



Dissociating several forms of commonness in birds sheds new light on biotic homogenization

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ABSTRACT

Aim We disentangle three facets of species commonness (local abundance, geographical range size, degree of habitat generalization) to identify how species segregate along these axes and how each of these facets determines the relative functional originality of each species (i.e. the mean trait distance of a species with others). At the community level we test whether changes in the relative abundances of species with different levels of commonness contribute to the spatial and temporal dynamics of species assemblages and to the local trend in functional homogenization.

Location France.

Methods Data from the French Breeding Bird Survey from 2001 to 2012 were used to represent the yearly change in species abundances of 198 species over 2057 plots. Functional originality and three commonness indices were calculated for each species related to their geographical range, habitat generalization and specific local abundances. These species-specific indices were then used to compute community-weighted means of commonness and functional originality. Hierarchical partitioning was used to investigate the relationships between each of the three facets of commonness and functional originality. Generalized additive models were used to estimate the spatial and temporal trends of each community index.

Results Species that are generalist and abundant but with a restricted range had higher functional originality. From 2001 to 2012, assemblages were increasingly composed of species with large ranges and of habitat generalists. The functional simplification of communities was mainly linked to the increase in species with large ranges and, to lesser extent, to a decrease in species with high local abundances.

Main conclusions The decomposition of commonness into complementary facets is useful for describing the causes and consequences of biotic homogenization at large spatial scales. Functional simplification can occur during a short time period and is driven mainly by the greater success of species with large ranges.

Keywords

Biotic homogenization, birds, commonness, functional diversity, range, rarity, specialization.

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INTRODUCTION

What makes species rare or common is of paramount importance in ecology and conservation biology (Preston, 1948; Kunin & Gaston, 1993). Two major research pathways have focused specifically on rarity: the first has tried to find some ecological or

evolutionary differences between rare and common species (Bevill & Louda, 1999) while the second has concentrated on the link between rarity and extinction risk (Dobson *et al.*, 1995).

Although most approaches have considered rarity or commonness as self-explanatory and straightforward concepts, some authors have highlighted the scale dependency and

multiple components of rarity. A given species can be common at a given spatial scale and become rare with respect to other scales (Hartley & Kunin, 2003). To clarify this issue, Rabinowitz (1981) proposed dissociating the rarity of a given species into three complementary facets: its geographical range, its local population size and its habitat specialization.

Several correlations between these three axes have been examined. The relationship between range size and abundance is probably one of the most investigated correlations (see Brown, 1984; Lawton, 1993; Gaston, 1996; Gaston *et al.*, 1997). Generally, the most widespread species have the highest local densities, which means that common species in terms of abundance are also common in terms of distribution (Gaston, 2003). One of the most likely hypotheses for explaining this pattern is the fact that locally abundant species with a large range also have a large habitat breadth, and are thus habitat generalists. This relationship between range size and habitat 'specialization' has been tested for several organisms (Pyron, 1999), suggesting that species with large ranges are often less specialized in their habitat than those with restricted ranges (Gaston & Spicer, 2001).

However, the ecological meaning of these relationships is obscured by several methodological difficulties. First, these relationships have rarely been tested using one specific dataset on several species monitored with the same protocol in a given area. Instead, meta-analyses have generally been conducted on several species monitored with different sampling designs in different places. This approach makes it more difficult to disentangle several forms of rarity independently of the variations in the sampling design and effort. Moreover, for a given species part of the relationship between several forms of rarity may derive from inherent sampling effects. For example, the range size of species with lower local abundance can be underestimated (Gaston *et al.*, 1997). The correlation between range size and niche breadth can also result simply from the increased probability of sampling species with larger ranges in a greater number of habitats. This potential sampling effect therefore inflates the habitat specialization of species with small ranges compared with those with larger ranges. Surprisingly, the possibility that habitat specialization partly results from this effect is often ignored. Instead, habitat specialization is often measured as simply the number of habitats where the species occurs or by a more continuous measurement of habitat preference that does not correct for range size (e.g. a measurement of density dispersion across habitats) (Devictor *et al.*, 2010a).

Overall, although the importance of dissociating and relating several forms of rarity was proposed more than three decades ago, only a few attempts have been made to use this approach (but see Espeland & Emam, 2011). A general framework investigating whether and how the three major axes of commonness (range size, local abundance and specialization) interact for a given group is lacking and species are still often considered 'rare' or 'common' without further specification.

Beyond the correlations between several facets of rarity at the species level, commonness and rarity are also used to characterize the dynamics of species assemblages, but without clearly dissociating these different components. For instance, among

the effects of global changes on species assemblages, the replacement of many species ('losers') by a few others ('winners') has been extensively documented across taxa (Clavel *et al.*, 2010). This process, so-called 'biotic homogenization' (BH), is considered a central topic for biogeography and conservation (Olden, 2006). Yet whether the gains in common species and the losses of rare species are contributing equally to BH remains unclear and has hardly been explicitly investigated. Biotic homogenization is thus often described as resulting from the spatial reorganization of communities towards assemblages with similar species (taxonomic homogenization) and is typically measured with similarity (or so-called beta diversity) indices (Olden & Rooney, 2006). However, BH can have different causes and consequences if it results from the success of species with large ranges, local abundances or niche breadths. For instance, local abundance or habitat specialization may help explain which species are primarily affected by local habitat disturbance (Filippi-Codaccioni *et al.*, 2010). To our knowledge, how each facet of commonness contributes to the process of BH has never been explored.

Moreover, measuring similarity indices (e.g. beta diversity) or the local increase in habitat generalists is not sufficient to measure other forms of BH (e.g. functional homogenization) which rely on changes in the variability of functional traits most likely to reflect species responses to changes in the environment and/or the impacts of those changes (Violle *et al.*, 2007). In other words, two communities with two different sets of species can be either highly similar or very different with respect to their functional traits (Luck & Smallbone, 2010). Whether BH also increases the functional similarity of communities has been comparatively little explored and what form of species commonness contributes to the functional diversity of species assemblages is therefore still unclear.

