LETTER

Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world

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Abstract

Functional and phylogenetic diversity are increasingly quantified in various fields of ecology and conservation biology. The need to maintain diversity turnover among sites, so-called beta-diversity, has also been raised in theoretical and applied ecology. In this study, we propose the first comprehensive framework for the large-scale mapping of taxonomic, phylogenetic and functional diversity and of their respective turnover. Using high-resolution data on the spatial distribution and abundance of birds at a country scale, we disentangled areas of mismatches and congruencies between biodiversity components. We further revealed unequal representation of each component in protected areas: functional diversity was significantly under-represented whereas taxonomic diversity was significantly over-represented in protected areas. Our results challenge the use of any one diversity component as a surrogate for other components and stress the need to adopt an integrative approach to biodiversity conservation.

Keywords

Beta-diversity, biogeography, community phylogeny, distribution, functional traits, protected areas, spatial analysis, turnover.

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INTRODUCTION

Community ecologists, macroecologists and conservation biologists have increasingly begun to quantify several facets of diversity within species assemblages. Taxonomic diversity (TD), the most commonly considered component of diversity is silent on functional and phylogenetic differences among species. Measuring phylogenetic diversity (PD) in species assemblages was then proposed as a promising way to explain the role of species interactions and biogeographic histories in community structure and composition (Webb *et al.* 2002). Meanwhile, functional diversity (FD), reflecting the diversity of morphological, physiological and ecological traits within biological communities (Petchey & Gaston 2006) was shown to better explain ecosystem functioning than other classical measures of diversity (review in Hooper

et al. 2005). At large scales, understanding spatial and temporal patterns of FD was also proposed as a useful route to disentangle among several assembly processes (Petchey *et al.* 2007). Finally, as between-species interactions and species functional roles involve complex and often unknown suite of traits, PD was proposed as a holistic characteristic of species assemblages that can even better explain ecosystem productivity than FD (Cadotte *et al.* 2009).

From conservation perspectives, FD and PD were both advocated as two important facets of diversity respectively for ensuring the provision of goods and services (Díaz *et al.* 2007) and for representing an evolutionary history of conservation interest (Mace *et al.* 2003; Knapp *et al.* 2008). All these types of diversity have also been recently decomposed in regional, local and among-sites components

(so-called gamma, alpha and beta diversities) (Lande 1996; Gaston *et al.* 2007; Graham & Fine 2008).

Surprisingly, despite this recent surge for disentangling the multiple components of biodiversity, the causes and consequences of the complementarities between these components are still unclear. In fact, two communities of equal TD may be composed of species with either highly similar or different phylogenetic histories (Webb *et al.* 2002; Forest *et al.* 2007). Similarly, any estimated measure of FD (or even the true FD that would capture all functional traits) can also be decoupled from PD if some functional traits are under strong stabilizing selection or owing to competitive interactions within lineages (Prinzing *et al.* 2008). Measuring each of these complementary biodiversity components is thus necessary for understanding the complete structure, composition and dynamics of natural communities (Webb *et al.* 2002; Maherali & Klironomos 2007).

Adopting an integrated view of biodiversity is also a great challenge for conservation planning. Indeed, global changes may have an impact on FD and alter species interactions and ecosystem functioning regardless of the change in TD (Díaz *et al.* 2006; Taylor *et al.* 2006; Flynn *et al.* 2009). Similarly, a decrease in PD may induce the loss of evolutionary history and future options (Mace *et al.* 2003; Forest *et al.* 2007; Emerson & Gillespie 2008). However, note that PD is silent on which lineages will speciate in the future, and on what and where the next adaptive radiation will take place (Krajewski 1991). A conservation dilemma can arise from the mismatch between TD, FD and PD: if communities with different levels of each diversity component are located in different places, areas with high TD may exclude high FD levels and diverse phylogenetic lineages (Forest *et al.* 2007; Naidoo *et al.* 2008; Cumming & Child 2009).

In theory, preserving several components of biodiversity simultaneously could be achieved by maximizing the protection of TD. Indeed, a complementary network of sites that encompasses all species will capture overall FD and PD. However, this policy is unfeasible and both past and current conservation strategies have instead focused on priority taxa or areas to protect rarity, endemism and distinctiveness (Myers *et al.* 2000; Kier *et al.* 2009). Moreover, effective strategies towards biodiversity conservation require not only the inclusion of individual species, functions or lineages in protected areas, but also sets of interacting species over large areas.

