organisms possess, PD was proposed as a relevant metric to study community structure as a complement to FD, because species' interactions and species' functions involve complex and often unknown sets of traits (Webb *et al.*, 2002). There is still, however, a lack of knowledge about how traits evolved and how evolutionary processes create complex patterns that cannot be described by phylogenetic relations alone (Diniz-Filho *et al.*, 2013).

Because patterns of SD, FD and PD often differ (Pavoine & Bonsall, 2011; Münkemüller *et al.*, 2012; Purschke *et al.*, 2013), the interpretation of the relationships between these facets of diversity has the potential to improve our understanding of the determinants of community composition (Cavender-Bares *et al.*, 2009; Mouquet *et al.*, 2012). The relationship between SD and FD (or PD) is expected to be positive partly because they are inherently linked by a sampling effect (Loreau *et al.*, 2001; Rodrigues *et al.*, 2005). Given two communities, the one that contains the greater number of species has a greater probability of presenting a higher FD (or PD) simply because trait values (or phylogenetic differences) will accumulate with the successive addition of species. Beyond this purely statistical effect, ecological theory suggests that two main ecological processes – habitat filtering and limiting similarity – drive community assembly. The habitat filtering hypothesis assumes that coexisting species are more ecologically similar to one another than would be expected by chance, because environmental conditions act as a filter that only allows a narrow spectrum of functional traits to persist locally (van der Valk, 1981). The limiting similarity hypothesis, on the other hand, assumes that biotic interactions, particularly competition, maximize the differentiation between coexisting species (MacArthur & Levins, 1967). Although they seem mutually exclusive, these processes largely depend on the spatial scale considered, and their relative contributions are often difficult to disentangle (Lavergne *et al.*, 2010).

Because manipulative experiments are difficult to perform when studying ecological systems at large spatial and temporal scales, other methods have been proposed to circumvent this difficulty. Among these methods, comparing the observed patterns of diversity to those expected on the basis of a null model is now widely used. The null-model analysis specifies a statistical distribution or randomization of observed data, designed to simulate species assembly without invoking ecological mechanisms (Gotelli & Ulrich, 2012). By comparing observed and null-model outcomes, competing hypotheses (e.g. habitat filtering or limiting similarity) about community assembly can be tested. Besides, null models are now extensively used to test whether the SD–FD (or SD–PD) relationship is simply produced by sampling effects, or if differences between observed and simulated FD (or PD) can reveal assembly rules (Kraft *et al.*, 2007; Petchey *et al.*, 2007; de Bello *et al.*, 2009). This comparison of observed FD (or PD) with simulated FD (or PD) is supposed to reveal the extent of habitat selection versus limiting similarity arising from biotic interactions (de Bello, 2011).

Other studies have already examined several aspects of the relationship between these facets of diversity (de Bello *et al.*, 2009; Cadotte *et al.*, 2011). Here, we propose a systematic framework for highlighting major sources of variability and confusion regarding the SD–FD and SD–PD relationships. Although some aspects of such analysis have been highlighted (e.g. the influence of the spatial scale or trait considered), others remain unclear (e.g. the influence of the number and identity of traits, and the complementarities between null models).

In this study, we used a large-scale data set on bird distributions to examine the robustness of the SD–FD and SD–PD relationships at a large spatial scale. We examined the consequences on the strengths and shapes of these relationships while: (1) shifting between abundance and presence–absence data; (2) varying the number of functional traits used in the measurement of FD; (3) changing the spatial scale (i.e. the spatial grain) over which diversity indices are calculated; and (4) modifying the definition of the null model, i.e. the constraints applied to the randomization procedure. Beyond the robustness test of the description of patterns of diversity to changes in different methodologies, we also tried to disentangle the variability resulting from methodological choices from those due to hidden ecological processes.