On one hand, a quantitative argument supports the idea that common species are more important than rare species from a functional perspective (Gaston & Fuller, 2008) because they are represented by more individuals or larger total biomasses. On the other hand, a qualitative argument suggests that rare species may support, on average, more original functions (Calba *et al.*, 2014). In a changing environment, trophic interactions also often imply that a few 'rare' species, such as large apex consumers, are essential for the maintenance of the functional composition of species assemblages and ecosystem functioning (Estes *et al.*, 2011). However, once again, whether and how the change in each facet of commonness (or rarity) contributes to the change in the functional diversity of communities have yet to be demonstrated.

Here, we used a high-resolution dataset for birds to address three main objectives. First, at the species level we proposed to disentangle commonness into three independent and complementary axes and link these axes with the functional originality of species. Secondly, at the community level, we assessed how species assemblages characterized by these three forms of commonness change in space and time. Finally, we tested how these changes contribute to the dynamics of functional homogenization.

METHODS

Bird data

Data from the French Breeding Bird Survey (FBBS), a large-scale, multiyear and multiplot monitoring programme, were used (Fig. 1). The FBBS followed a standardized protocol within metropolitan France from 2001 to 2012 (Jiguet *et al.*, 2012). In short, a 2 km × 2 km plot was selected at random in a 10-km radius around the residence of each skilled volunteer ornithologist. This random selection ensured both the survey of varied habitats and representative sampling. In each plot, 10 point counts were evenly distributed across the different habitat types available within the plot (Fig. 1). Then, in each point count, the birdwatcher recorded all birds seen and heard during 5 min in two sessions during the breeding season. Only plots sampled for at least 2 years were used for the analysis ($n = 2057$, with an average of 841 plots monitored each year). In this study we only used the data for the 198 species that breed regularly in France.

Measuring the three facets of commonness of each species

For each species, local abundance was estimated by first taking, for one point and one year, the maximum abundances between

the two sessions where the species had been recorded. We then calculated the mean maximum abundances per point from 2001 to 2012. This index was called the species abundance index (SAI).

For each species, the range was estimated as the total area covered by the distribution of the species within the boundaries of the French metropolitan territory. We used the species distribution maps of BirdLife International & NatureServe (2012), a freely available data base commonly used in the literature, with which we intersected the boundaries of France on a geographical information system (GIS). This provided, for each species, a species range index (SRI) expressed in 10^4 km². Note that we also explored other SRIs (not presented here) using, successively, the number of plots where the species had been recorded from 2001–12 in the French BBS (SRI₂) and the range area estimated by the most recent French Breeding Bird Atlas (2009–12) (SRI₃). SRI is highly correlated with SRI₂ (linear model, $+0.026414 \pm 0.001827$ SE, $F_{1,196} = 209$, $P = 0.026$, $R^2 = 0.52$) and with SRI₃ (linear model, $+9.645 \times 10^{-5} \pm 3.281 \times 10^{-6}$ SE, $F_{1,196} = 864$, $P < 0.001$, $R^2 = 0.82$).

Habitat specialization was estimated using the species specialization index (SSI) (Julliard *et al.*, 2006), which was obtained using the habitat description provided by observers in the field. Each observer classified each of his/her point counts among 18 pre-defined habitat classes (listed in Appendix S1 in Supporting