Effective conservation strategies in a changing world should also rely on the maintenance of species, functional and evolutionary processes at different spatial scales (Gering *et al.* 2003; Brooks *et al.* 2006; Lee & Jetz 2008). To do so, each component of diversity should be maintained at the local (alpha-diversity) and regional (gamma-diversity) scales but also among localities (so called spatial turnover or beta-diversity) (Buckley & Jetz 2008; Jankowski *et al.* 2009). Mapping beta-TD was thus recently proposed as an additional tool to improve conservation strategies (Gaston *et al.* 2007; McKnight *et al.* 2007). However, mapping the spatial distribution of both beta-FD and beta-PD has never been achieved (but see Graham & Fine 2008; Graham *et al.* 2009), and their congruence with beta-TD is virtually unknown.

Here, we propose the first comprehensive approach that decouples TD, FD and PD and their respective turnover and discuss theoretical and applied consequences of mapping and relating these complementary facets of diversity. To do so, we used a single, large-scale, standardized monitoring scheme to follow the abundance of 229 bird species across France during 7 years. We provide a simple conceptual and practical solution to map each component of biodiversity for this taxonomic group and further assessed the ability of the national protected area network to embrace each biodiversity component. We found large spatial mismatch between biodiversity components leading to an unequal representation of TD, PD and FD in protected areas. This work gives insights on the ecological and evolutionary forces that drive each biodiversity facet and suggests the need for an integrative approach to biodiversity conservation.

MATERIAL AND METHODS

Bird data

The French breeding bird survey (FBBS) is a large-scale, breeding-bird monitoring scheme that has followed a standardized protocol in 2×2 km plots since 2001 (Julliard *et al.* 2006). The plots are located randomly, which ensures the survey of varied habitats (including intensive farmlands, forests, suburbs and cities) and representative sampling: 12.5% of plots were included in protected areas, which cover *c.* 12.5% of the national territory (Fig. 1).

Briefly, for each species, we calculated the average abundance in all plots monitored at least two years during 2001–2007 ($n = 1037$). The FBBS is designed to monitor terrestrial breeding species, so marine and vagrant species were excluded from our analyses. The remaining 229 species were recorded on at least two different point counts. These species accounted for more than 99.99% of all individual birds recorded by the FBBS and represent the great majority of the French breeding avifauna.

Breeding birds in France provide a good dataset for this study because (1) strong environmental gradients exist across the country in accordance with varying climates from Mediterranean to continental and alpine; (2) the availability of a high-quality, large-scale, multi-year and multi-site survey; (3) high-quality knowledge of the phylogeny and
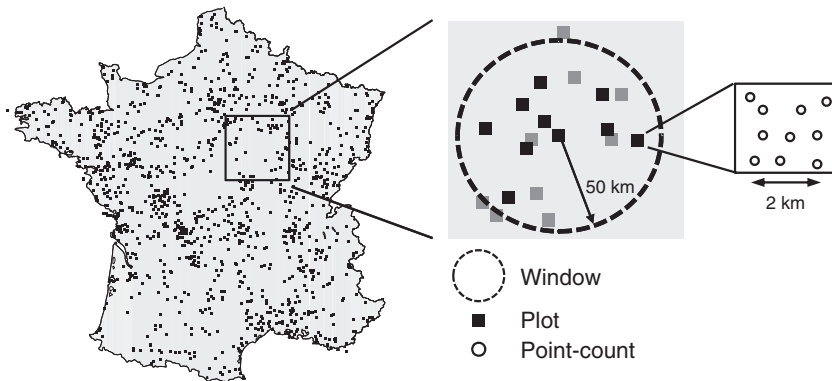
Gamma diversity: Diversity of the window
Beta diversity (or turnover): diversity between plots within the window
Alpha diversity: diversity of a given plot within the window

Figure 1 Spatial distribution of surveyed plots and sampling design.

functional traits of birds; and (4) the high diversity of avian functional traits with multiple known links with ecosystem functioning (Şekercioğlu 2006).

Partitionning taxonomic, functional and phylogenetic diversity

We used a systematic approach to map diversity and turnover between plots that are not regularly distributed over the study area. We considered each plot to be the center of a 50 km radius window, within which nine additional plots were randomly selected (Fig. 1). This approach provided 1037 windows that were of similar spatial extent and were composed of 10 plots (Fig. 1).