MATERIALS AND METHODS

Bird data

The data come from the French Breeding Bird Survey (FBBS), currently the main scheme for monitoring the spatial and temporal population changes of France's common breeding birds. This monitoring has been carried out since 2001 by volunteer observers following a standardized protocol in space and time.
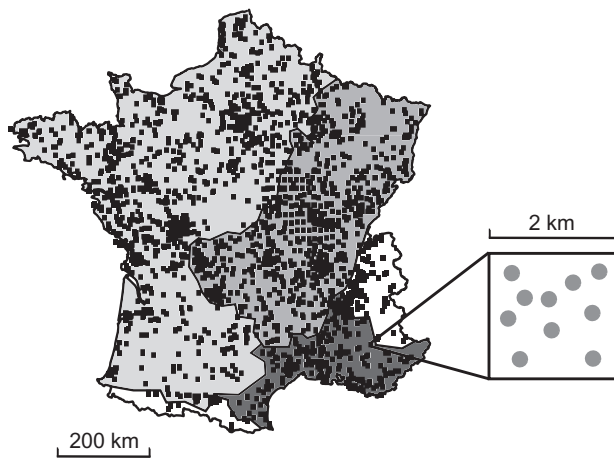
Figure 1 Spatial distribution of surveyed plots and sampling design for bird assemblages in mainland France. The colour ranges represent biogeographical areas: Atlantic (light grey), continental (grey), Mediterranean (dark grey), and mountain (white).

Each observer provides his home locality, and a 2 km × 2 km plot to be prospected is randomly selected within 10 km of this location. In this plot, the observer selects 10 point counts (Fig. 1), within which all individuals are recorded during a 5-minute period. Point counts must be separated by at least 300 m and their distribution must be representative of the main habitats with the landscape. They are sampled in the same order by the same observer each year. Each plot was monitored in two annual visits during spring, one before and one after 8 May, with 4–6 weeks between the two visits (Jiguet *et al.*, 2011). To be validated across years, the count must be repeated on approximately the same date each year (± 7 days from April to mid-June) as well as at the same time of day (± 15 min; 1–4 h after sunrise). For a given point count and species, the larger of the two annual counts is retained. We considered thereafter that a community is defined by the species co-occurring in a given plot. We used the plots monitored for at least two years during the period 2001–2010 ($n = 1914$) and the species recorded on at least two different plots. The resulting 228 species accounted for more than 99% of all individual birds recorded by the FBBS.

Calculating diversity indices

We used quadratic entropy (Botta-Dukát, 2005) to calculate the diversity indices of each community. This index incorporates both the relative abundances of species and biological information about the dissimilarity between species that can be based on taxonomic, functional or phylogenetic distances (Ricotta & Szeidl, 2009). It is defined as $Q = \sum_{i}^{S} \sum_{j}^{S} p_i p_j d_{ij}$, where S is the number of species, p_i and p_j are the relative abundances of the i-th and j-th species in the community and d_{ij} is the distance between these species. This index represents the average distance between two individuals selected randomly from the commu-

Table 1 Functional traits used to estimate functional diversity of bird species assemblages in France. Trait data were obtained from Petchey *et al.* (2007) and Devictor *et al.* (2010).

Trait type	Trait	Type of metric
Resource quantity	Body mass	Continuous
	Life span	Continuous
	Clutch size	Continuous
Main component of diet(s)	Plants	Binary
	Invertebrates	Binary
	Vertebrates	Binary
Main foraging method(s)	Pursuit	Binary
	Gleaning	Binary
	Pouncing	Binary
	Grazing	Binary
	Digging	Binary
	Scavenging	Binary
	Probing	Binary
Main foraging substrate(s)	Water	Binary
	Mud	Binary
	Ground	Binary
	Vegetation	Binary
	Air	Binary
	Aerodynamic index	Continuous
Main foraging period	Migratory status	Binary
	Nocturnal	Binary
Nest location	Canopy/ground/hole	Categorical

nity with replacement. Quadratic entropy can be used to calculate SD, FD and PD similarly, which facilitates their comparison (Devictor *et al.*, 2010; Pavoine & Bonsall, 2011). We calculated SD by setting $d_{ij} = 1$ for all $i \neq j$. SD is thus equivalent to the Gini–Simpson diversity index (Ricotta & Szeidl, 2009). We calculated FD and PD by using d_{ij} as a measure of the pairwise functional or phylogenetic distance, respectively, between species i and species j.

Functional distances were calculated using a list of 22 functional traits (Petchey *et al.*, 2007; Devictor *et al.*, 2010) that contained information for all of the 228 species recorded. These functional traits measure various aspects of resource use by birds, such as the quantity and the quality of resources consumed, the feeding behaviour, and the activity period (Table 1). All of these traits play important roles in species interactions and ecosystem functioning, and can be considered a good source of functional information (Lepš *et al.*, 2006). From these traits, we calculated the Gower distance, which is widely used to represent distances of entities characterized by a mixture of quantitative and qualitative attributes (Legendre & Legendre, 1998). The Gower distances were measured with the function *daisy* of the R package CLUSTER. The phylogenetic distances between 220 species were directly extracted from a dated, calibrated molecular phylogenetic tree assembled by Thuiller *et al.* (2011): consistent estimates of branch lengths were available for this phylogeny.