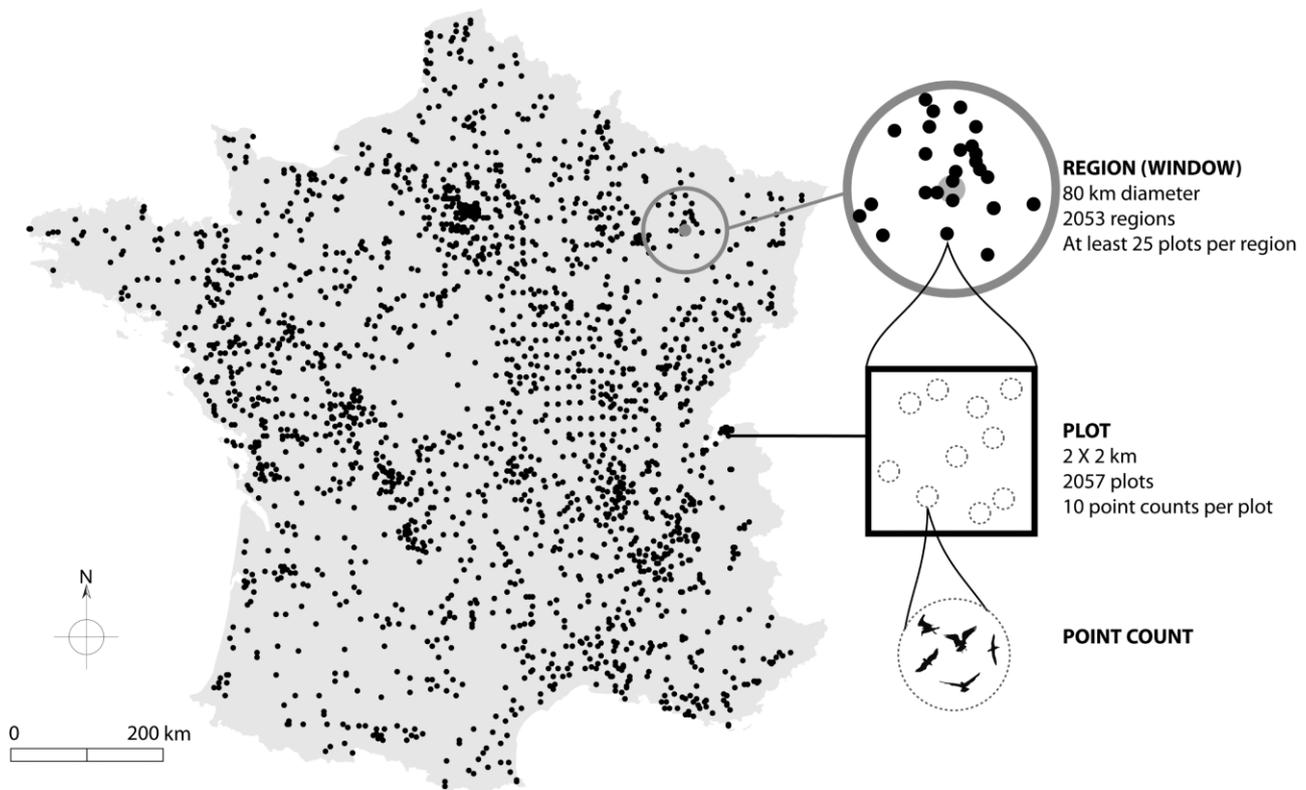


Figure 1 Spatial distribution and definition of the data considered. Birds were sampled by observers in 2 km × 2 km plots. In each plot, birds were recorded in 10 point counts with a standardized protocol. Temporal regional trends presented in this study were calculated within a moving window of radius 80 km.

Information). The SSI was then calculated as a measure of variance of average abundance among the 18 habitats during the period 2001–12. The coefficient of variation (i.e. the standard deviation divided by the mean) was used to obtain a metric statistically independent from species average abundance. SSI thus reflects how much species are narrowly or widely distributed across habitats (Julliard *et al.*, 2006). This so-called SSI has now been extensively used to characterize habitat specialization in birds (Devictor *et al.*, 2008; Filippi-Codaccioni *et al.*, 2010; Barnagaud *et al.*, 2011; Le Viol *et al.*, 2012).

However, in this approach two aspects of commonness are implicitly mixed. In fact, a species can be generalist in part because it is widely distributed and specialist in part because it is localized, regardless of its true preference for a given set of habitats. To estimate habitat specialization corrected for this potential sampling effect related to species range, we used a randomization algorithm as follows. The habitats described by observers among the monitored plots in the dataset were randomized 1000 times and 1000 simulated SSI were calculated for each species. Thus, for each species, the number of plots occupied and its local and total abundances were maintained. In each randomization, only the habitat types were randomly distributed among the occupied plots. This generated expected SSI values for the given species assuming that it can occupy any habitat. Therefore, each of these randomizations provided a specialization index simply generated by the numerical characteristics of the species, regardless of their true ecological association with particular habitats. In other words, these simulated SSI values resulted from the spatial distribution of the species and its abundance profile but from a randomized habitat preference. In this way, a 'corrected SSI' was obtained by subtracting the simulated SSI values from the observed SSI values divided by the standard deviation of the simulated values. These corrected SSI values represent the true ecological preference, independent from other forms of commonness.

For consistency among indices (i.e. an increase in an index represents an increase in commonness), the opposite of this corrected SSI was used to obtain a 'generalization' index ($SGIc = -SSI_{corrected}$) instead of a specialization index, and we modified it as [(maximum of the SGIc) – (value of the SGIc)] to only have positive values. Thus, the higher the SGIc, the more generalist the species is for habitat, independent of its range and local abundance. Similarly, higher SRI and SAI correspond to greater commonness with respect to their range size and their local abundance, respectively.

Measuring the species-specific functional originality

Species-specific functional originality was measured from 22 functional traits extracted from Devictor *et al.* (2010b) (Appendix S2). These traits encompassed life-history traits and feeding habits (Petchey *et al.*, 2007), and were identified as being important in determining the response of bird species to environmental change and in determining the contribution of bird species to ecosystem functions (Sekercioglu, 2006). From these traits, we calculated the Gower distance to represent pairwise trait

distances estimated from the species trait matrix (Legendre & Legendre, 1998). Gower distance accounts for both continuous and qualitative traits and were measured with the function 'daisy' of the R package 'cluster'. We then estimated the functional originality of each species by calculating the mean trait distance between each species and the others (Calba *et al.*, 2014). Note that this metric is highly similar to other measurements of species originality (Pavoine *et al.*, 2005).

Community-weighted mean indices

At the community level, one of the difficulties in studying the relationships between commonness and BH is selecting the appropriate metrics. Here, community-weighted means (CWMs) were used, as they offer a simple and flexible approach to assess the spatial and temporal dynamics of community composition with respect to particular traits of interest. To calculate the CWM, a quantitative trait, X_i , is attributed to each species, reflecting a specific characteristic of interest (e.g. one facet of commonness). Then, any given species assemblage at a given point in space and time can be characterized by averaging X_i , either across the individuals present in this assemblage at that time (if abundance data are available) or simply across species (if only presence–absence data are used) (Webb *et al.*, 2010; Newbold *et al.*, 2012). Therefore

$$CWM = \sum_{i=1}^n a_i X_i / A,$$

where a_i designates the abundance of species i in this assemblage (note that $a_i = 1$ for all i if only presence–absence data are available), X_i is the specific trait of species i and A is the total abundance. Several aspects of change in community composition can thus be assessed using the same metric simply by changing the specific trait (X_i) considered. This avoids the difficulty of comparing indices with different mathematical properties.

Thus, for each plot each year, the community range index (CRI), community area index (CAI) and community generalization index (CGIc) were calculated, representing the community-weighted mean calculated with each facet of commonness (CRI, CAI and CGIc were calculated with the above formula with X_i corresponding to SRI, SAI and SGIc, respectively). Each of these indices was expected to increase following the local relative increase in individuals belonging to species with larger ranges, higher local abundances or greater generalization. Similarly, we also calculated a community functional index (CFI) measuring the functional originality of a community.