We then used the additive partitioning of Rao's quadratic entropy as a common framework for partitioning each biodiversity facet (Ricotta & Sweidl 2009). In this approach, the diversity of each window (Q_γ) is given by $Q_\gamma = \bar{Q}_\alpha + Q_\beta$, where $\bar{Q}_\alpha$ represents the average diversity of the plots within window, and Q_β the turnover among plots within window (Fig. 1). For a given plot with S species, the Rao quadratic entropy is given by $Q_k = \sum_{i=1}^{S} d_{ij}p_ip_j$ where p_i and p_j are the relative abundances of the ith and jth species and d_{ij} is the distance (i.e. functional or phylogenetic) between species ($d_{ij} = 0$ for $i = j$). Note that for TD, d_{ij} is simply set to 1 for all pairs of species ($i \neq j$) so that Q_k reduces to the Simpson index (Ricotta 2005). Hence, Q_k represents the expected dissimilarity (in terms of identity, functional or phylogenetic distance) between two individuals selected at random in the plot. A weight can be attributed to each plot to reflect relative sampling effort. As the sampling effort was constant in this study (each plot was monitored during the same amount of time and each window had exactly 10 plots), weighting was not necessary and, for a given window, $\bar{Q}_\alpha$ was simply the average of Q_k across the 10 plots of that window. The regional FD Q_γ is equivalent

to Q_k but is calculated at the regional (window) level and thus represents the distances between all pairs of species i and j within and between all pairs of plots weighed by their frequencies. Finally, beta diversity of the window is given by $Q_\beta = Q_\gamma - \bar{Q}_\alpha$ (note that the multiplicative partitioning given by $Q_\beta = Q_\gamma / \bar{Q}_\alpha$ could be used as well; Jost *et al.* 2010).

We further used a correction proposed first by Jost (2007). Jost showed that many diversity indices, including Simpson diversity, can have counterintuitive ecological properties. The importance of using this correction was further underlined by Ricotta & Szeidl (2009) for Rao. If not corrected, β-diversity values are underestimated and can be meaningless in case of complete species turnover between communities. Correct and unbiased metrics of gamma and beta diversities are obtained by applying a simple correction given by $Q_{\gamma jost} = 1/(1 - Q_\gamma)$ and $Q_{\beta jost} = (Q_\gamma - \bar{Q}_\alpha) \times 100/(1 - \bar{Q}_\alpha)$. Finally, $Q_{\beta jost}$ was expressed as a percentage of the regional diversity. The same approach was used for the partitioning of TD, FD and PD.

Note that these metrics combine the difference between the functional (or phylogenetic) distances between species and the structure in relative abundances in species assemblages. In doing so, species at low abundance in most sites yet with important functional roles (or distinct phylogenetical history) could have small contribution to FD (or PD). To assess the influence of using presence–absence instead of abundance data, we also calculated the same metrics with presence–absence. In this case, $Q_{\gamma jost}$ corresponds to the mean pairwise (functional or phylogenetic) distance separating species in the community (Webb *et al.* 2002) and $Q_{\beta jost}$ the turnover in the distances (functional or phyloegnetic) between species in that community.

Using Rao as a common framework allowed us to compare all facets of diversity with and without considering species relative abundances. Note that other approaches are

possible to calculate PD and FD and their respective turnover (Petchey & Gaston 2006; Graham & Fine 2008). For instance, PD (or FD) of a given region can simply reflect the sum of the branch lengths connecting species present in that region (Faith 1992). Then, PD (or FD) can be partitioned into local, regional and between plots components using the partitioning of diversity proposed by Lande (1996) or using other turnover metrics (Graham & Fine 2008).

Functional and phylogenetic distances between species

Functional diversity was obtained using all pairwise distances between the 229 bird species based on 22 functional traits (Petchey *et al.* 2007). These functional traits (see Table S1) were either quantitative or qualitative, and measured various aspects of resource use by birds. All of these traits are playing important roles in species interactions and ecosystem functioning (Şekercioğlu 2006) and were taken from Cramp (1977–1994). Correlations between these functional traits could influence the estimate of functional distances between species (Petchey & Gaston 2006). In particular, FD could be influenced by the most correlated traits, although one or few uncorrelated traits could be more important for functional roles. To decrease the potential influence of highly correlated traits, we therefore used Hill & Smith (1976) multivariate technique to create scaled orthogonal composite traits. This multivariate analysis allows the creation of independent composite traits with mixed quantitative variables and factors. The coordinates of species along the first eight axes of this multivariate analysis (corresponding to 71% of variation in the functional space) were used to build a functional dendrogram depicting the functional relationships among species using hierarchical classification. Because cophenetic distances estimated from hierarchical classification may depend on the distance and clustering method, we used a consensus approach proposed by Mouchet *et al.* (2008). This method tests all combinations of distances and clustering methods and then selects the most reliable dendrogram to estimate ultrametric functional distances between species pairs (given in Figure S1).