We further applied a simple correction [$Q_{corr} = 1/(1 − Q)$] first proposed for the Gini–Simpson index (Jost, 2006) and then

Table 2 Constraints of the different null models on the structural features of French bird occurrence data and their consequences. All randomization procedures consist of changing the identity of species on the species-by-site abundance matrix. The identities of species are sampled without replacement for each site in order to maintain the species richness at each site. Randomization procedures differ in the sampling pool and with respect to the species' relative abundance. Null models therefore have different consequences on the environmental filtering and the relative species abundance (minus signs indicate that there is no effect or little effect, whereas positive signs indicate an effect, more or less important).

	Constraints		Consequences		
Null model	Species richness per site maintained	Pool of sampling	Sampling according to species relative abundances	Environmental filtering	Relative species abundances
M1	Yes	France	Yes	+++	–
M2	Yes	Biogeographical area	Yes	+	–
M3	Yes	Site	No	–	+++

extended to quadratic entropy (Ricotta & Szeidl, 2009) in order to avoid counterintuitive ecological properties of the indices.

General linear mixed models

To describe the SD–FD (or SD–PD) relationship, we first performed linear and log-linear models. As we found very little difference between the relationships obtained (by comparing the associated R^2 values), we chose to go into detail only using linear models. We needed to account for spatial correlation within the data set because closely spaced assemblages were likely to be more similar in their species composition than more distant assemblages. We therefore used generalized linear mixed models (Pinheiro & Bates, 2009), in which FD (or PD) was considered the response variable and SD the continuous explanatory variable. This model also accounted for spatial dependence in the errors by defining a spatial correlation structure derived from a semivariogram analysis. Different theoretical semivariograms were tested (including linear, exponential, spherical, Gaussian and rational quadratic). The best-fitting semivariogram was selected (Fortin *et al.*, 2002) and incorporated in the mixed model.

Robustness of the SD–FD and SD–PD relationships

A general model of the SD–FD relationship was first performed at the scale of France using all plots as independent samples. In a first step, we investigated the robustness of this relationship by changing some aspects of our methodological approach.

(1) First, we performed exactly the same analysis as with presence–absence data. For this, we assigned an abundance of 1 to each species present in a plot and recalculated SD and FD.

(2) We then tested the robustness of the SD–FD relationship to changes in the number and identity of functional traits considered. For this, we recalculated FD using only 3, 6, 9, 12, 15, 17 and 20 traits, with 500 randomized sets of traits at each of these numbers.

(3) We also tested the influence of the spatial scale or grain, i.e. the contiguous area at which data are aggregated (Whittaker

et al., 2005). Thus, we increased the size of the assemblages from which we calculated diversity indices. We used a systematic approach to form larger assemblages of species by considering each plot to be the centre of a 25-km, 50-km or 75-km radius window, within which 4, 16 and 34 additional plots, respectively, were randomly selected and aggregated.

Finally (4), we tested the influence of the particular null model used on the SD–FD relationship by comparing the results obtained with three alternative null models differing in their specific constraints (Table 2). For this, we used null-model procedures often employed in community ecology that are based on permutations of species identities in the species-by-site abundance matrix (e.g. in Stevens *et al.*, 2003; Petchey *et al.*, 2007; de Bello *et al.*, 2009; Flynn *et al.*, 2009; Thompson *et al.*, 2010). For null model 1 (M1), species were sampled from the pool of France – i.e. the pool of 228 species – according to their relative abundance. For null model 2 (M2), species were sampled from the biogeographical pool, i.e. the pool of species recorded in the biogeographical area where the site was located, according to their relative abundance. We defined four biogeographical areas – Atlantic, continental, Mediterranean and mountain (Fig. 1) – whose species pool varied in size from 154 to 206 species. For null model 3 (M3), species were sampled from the site pool. This latter model simply consisted of swapping the abundances of species in each plot; the commonness or rarity of species was therefore not maintained. Overall, these three null models had different consequences regarding the maintaining of the environmental filtering and the relative abundance of species (Table 2). For each model, we repeated the randomization 1000 times to produce a distribution of simulated FD and PD values.