Statistical analyses

The relationship between SAI, SRI and SGIc and species-specific functional originality were first tested at the species level. Hierarchical partitioning of R^2 was used in order to determine the proportion of variance of functional originality explained independently by each facet of commonness (Chevan & Sutherland,

1991; Mac Nally, 2000). This method enables the identification of variables whose independent correlation with the dependent variable yields high explanatory power.

Whether the three forms of commonness were more similar between closely related species than between distantly related species in the phylogeny was also tested using Pagel's λ . This approach uses a tree lambda-transformation that compares the phylogenetic trait distribution with that expected in a scenario of Brownian trait evolution (null hypothesis, $\lambda = 0$) (Pagel, 1999; Münkemüller *et al.*, 2012). Phylogenetic signals were obtained by testing a generalized least square (GLS) model using each species commonness index value as a dependent variable, assuming the absence of any independent variable (species commonness index *c.* 1) but a correlation structure imposed by the phylogenetic relatedness among species (using `corPagel` as an argument in the package 'ape' in R). This test provides an estimate of the amount of phylogenetic relatedness of each species commonness index with respect to a scenario of Brownian trait evolution.

To assess the temporal trends in each CWM, we needed to account for non-independence of the plots, the potential influence of spatial gradients, temporal autocorrelation (if any) and nonlinear temporal changes in the indices. To handle these multiple constraints, we used a two-step approach (Monnet *et al.*, 2014). A first model was used to calculate averages and uncertainties in each CWM value in each year individually. This model used nonlinear mixed models (GAMM) in which each CWM was considered the dependent variable, year was considered a factor, and plot a random effect. To account for structural spatial gradients in this model, we fitted geographical coordinates using a smoothing function (two-dimensional thin plate regression splines) as a trend-surface of the dependent variable (Dormann *et al.*, 2007) according to the methods proposed by Wood (2006). We did not fix a priori the number of degrees of freedom for the smooth but used the penalized optimization procedure of the R package 'mgcv'.

Note that this first model does not make the assumption that indices have linear temporal trends but summarizes the effect of each year individually. The plots resulting from this model reflect the year-to-year changes in each index and possible variations in their uncertainty (e.g. due to variations in the number of sampled plots each year) accounting for spatial gradients. As we did not find support for any temporal autocorrelation in the residuals (using the 'acf' function in R) we ignored this potential source of non-independence.

We then used a second model to test the general national trend of the yearly averages in each CWM. In this second model, the yearly average (estimated in the first model) was considered as the dependent variable, and year as a continuous dependent variable. Also, the uncertainty (inverse of the standard error) of each yearly average was considered as a weight in this model. In this second model, we therefore tested whether the average of the indices had increased from 2001 to 2012. Note that testing the linear trend of each CWM directly in one general model (i.e. using year as a continuous variable in the first model) provide similar qualitative results (not shown).

Beyond the general national trends estimated above, we wanted to highlight whether the temporal trends in CWMs were related to each other locally. To estimate the spatial distribution of the temporal dynamics of each CWM, a moving window algorithm was built as follows (Devictor *et al.*, 2010b). Each plot was considered the centre of a window of radius 80 km, within which all additional plots included in the window were selected (Fig. 1). This radius was chosen so that each given window encompassed at least 25 plots. We did not choose to select a fixed number of plots in each window because the number of plots should influence the standard error of the trends, not the direction or the mean of the trends, and our objective was to estimate, for each window, the most accurate trend. This approach provided 2053 windows that were of similar spatial extent and that are composed of at least 25 plots. The temporal trend of each CWM within each window was then calculated using a linear mixed model with community commonness metrics (CAI, CGIc, CRI and CFI) as dependent variables, year as a continuous independent variable and plot as a random factor. The relationship between each local trend (i.e. calculated in each window) of each community commonness index (CAI, CRI and CSI) and CFI was tested. In these models, spatial autocorrelation was accounted for using a GLS model in which the spatial structure was used to model the error term correlation structure. Our spatial structure was best described by an exponential semi-variogram. From the minimal variance of residuals between two points, the nugget (6.11), variance increased with distance until the range was reached (56 km). This non-independence in the data yielded by spatial autocorrelation was included in the GLS.

RESULTS

Species-specific estimates of the several forms of commonness

Figure 2 presents the three facets of commonness (i.e. geographical range, local habitat generalization and local abundance). Of the 198 species considered, only eight can be considered as being common by all three measures of commonness (category 1); on the other hand, 11 species were considered rare under all three measures in having small ranges, being local specialists and with low local abundance (category 8). Between these two extreme categories, all other species are more or less common with respect to one or two forms of commonness.

Interestingly, correcting species specialization (SSI) using the bootstrap algorithm strongly affected the raw values of habitat specialization (Appendix S3). Therefore, if this correction is ignored, many species are misleadingly considered specialist or generalist simply because of the size of their geographical range.