Note that although multivariate analysis creates independent combination of traits, only eight axes were selected to build the functional dendrogram. Yet, all axes could hold important functional combinations of traits. We therefore conducted similar analysis using a functional dendrogramm directly based on the 22 traits and found similar qualitative results.

Phylogenetic diversity and phylogenetic turnover were obtained in the same manner, but the phylogenetic ultrametric distances between species were directly calculated from phylogenetic trees. First, we used a complete phylo-

geny for the 229 species considered. This tree resulted from a super tree derived from different studies using different methods (Jønsson & Fjeldså 2006; Møller 2006). For this phylogeny, consistent estimates of branch lengths were unavailable. Therefore, all branch lengths were considered to be equal to 1 and the tree converted in a smoothed ultrametric tree. To assess the robustness of our results to the particular phylogeny considered, the same analysis was also repeated with a more precise phylogeny including branch lengths (Thomas 2008) but which only included a subset of the studied specie. Note that this other phylogeny was the most complete and recent molecular phylogeny available for a maximum number of bird species considered in our study (148 species among the 229).

Finally, matrices of pairwise distances between species were derived from the functional and from the two phylogenetic trees. For a given distance matrix, all pairwise distances were standardized so that the maximum distance between species equaled 1. All diversity metrics were then calculated using these matrices.

Statistical analysis

To test the statistical congruence between diversity components, we performed generalized linear mixed models that accounted for spatial dependence between samples. These models are generalized linear models with an exponential covariance structure that accounted for spatial autocorrelation between samples (Pinhero & Douglas 2000). Therefore, all presented tests were corrected for spatial autocorrelation.

Taxonomic diversity can intrinsically influence the functional and phylogenetic turnover (Harrison *et al.* 1992; Lennon *et al.* 2001). Indeed, a lack of taxonomic turnover will prevent functional and phylogenetic turnovers and high taxonomic turnover tends to be associated with high functional and phylogenetic turnovers by sampling effect. Therefore, to disentangle the distribution of functional and PD from the spatial gradient in TD (Forest *et al.* 2007), we further mapped the residuals of the linear regressions of functional (and phylogenetic) diversity on TD. All calculation of indices and statistical analyses were performed with R statistical software (using packages ape, clue, ade4 and nlme).

Protected area assessment

We mapped the spatial distribution of each diversity component using a kriging interpolation technique based on the spatial autocorrelation structure of variables. This technique provides the best and unbiased predictions of variables recorded in discrete sample points over a given area (Cressie 1993).