All calculation of indices, statistical analysis, and null model simulation were performed with the statistical software R 2.12.1 (R Core Team, 2012) using packages ADE4, CLUSTER, GSTAT, NLME and SPDEP.

RESULTS

At the scale of France, FD was positively correlated to SD ($F_{1,1912} = 626, P < 0.001, r^2 = 0.18$, slope $= 0.0026 \pm 0.0001$ standard error) (Fig. 2). This result shows that 82% of the variation in

Figure 2 Relationship between species diversity and functional diversity of bird assemblages in mainland France calculated with (a) abundance data, and (b) presence–absence.
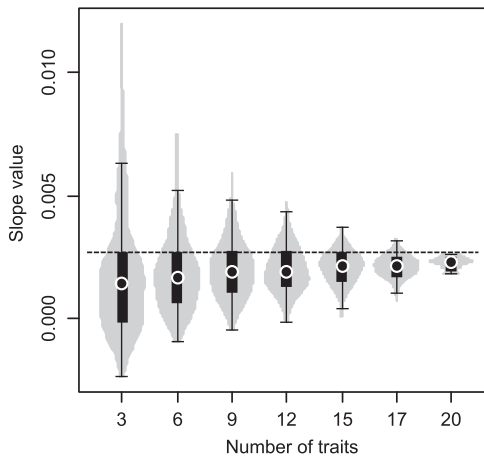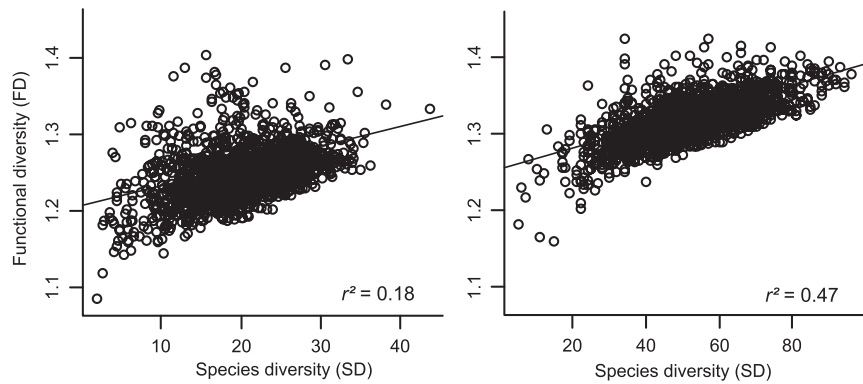
Figure 3 Slope values of the relationship between species diversity and functional diversity of bird assemblages in mainland France obtained with different numbers of functional traits included (3–20) in the analysis. White open circles represent the mean slope values, black lines represent the first and the third quartiles, black bands represent the second quartiles, and grey shapes represent the distributions of slope values obtained after 500 simulations. The dashed line is the slope value obtained with 22 traits.

FD remained unexplained by that of SD. FD was still positively correlated to SD with presence–absence data ($F_{1,1912} = 1847$, $P < 0.001$, $r^2 = 0.44$, slope $= 0.0018 \pm 0.00004$) and the difference between the slopes was significant (repeated-measures ANOVA: $F_{1,1911} = 152$, $P < 0.001$).

Reducing the number of functional traits used to calculate FD gradually decreased the average value of the slope of the SD–FD relationship (Fig. 3). The average slopes obtained after 500 simulations ranged from 0.0016 ± 0.0022 for 3 traits to 0.0022 ± 0.0003 for 20 traits, and the difference between these two extreme slopes was significant (ANOVA weighted by standard error: $F_{1,988} = 178$, $P < 0.001$). Thus, all average slopes were lower than the slope observed with 22 traits. Moreover, we noted that with the removal of up to 12 traits, even negative relationships could be obtained (Fig. 3). The negative SD–FD relationships represented 26% of the 500 relationships simulated with three traits and 2% of those simulated with nine traits. We then

focused on the identity of traits included when the relationships were negative. Several traits were more frequently involved in these relationships (e.g. scavenging, vegetation, nocturnal, air and mud; all > 50%) whereas others were not (e.g. migration, plants, ground, gleaning and pursuit; all < 5%). We also investigated the stronger positive relationships and found that the frequencies of the traits involved differed from that leading to the negative relationships. In other words, specific traits contributed to reinforce or to decrease (or even qualitatively change) the positive SD–FD relationship.