The general model relating species functional originality to the three forms of commonness explains 11.94% of the total variability in functional originality. A hierarchical partitioning of this model further reveals that among this 11.94%, species functional originality is significantly (Z -score ≥ 1.65 ; $P < 0.05$) and best explained by species generalization (positive relation; 57.72% of the total variance explained by the three commonness

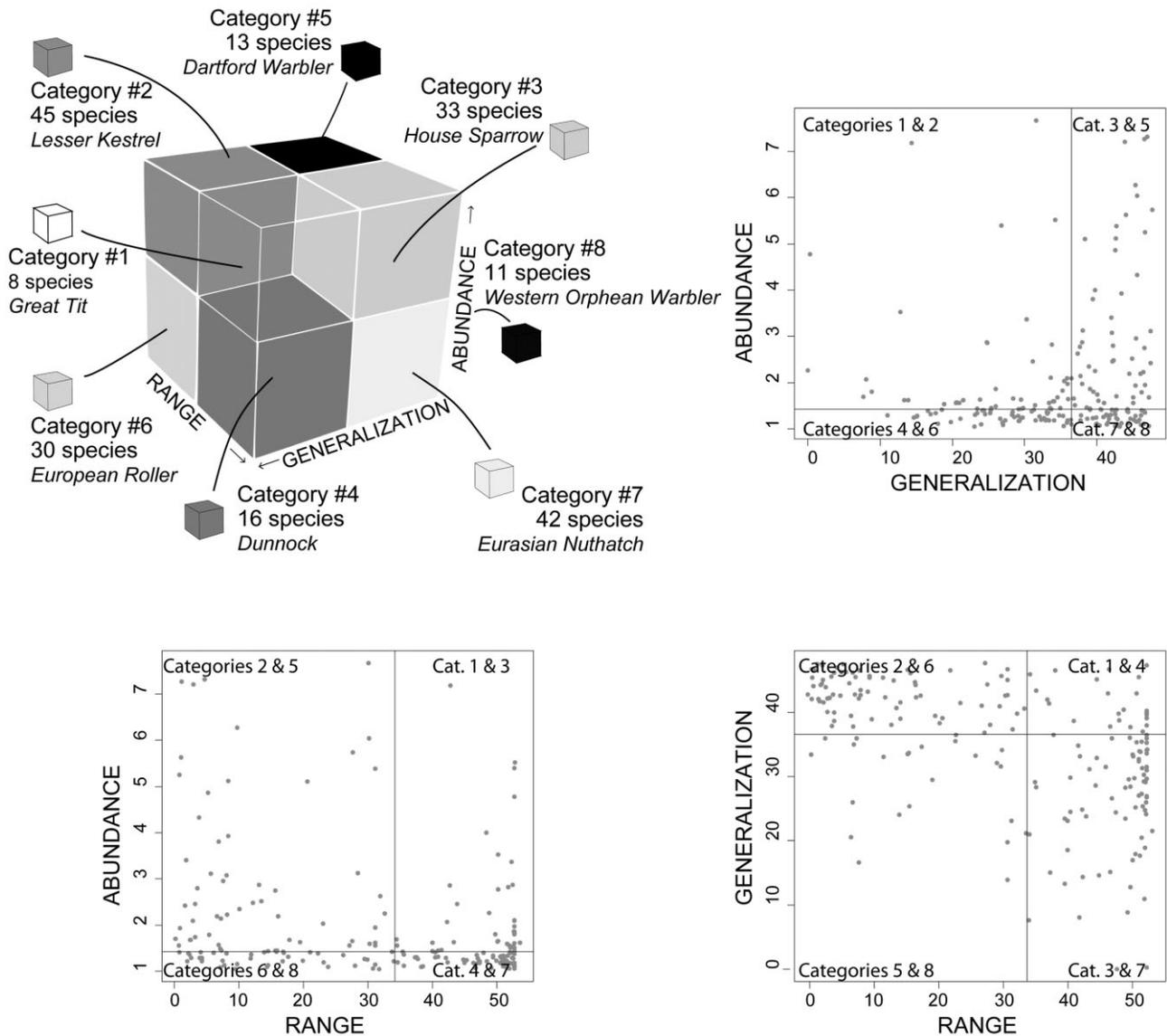


Figure 2 Visualization of the three facets of commonness for the 198 bird species studied. ‘Abundance’ and ‘generalization’ were calculated from the data of the French Breeding Bird Survey (2001–12). The first one corresponds to a species abundance index (calculated as the mean maximum abundance per sampling point and expressed in number of individuals) and the second one to a species generalization index (calculated as the opposite value of the variance of average abundance among available habitats, corrected for differences in species ranges – see Methods for details). The values of the axis related to species generalization were transformed [(maximum of the index) – (value of the index)] to have only positive values. ‘Range’ was calculated from BirdLife International & NatureServe (2012) and corresponds to the geographical range of a species within France (expressed in 10^4 km²). Species were split into two categories along each axis according to their higher or lower position in relation to the median values of each axis, thus giving eight possible categories across all axes. On each of the three two-dimensional plots, black horizontal and vertical lines represent the median values of *y*- and *x*-axes, respectively.

facets, $P < 0.05$), next by species abundance index (positive relation; 28.61% of the total variance explained, $P < 0.05$) and finally by species range (negative relation; 13.68% of the total variance explained, $P < 0.05$). Moreover, there is a significant phylogenetic signal for each commonness facet (SGIc, $\lambda = 0.21$; SRI, $\lambda = 0.24$; SAI, $\lambda = 0.55$; all $P < 0.001$) as well as for functional originality ($\lambda = 0.72$, all $P < 0.001$). These results show each facet of commonness tend to be phylogenetically clustered.

Note, however, that this signal is particularly strong for SAI and even stronger for functional originality but rather weak for SGIc and SRI.

Temporal and spatial trends of commonness indices

The temporal trends of community-weighted means, calculated with each form of commonness, were then estimated (Fig. 3).