Using the official coverage of all existing French protected areas (available online from the World Database on Protected Areas: http://sea.unep-wcmc.org/wdbpa/), we also assessed whether windows with more or less high levels of each biodiversity component were included in the protected area network. Rather than choosing an arbitrary threshold to focus on so-called biodiversity hotspots, we used a continuous approach: for each biodiversity component (TD, FD and PD and their relative turnovers), we ranked all windows from the most to the least diverse, presenting a decreasing diversity gradient. We then estimated the cumulative percentage of windows included in protected areas along this gradient. We then tested whether the 20% of windows with the highest values for each diversity component were more or less protected than expected by chance. To do so, we performed a permutation test in which the protected windows were randomly distributed among all windows (1000 times), and then we calculated the proportion of protected windows among the 20% of windows with the highest diversity values. For each
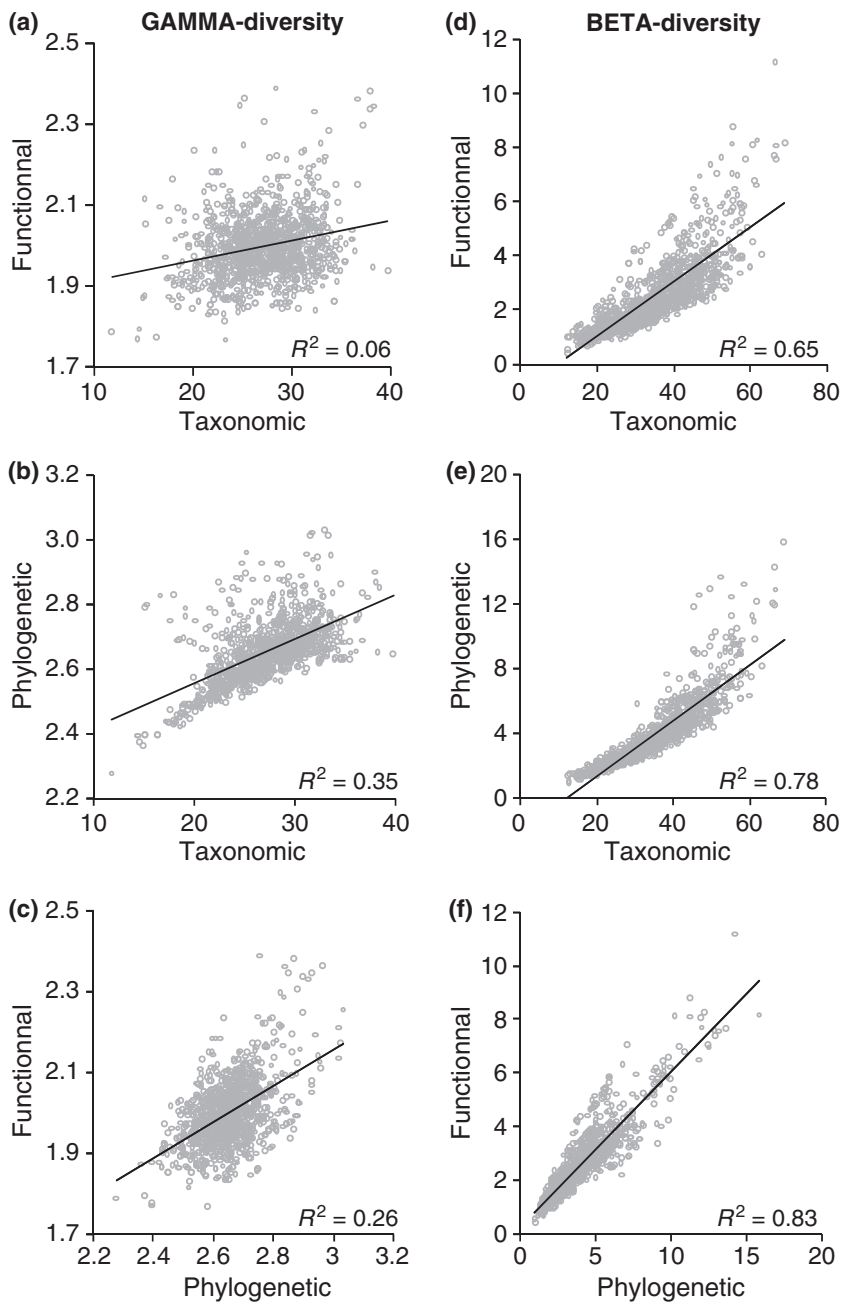

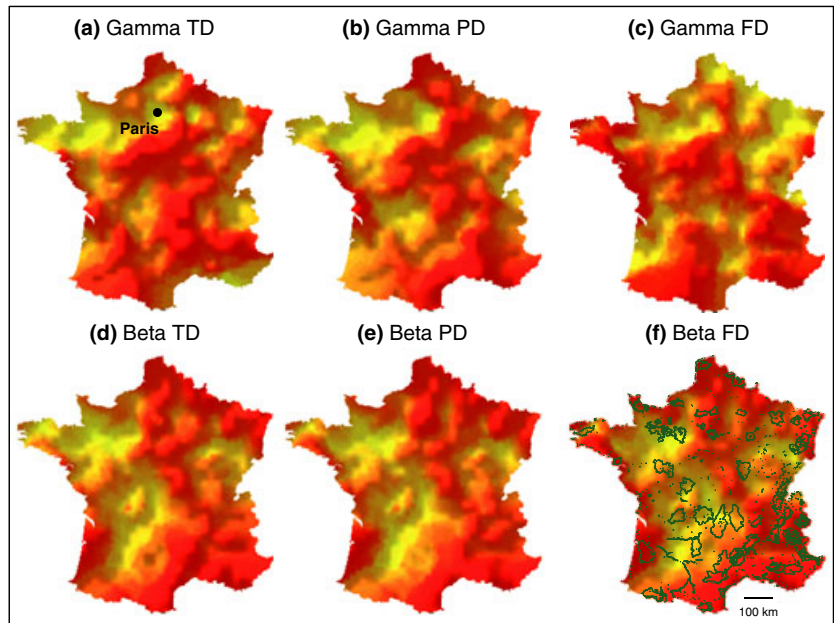**Figure 2** Plots of the relationships between each component of gamma and beta diversity.