For all the spatial scales used to calculate diversity indices, FD was positively correlated with SD, but the slopes varied significantly among regions of different sizes (repeated-measures ANOVA: $F_{1,4918} = 66$, $P < 0.001$). The slope was steeper for relationships calculated over broader spatial scales. Thus, the slope for the 25-km region (0.0016 ± 0.0002) was shallower than for the 50-km region (0.0019 ± 0.0002), and both were lower than the slope for the 75-km region (0.0023 ± 0.0001). However, at the scale of the plot (2-km region), the slope was steeper (0.0026 ± 0.0001) than at broader scales.

The FD observed in bird communities was lower than FD simulated with the three null models (Paired t-test: $P < 0.001$). This pattern is reflected in the relationship between observed and simulated FD (Fig. 4a–c). The slopes of the relationships simulated with null models 1 (M1) and 2 (M2) were lower on average than the observed slope (96.5% and 80.4%, respectively, were lower than 0.0026) (Fig. 4d,e). With null model 3 (M3), on the other hand, almost all of the slopes were steeper (99.9%) than the observed slope (Fig. 4f).

Similar results were observed regarding the robustness of the SD–PD relationship. First, at the scale of France, PD was positively correlated with SD both based on abundance data ($F_{1,1912} = 39$, $P < 0.001$, $r^2 = 0.11$, slope $= 0.0031 \pm 0.0005$) and on presence–absence data ($F_{1,1912} = 90$, $P < 0.001$, $r^2 = 0.47$, slope $= 0.0016 \pm 0.0001$) (Appendix S1 in Supporting Information). The slopes, however, varied significantly between abundance and presence–absence data (repeated-measures ANOVA: $F_{1,1911} = 431$, $P < 0.001$). For all spatial scales used to calculate the diversity indices, PD was positively correlated with SD, but the slopes of the correlations varied significantly among regions of different sizes (repeated-measures ANOVA: $F_{1,4918} = 17$, $P < 0.001$). The slope for the 25-km region (0.0024 ± 0.0004)

Null model 1

Null model 2

Null model 3
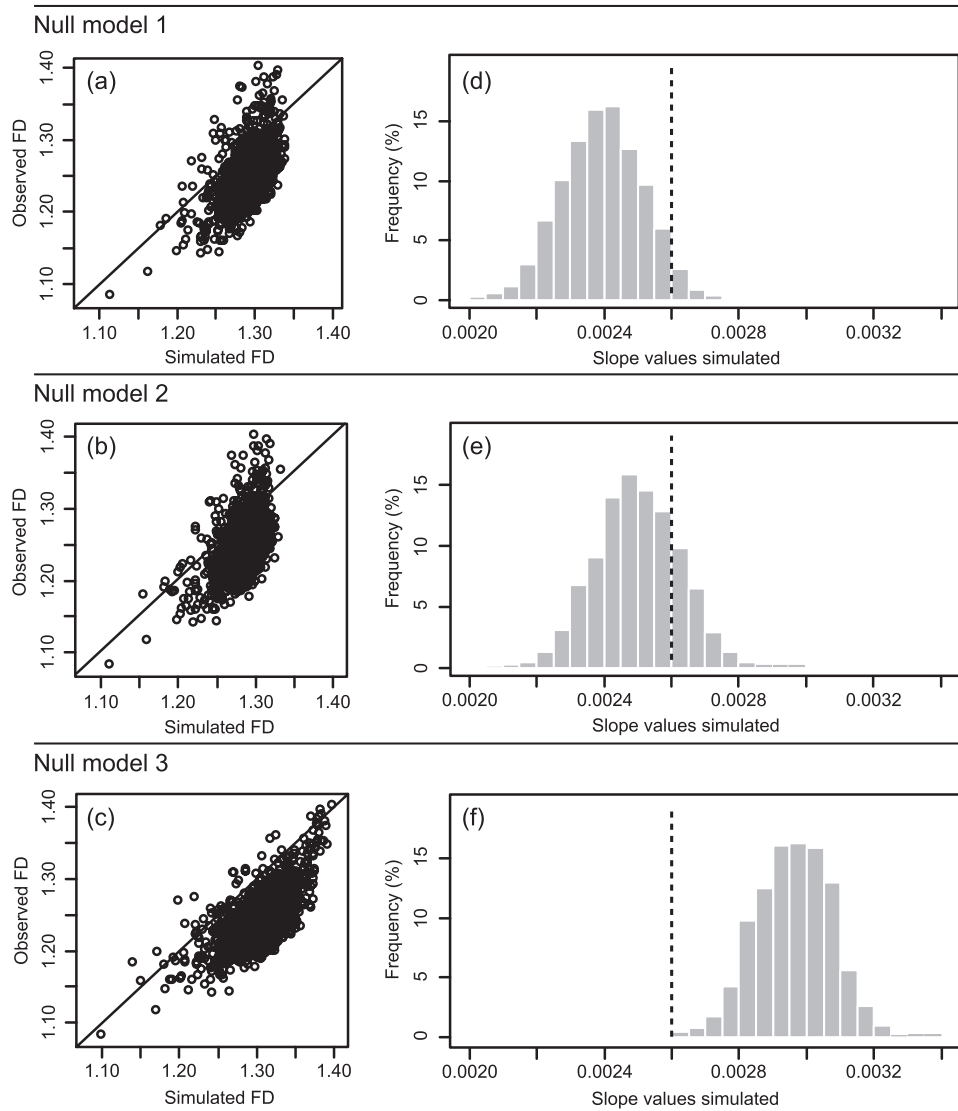
Figure 4 (a–c) The relationships between simulated functional diversity (FD) and observed FD of bird assemblages in mainland France; the solid line is the 1:1 relationship. (d–f) The distributions of slope values of the simulated relationships between specific diversity (SD) and FD; the dashed line is the observed slope value. These results were obtained after 1000 simulations of: (a,d) null model 1, where species are sampled from the France pool according to their relative abundance; (b,e) null model 2, where species are sampled from the biogeographical pool according to their relative abundance; and (c,f) null model 3, where species are sampled from the site pool irrespective of their relative abundance.