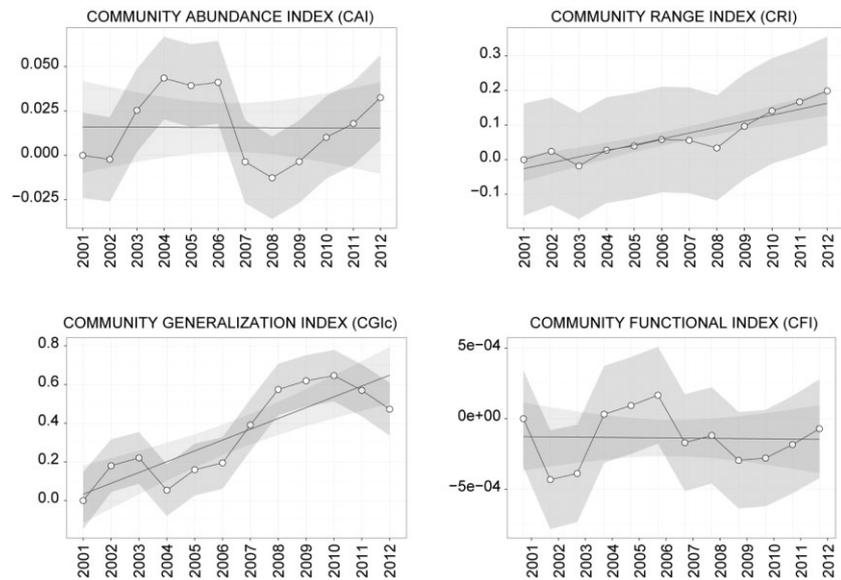


Figure 3 National temporal trends of each index from 2001 to 2012 as estimated by generalized additive mixed models (GAMMs) with associated standard errors in grey areas. Black lines correspond to the linear temporal trends of these indices, based on linear regressions with each yearly change as the explanatory variable and year as a continuous variable. As for GAMMs, grey areas also show standard errors associated with these linear models. In each graph the first year (2001) was set at zero.

There are high year-to-year variations in CAI ($-6.808 \times 10^{-5} \pm 1.808 \times 10^{-3}$ SE, $F_{1,10} = 0.001$, $P = 0.97$, $R^2 = 0.0001$) which is different from the other trends observed in the CRI and the CGIc. In other words, the change in the composition of local communities is not biased towards species with higher or lower species-specific abundances. In contrast, there are directional changes in the CRI ($+0.0174 \pm 0.0033$ SE, $F_{1,10} = 27.42$, $P = 0.0004$, $R^2 = 0.73$) and CGIc ($+0.0564 \pm 0.0104$ SE, $F_{1,10} = 29.45$, $P = 0.0003$, $R^2 = 0.75$) which both regularly increase over time. Therefore, communities tend to be enriched in species with large ranges (SRI) and large habitat breadth (SGIc).

At the national scale, there is a weak and non-significant decrease in the functional originality (CFI) of assemblages ($-2.412 \times 10^{-7} \pm 1.712 \times 10^{-5}$ SE, $F_{1,10} = 0.0002$, $P = 0.99$, $R^2 = 1.985 \times 10^{-5}$). Therefore, while the composition of communities has changed towards species with large ranges and generalization, this does not substantially translate to the increase or decrease in functional originality of assemblages at the national scale.

Testing the relation between the local trends in each community commonness metric with the local trends in functional diversity, however, reveals that functional diversity decreases with the increase in CRI locally ($-1.298 \times 10^{-3} \pm 4.7669 \times 10^{-5}$ SE, $P < 0.001$). To a lesser extent, functional diversity increases with the increase in CAI ($+0.0049 \pm 0.0003$ SE, $P < 0.001$) and with the increase in CGIc ($+9.610 \times 10^{-5} \pm 0.0001$ SE, $P = 0.055$) (Fig. 4).

DISCUSSION

Adapting the conceptual framework proposed by Rabinowitz (1981) to describe the different forms of rarity, we found that commonness is a multifaceted concept, emphasizing that 'there are multiples routes to being common' (Gaston, 2011). In fact,

we found a great variability among species range, habitat specialization and local average abundance. More interestingly, the distribution of breeding birds in France does not seem to be evenly shared within each of the three categories of commonness.

However, this classification requires caution. First, although the position of each species along each axis makes sense, it is more or less arbitrary to delineate discrete classes of commonness. Such delineation inevitably depends on both the scale and the thresholds chosen for each axis (e.g. median values were used here). Thus, the proposed categories should be viewed as a qualitative approach to segregating species into major types of commonness (Fig. 2). Second, our approach ignores intraspecific variations among individuals, populations or subspecies (Bolnick *et al.*, 2011). Third, these categories only make sense for the particular dataset considered. In the FBBS, only the most common species are sampled within a single country. Therefore, the distinction of different kinds of commonness might be only relevant for a subset of the most common species among the whole national breeding avifauna. Consequently, the least common species we identified (category 8) are far from being the rarest birds breeding in France. Finally, the calculation of each of the three indices is based on French data from 2001 to 2012 and thus corresponds to a national range size, local abundance and local generalization estimated for a given time period. In other words, a common species in France is neither necessarily common in other countries nor will it have a constant commonness in the future. For instance, it is likely that habitat specialization can change over time for a given species (Barnagaud *et al.*, 2011).

However, we have revealed several properties of commonness at the species level that should be independent of the dataset considered. For instance, we have shown that the higher the number of plots occupied by a given species, the more chance it has of being found in a wide range of habitats and thus of being