Figure 3 Spatial distribution of taxonomic, phylogenetic and functional diversity and their relative turnover. (a–c) Maps of taxonomic, phylogenetic and functional gamma-diversity, respectively (10 quantile intervals from yellow to dark red). (d–f) Maps of diversity turnover (beta-diversity) for each respective component. (f) The protected area network boundaries are drawn on the map of functional turnover.

diversity component, the probability that the observed proportion was higher or lower than expected by chance was then calculated by comparing the simulated proportions with the observed values.

RESULTS

Overall, we found that FD and PD were positively related to TD ($F_{1,1035} = 175.3$; $P < 0.0001$; $r^2 = 0.06$; $n = 1037$; and $F_{1,1035} = 809.4$; $P < 0.0001$; $r^2 = 0.35$; Fig. 2a,b). These results show that c. 94% and 65% of the variation in FD and PD, respectively, remained unexplained by TD. Mapping these relationships revealed important spatial mismatches and congruencies between biodiversity components (Fig. 3).
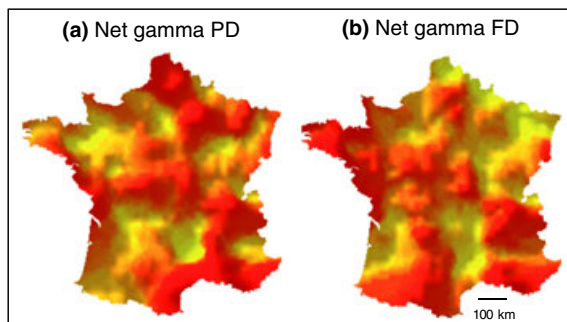

Figure 4 Spatial distribution of net phylogenetic and functional diversity. The residuals from linear regressions of (a) phylogenetic and (b) functional diversity on taxonomic diversity (coloured along 10 quantiles from yellow to dark red).

For instance, in the south and center of France some areas had high FD but low PD and TD values, whereas northeastern France could have high TD and PD but low FD values (Fig. 3a–c). Functional and phylogenetic residuals were still weakly correlated ($r^2 = 0.20$) and large areas with high net PD (i.e. areas with higher values of FD than predicted by TD) were not congruent with areas of high net FD (Fig. 4a,b).

Regarding beta-diversity patterns, we found that functional and phylogenetic turnovers were both positively related to taxonomic turnover ($F_{1,1035} = 2108.5$; $P < 0.0001$; $r^2 = 0.65$; and $F_{1,1035} = 2994.6$; $P < 0.0001$; $r^2 = 0.78$; respectively, Fig. 2d,e). The relation between functional and phylogenetic beta-diversity was even stronger ($F_{1,1035} = 3467.7$; $P < 0.0001$; $r^2 = 0.83$, Fig. 2f). Contrary to gamma diversities, we mostly highlighted areas of spatial congruence and only small and localized mismatches between beta diversity facets (Fig. 3d–f).