was lower than the slope for the 50-km region (0.0041 ± 0.0004) and that for the 75-km region (0.0042 ± 0.0003). Finally, the PD observed in bird communities was lower than the PD simulated with the three null models (paired *t*-tests: $P < 0.01$). This pattern is reflected in the relationship between observed and simulated PD (Appendix S2a–c). All null models produced very different simulated slopes compared to the observed one. Indeed, the slopes of the relationships simulated with M1 were almost higher than the observed slope (97.8% were higher than 0.0031) (Appendix S2d), whereas all those simulated with M2 and M3 were much higher than the observed slope (Appendix S2e,f).

DISCUSSION

Robustness of the SD–FD and SD–PD relationships

For calculating diversity indices, quadratic entropy is a very flexible index that is now widely used in ecology and conservation (Pavoine & Bonsall, 2011). This metric represents the average difference (either functional or phylogenetic) between two individuals selected randomly, with replacement (Botta-Dukát, 2005). If presence–absence data rather than abundances are used, it represents the mean distance between the occurring

species. Interestingly, when the quadratic entropy is used with presence–absence and phylogenetic distances, it is equivalent to the mean pairwise phylogenetic distances (MPD) often used in phylogenetic analysis (Webb *et al.*, 2002). Using this metric, we found that accounting for species abundances increases the slope of the SD–FD (or SD–PD) relationship, which in turn reduces significantly the perception of functional (or phylogenetic) redundancy within communities. The idea that including differences in abundance among species has important consequences for patterns of diversity is not novel (Díaz & Cabido, 2001), even if it has only recently been explicitly studied (Newbold *et al.*, 2012). Most animal community studies are still based on presence–absence data (Petchey *et al.*, 2007; Flynn *et al.*, 2009; Strauß *et al.*, 2010; Guillemot *et al.*, 2011).