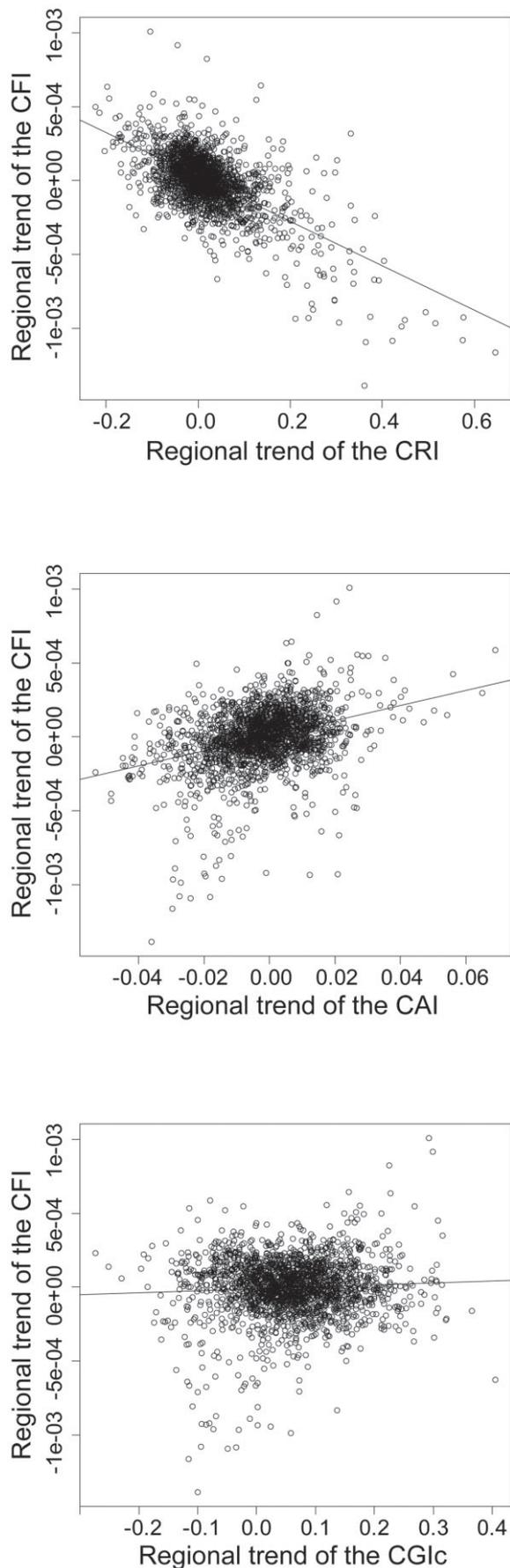


Figure 4 Relationships between regional trends (calculated in each window of radius 80 km composed of 25 plots) in functional originality and the regional trends of each community commonness metric. Solid lines represent the linear trends. CAI, community abundance index; CRI, community range index; CGIc, community generalization index; CFI, community functional index.

considered a habitat generalist. For this reason, we believe that many species can be mistakenly considered habitat generalists because of their large range (the correlation between the generalization index and the range index gets much weaker when the generalization index is corrected; see Appendix S4). We have also found that commonness is a trait that is phylogenetically clustered, and that it is noticeably pronounced for SAI. It is indeed known that particular genera or families tend to be gregarious (e.g. Corvidae, Laridae, Hirundinidae). In contrast, habitat specialization and species ranges are not expected to be particularly clustered (Forister *et al.*, 2012). In addition, we have found an even stronger phylogenetic signal for functional originality, as expected from the strong phylogenetic conservatism of the traits considered. If the regional decrease in community originality is confirmed, this could indicate that specific lineages are more prone to local decrease than others (Thomas, 2008). In any case, these results plead for an even more complete study of changes in community composition in space and time with a specific focus on functional and phylogenetic diversity (Monnet *et al.*, 2014).

Moreover, the relationships we have found between the three facets of species commonness and their functional originality complement the findings of Gaston & Fuller (2008), according to whom species with large numbers of individuals (i.e. abundant species) contribute more than rare species to ecosystem functions. We have indeed shown that species with high local abundances and generalization tend to have more original functions. However, our results further suggest that functional originality is also negatively related to species range sizes. This is in accordance with the recent study of Mouillot *et al.* (2013) revealing that rare species (considering both range size and local abundance in their study) support the most distinct combination of traits. However, our results on the relationships between species commonness and species functional originality require caution since the three forms of commonness barely explain 12% of the total variability in functional originality.

We then expressed the species-specific differences among the three forms of commonness at the community level in space and time. The spatio-temporal trends we highlighted are based on a rather short-time period (2001–12) that implies that whereas such changes have to be interpreted with caution, directional changes can be detected in some commonness facets over 11 years.

At the national scale, we found that although CAI does not show a clear temporal trend, both CRI and CGIc increased significantly from 2001 to 2012, reflecting that species assemblages are increasingly dominated by species with large ranges and large habitat breadths. The increase in average specialization

(CGIc) has already been demonstrated for breeding birds in several European countries (Le Viol *et al.*, 2012). Such results have even led to the consideration that habitat generalists are the winners of current global changes (Davey *et al.*, 2012). Here, although we used an index of generalization corrected by potential artefacts related to species range size, this trend remains valid. However, to our knowledge, the enrichment of bird communities with species with large ranges (as demonstrated by the marked increase in CRI) has never been documented. This suggests that species with large ranges are probably those that are benefiting from global changes compared with species with restricted ranges. One can hypothesize that widely distributed species are characterized by higher genetic variability, phenotypic plasticity and thus better reactivity to global changes.

Beyond these national trends, we have also clearly demonstrated that, in the same regional areas (within the same 80-km radius), the decrease in functional diversity (CFI) is mainly linked with the increase in CRI and with the decrease in CAI. We can thus consider that the increase in species with a large range and the decrease in numbers of species with high local abundance lead to functional BH independently of their degree of habitat specialization.

CONCLUSION

By separating species commonness into three complementary forms, we have found that there are different ways of being common for a given species according to its local abundance, its range size and its habitat specialization. We have further shown that species that are the most generalist and abundant but with restricted ranges tend to be more functionally original. At a national scale, we have revealed an increase in the relative abundance of species with large ranges and habitat breadths and a non-significant decreasing trend in functional originality. However, we have shown that the local decrease in functional diversity is clearly linked to the enrichment of the most widespread species within communities. Our results open up new research avenues in the understanding of the consequences of commonness on community dynamics and on the process of BH occurring at a large scale.

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REFERENCES

- Barnagaud, J.-Y., Devictor, V., Jiguet, F. & Archaux, F. (2011) When species become generalist: on-going large-scale changes in bird habitat specialization. *Global Ecology and Biogeography*, **20**, 630–640.
- Bevill, R.L. & Louda, S.M. (1999) Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology*, **13**, 493–498.
- BirdLife International & NatureServe (2012) *Bird species distribution maps of the world. Version 2.0*. BirdLife International and NatureServe, Cambridge, UK and Arlington, MA.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, **26**, 183–192.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124**, 255–279.
- Calba, S., Maris, V. & Devictor, V. (2014) Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds: separating ecological drivers from methodological choices. *Global Ecology and Biogeography*, **23**, 669–678.
- Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *The American Statistician*, **45**, 90–96.
- Clavel, J., Julliard, R. & Devictor, V. (2010) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and Environment*, **9**, 222–228.
- Davey, C.M., Chamberlain, D.E., Newson, S.E., Noble, D.G. & Johnston, A. (2012) Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, **21**, 568–578.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252–261.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. (2010a) Defining and measuring ecological specialization. *Journal of Applied Ecology*, **47**, 15–25.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010b) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, **13**, 1030–1040.
- Dobson, F.S., Yu, J. & Smith, A.T. (1995) The importance of evaluating rarity. *Conservation Biology*, **9**, 1648–1651.
- Dormann, C.F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., de Blust, G., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J.P., Schmidt, T., Speelmans, M., van Wingerden, W.K.R.E. & Zobel, M. (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography*, **16**, 774–787.
- Espeland, E.K. & Emam, T.M. (2011) The value of structuring rarity: the seven types and links to reproductive ecology. *Biodiversity and Conservation*, **20**, 963–985.

- Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Filippi-Codaccioni, O., Devictor, V., Bas, Y., Clobert, J. & Julliard, R. (2010) Specialist response to proportion of arable land and pesticide input in agricultural landscapes. *Biological Conservation*, **143**, 883–890.
- Forister, M., Dyer, L.A., Singer, M.S. & Stireman, J.O. (2012) Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. *Ecology*, **93**, 981–991.
- Gaston, K.J. (1996) The multiple forms of the interspecific abundance–distribution relationship. *Oikos*, **75**, 211–220.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.
- Gaston, K.J. (2011) Common ecology. *BioScience*, **61**, 354–362.
- Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution*, **23**, 14–19.
- Gaston, K.J. & Spicer, J.I. (2001) The relationship between range size and niche breadth: a test using five species of *Gammarus* (Amphipoda). *Global Ecology and Biogeography*, **10**, 179–188.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.
- Hartley, S. & Kunin, W.E. (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, **17**, 1559–1570.
- Jiguet, F., Devictor, V., Julliard, R. & Couvet, D. (2012) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica*, **44**, 58–66.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.
- Kunin, W.E. & Gaston, K.J. (1993) The biology of rarity: patterns, causes and consequences. *Trends in Ecology and Evolution*, **8**, 298–301.
- Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, **8**, 409–413.
- Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, A., Pearce-Higgins, J.W., Reif, J., Van Turnhout, C. & Devictor, V. (2012) More and more generalists : two decades of changes in the European avifauna. *Biology Letters*, **8**, 780–782.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.
- Luck, G.W. & Smallbone, L.T. (2010) The impact of urbanization on taxonomic and functional similarity among bird communities. *Journal of Biogeography*, **38**, 894–906.
- Mac Nally, R. (2000) Regression and model building in conservation biology, biogeography and ecology: the distinction between and reconciliation of ‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation*, **9**, 655–671.
- Monnet, A.C., Jiguet, F., Meynard, C.N., Mouillot, D., Mouquet, N., Thuiller, W. & Devictor, V. (2014) Asynchrony of taxonomic, functional, and phylogenetic diversity in birds. *Global Ecology and Biogeography*, **23**, 780–788.
- Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E., Renaud, J. & Thuiller, W. (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, **11**, e1001569.
- Münkemüller, T., de Bello, F., Meynard, C.N., Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N. & Thuiller, W. (2012) From diversity indices to community assembly processes: a test with simulated data. *Ecography*, **35**, 468–480.
- Newbold, T., Butchart, S.H.M., Şekercioğlu, C.H., Purves, D.W. & Scharlemann, J.P.W. (2012) Mapping functional traits: comparing abundance and presence–absence estimates at large spatial scales. *PLoS ONE*, **7**, e44019.
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039.
- Olden, J.D. & Rooney, T.P. (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, **15**, 113–120.
- Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.
- Pavoine, S., Ollier, S. & Dufour, A.B. (2005) Is the originality of a species measurable? *Ecology Letters*, **8**, 579–586.
- Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007) Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, **76**, 977–985.
- Preston, F.W. (1948) The commonness and rarity of species. *Ecology*, **29**, 254–283.
- Pyron, M. (1999) Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. *Journal of Biogeography*, **26**, 549–558.
- Rabinowitz, D. (1981) Seven forms of rarity. *The biological aspects of rare plant conservation* (ed. by H. Synge), pp. 205–217. Wiley, New York.
- Sekercioğlu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, **21**, 464–471.
- Thomas, G.H. (2008) Phylogenetic distributions of British birds of conservation concern. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2077–2083.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. & Leroy Poff, N. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, **13**, 267–283.
- Wood, S. (2006) *Generalized additive models. An introduction with R*. Chapman and Hall/CRC, Boca Raton, FL.

SUPPORTING INFORMATION

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

Appendix S1 Habitat classes used to calculate the Species Specialization Index.

Appendix S2 List of functional traits to compute functional indices.

Appendix S3 Pair correlations between each Species Commonness Index for the 198 species studied.

Appendix S4 Pair correlations between each Community Commonness.

BIOSKETCH

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