We also observed that a higher number of functional traits included in the calculation of FD leads to a steeper slope of the SD–FD relationship, i.e. a lower functional redundancy detected within the community. This finding suggests that the 22 functional traits examined in our study are partly uncorrelated, consistent with the results of other studies that reported that a greater number of uncorrelated traits decreases the ability to detect functional redundancy (Micheli & Halpern, 2005; Petchey *et al.*, 2007). Part of this relationship (Fig. 3) is expected and results from the higher variance necessarily produced with fewer traits, but we also found that the slope of the relationship can become negative when only a few traits (up to 10 in our case) are used to calculate FD. Thus, more species-rich communities do not always have higher FD when measured with quadratic entropy. Indeed, the addition of a new species into the community can increase SD, but it may decrease the average dissimilarity among species if, globally, that species shares the same traits as the others (Botta-Dukát, 2005). Consequently, following an increase of SD, FD may increase or decrease according to the species' functional traits. We further identified some traits which are over-represented in negative relationships. They do not belong to a particular type of trait. They represent, at least to some extent, almost every type of trait that we considered: diet (plants), foraging substrate/habitat (vegetation, air, mud or ground), foraging method (scavenging, gleaning or pursuit) and foraging period (nocturnal or migration). Rather, these traits are distinguished by the unequal distribution of their modality among species. In other words, one of their states is represented by few species. The consequences of these results on the ability of a particular metric to reflect functional diversity is clearly context-dependent. Our results suggest that the robustness of those metrics to change in the characteristics of the traits considered (range, distribution) must be assessed carefully. Overall, these analyses show that increasing the information yielded by the indices considered (abundances and number of traits) decreases the level of functional redundancy reported.

We also found that the slope of the SD–FD relationship is sensitive to the spatial scale used. The variability of slopes we observed could be attributable to the fact that we captured different types of processes according to the scale considered. For instance, at a small scale (2 km), the relationship seems to be very sensitive to sampling effect, leading to a steep slope. At broader scales (25–75 km), it is likely that habitat diversity increases with the size of the assemblage, steepening the slope of the SD–FD relationship (Devictor *et al.*, 2010). Therefore, this scale-dependency analysis can reveal the spatial extent at which the effect of a given process on FD becomes negligible (sampling effect) while others become dominant (environmental filters). Regarding PD, we also found that for large scales (25–75 km), the slope of the SD–PD relationship increases with the size of the assemblage, but PD seems to be less sensitive to sampling effect than FD at small scales (2 km). Indeed, at broader scales (50–75 km), the slope of the SD–PD relationship becomes higher than at small scales (2 km). This result suggests that FD and PD can have different sensitivities to similar processes (Purschke *et al.*, 2013) and studying them simultaneously is likely to better capture and explain the distribution of diversity among communities (see below) (Münkemüller *et al.*, 2012).

Robustness of the null-model analysis

We investigated the influence of the randomization procedure on the interpretation of the SD–FD and SD–PD relationships by means of null models. For all randomization procedures, we found that observed FD was lower than simulated FD, indicating that species that actually co-occur in realized assemblages are more similar in their functional traits than a random set of species of identical number. This result is consistent with other studies that used similar null models (Petchey *et al.*, 2007; de Bello *et al.*, 2009; Thompson *et al.*, 2010). The deviation between observed and simulated FD is usually explained through the habitat filtering hypothesis. Indeed, for M1 and M2, species are drawn from very large pools (France or biogeographical area), and this procedure does not account for habitat filters, particularly those acting at local scale. This randomization allows the co-existence of species with very different functional traits, leading to high community FD. The deviation from observed FD was lower when species were sampled from the biogeographical pool of the plot. In a similar analysis of FD in bat communities, Stevens *et al.* (2003) found that many differences between observed and simulated patterns of FD became insignificant when species were sampled so as to account for regional constraints. We also found that for all randomization procedures, observed PD was lower than simulated PD, indicating that species that co-occur in realized assemblages are more phylogenetically related than a random set of species of identical number. Some authors (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009) suggested that when close relatives occur together more than expected (phylogenetic clustering), the underlying process was habitat selection on shared physiological tolerances, i.e. trait conservatism. Thus, all of these results seem to support the habitat filtering hypothesis.

Habitat filtering cannot, however, explain the deviation between observed and simulated FD and PD for M3. In this randomization procedure, species identity is conserved within a plot, so all the environmental filters are maintained (Table 2). The only change affects the relative abundances of species, which were swapped within each plot. Thus, this null model
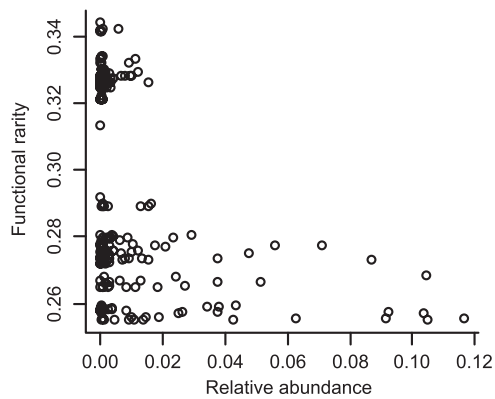
Figure 5 Relationship between relative abundance and functional rarity of 228 bird species in France, estimated from 22 functional traits.

randomizes only the relative species rarity (or commonness). It provides simulated communities with high frequencies of species that are normally rare in real communities, leading to higher FD values because of their original traits. To confirm this hypothesis, we estimated the functional originality of each species by calculating the mean functional distance between each species and the others. In this way, the more a species is isolated in the functional dendrogram, the more important is the mean distance that characterizes its originality. We found that the relationship between abundance and functional originality of species (Fig. 5) segregates rare and functionally original species from species that are more abundant and less original with respect to their traits. Interestingly, these results are similar to those obtained by Thompson *et al.* (2010) with plant communities. In other words, our results suggest that a pool of rare species has mostly unique traits, whereas common species tend to have shared traits. As rare species became more abundant in communities simulated with M3, this produces a higher simulated than observed FD.

Moreover, we found that the slopes of the SD–FD relationship obtained with M3 are mostly greater than observed. According to the previous explanation, linking species abundances to the functional originality, this result suggests that a higher proportion of rare species is observed in species-rich communities, which increases the FD in those communities and finally leads to steeper slopes for simulated than for observed data. This seems to be consistent with the framework recently proposed by Mayfield & Levine (2010), in which trait convergence – within relatively homogenous environmental conditions – can be explained by the exclusion of less competitive species and the dominance of species with similar and particularly competitive functional traits. Interestingly, although we show that more common species exhibit less original functional traits on average, others have recently shown that common species are also those with less vulnerable traits (Mouillot *et al.*, 2013). Whether the combination of particular functional traits can be interpreted as a cause or a consequence of rarity remains an

open question. Our results suggest, however, that the increase in most common and generalist species observed worldwide (Clavel *et al.*, 2010) probably affects the functional originality of local assemblages.

Concluding remarks

Our study suggests that throughout the investigation, from the description of a relationship to its interpretation in terms of processes, the results were influenced by the metrics or procedures used. Indeed, we found that both the shape and the strength of the SD–FD and SD–PD relationships vary with methodological changes and this sometimes reveals interesting findings.

The lack of robustness of a given result to change in the method used is most often considered as a weakness. Indeed, researchers have to make several key decisions during the collection and the analysis of data, and one often considers that, ideally, we must reduce the effect of arbitrary decisions on scientific conclusions (Poos *et al.*, 2009). However, ecologists have already noted the difficulty or even impossibility of building a perfect model (truly null or purely statistical) that could materialize the distribution of species in the absence of a particular process (Gotelli & Ulrich, 2012). Here, our results suggest that rather than selecting one best null model in order to interpret a pattern, we can fruitfully use contrasting results obtained with different null models, each of which is justified. Indeed, we have shown that different processes (e.g. habitat filtering) and properties (e.g. the link between relative abundance and functional originality, or the uneven distribution of species within the data set) can emerge from this kind of robustness analysis.

The method of producing new findings from those already known uses the principle of the bootstrap technique. This technique is used in some fields such as physics, computer sciences or statistics, and refers to a self-sustaining process that proceeds without external help. The term 'bootstrap' is a reference to Baron Münchhausen who, briefly ignoring the laws of gravity, gets out of a swamp by pulling himself up by his own hair, or in another version, by his boot-straps. This metaphor can be applied to our approach, because we are able to highlight new properties from the same data set only by changing some elements which structure the SD–FD and SD–PD relationships (e.g. the abundance data, the functional traits, or the null model constraints).

To conclude, we argue that, rather than trying to entirely eliminate the influence of specific methodological choices when conducting large-scale analyses (which seems to be a rather illusory goal), we can successfully investigate the multiple sources of variation, including those due to subjective methodological choices. We believe that this investigation can help us to separate ecological meaningful information from pure artefacts and to distinguish alternative processes, in order to better understand the structure and composition of ecological communities at large spatial scales.

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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 Relationship between species diversity and phylogenetic diversity of bird assemblages calculated with (a) abundance data, and (b) presence–absence data.

Appendix S2 Relationships between simulated and observed phylogenetic diversities of bird assemblages with null models M1 (a), M2 (b) and M3 (c). Distributions of slope values of the simulated SD–PD relationships with null models M1 (d), M2 (e) and M3 (f).

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