Our quantitative results are obviously dependent on the traits and on the phylogeny considered. However, we conducted a similar analysis using a different phylogeny (including branch lengths) for a subset of 148 species and found similar qualitative results (Figure S2). In particular, we found again large areas of mismatch between gamma diversities and mostly overlap between areas of high (or low) beta diversities. Alternatively, our results could be driven by changes in species relative abundance rather than by true differences in phylogenetic and functional compositions. However, using presence–absence, we still highlighted large areas of mismatch and congruencies between diversity facets (Figure S3).
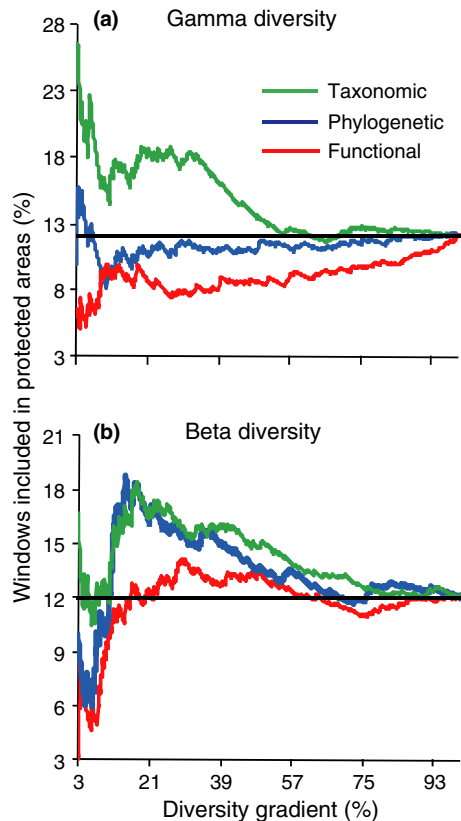
Figure 5 Cumulative proportion of taxonomic, phylogenetic and functional gamma and beta diversities included in the protected area network. (a) For each diversity component, we ranked the 1037 windows from the most to the least diverse. Along this decreasing diversity gradient (X-axis, expressed as a percentage), we calculated the cumulative percentage of protected windows (Y-axis). For any given value of the diversity gradient (at least for a representative sample size of windows, i.e. more than 3%), if the protected area network is unbiased, one expects the proportion of protected windows to match the overall proportion of protected windows among all windows (i.e. 12.5%). Therefore, proportions of protected windows located over and under the horizontal black line, respectively, reveal the over- and under-representation of plots located in protected areas. For instance, the 3% of windows with the highest functional diversity values (red line) are under-protected, whereas the 3% of windows with the highest taxonomic diversity are well-protected (green line). (b) A similar analysis was conducted for the turnover (beta diversity) of each diversity component.

The aim of the protected area assessment was to reveal, for any given diversity level included in the monitored windows, the proportion of protected windows. This assessment was based on the cumulative proportion of windows included in the protected area network, classified from the most to the least diverse window. This representation allows testing whether the proportion of protected

windows holding any level of biodiversity, is over or under-protected from what is expected by chance. As 12.5% of the whole territory is protected, we expected for any level of diversity and for each component to find at least 12.5% of protected windows. Instead, we found that gamma-TD, PD and FD were not equally captured within the protected area network (Fig. 5). For instance, among the windows holding the upper 20% of TD, 18.7% are protected and this proportion is higher than what is expected by chance (12.5% of the whole territory, permutation test, $P < 0.001$, $n = 1000$).

By contrast, among the windows having the top 20% of PD values, only 11% are protected (which is not different from expected by chance, $P = 0.26$). For the same level of diversity, FD is even more underprotected: among windows having the top 20% of FD values, only 9% are protected, which is less than what is expected by chance ($P = 0.04$) (Fig. 5a). Note that for any level of diversity, TD is generally overprotected (i.e. the green line is generally above the black line), whereas PD and FD are generally underprotected.

A similar analysis for beta-diversity revealed a different pattern (Fig. 5b): the 20% of windows with the highest beta-TD and beta-PD values are overprotected (16.7% vs. 16.8%, $P = 0.01$), whereas the proportion of protected windows with the highest 20% turnover of FD is not different from what is expected by chance (12.0%, $P > 0.1$).

DISCUSSION

We found that for a given taxonomic group, disentangling and mapping each diversity component separately reveals only partial congruence between TD, PD and FD (for either gamma or beta diversity). Furthermore, we revealed a partial and unequal coverage of each diversity component by protected areas.

Whether a given diversity component is a good surrogate for other components depends on the data available, the objectives, but also the area considered. For instance, the north-west coast of France (Brittany) concentrates high FD but low PD and TD, whereas the north-east exhibits both areas of high TD and PD but low FD and areas with high PD but low TD and FD diversity. Note that we also found areas of congruence between the different diversity facets. For instance, we found high gamma and beta diversities around the Mediterranean region regardless of the component considered. The Mediterranean basin is known to be an exceptional ecoregion in which the paleogeography and historical land-use have created complex mosaic of habitats (Médail & Quézel 1999; Myers *et al.* 2000) which probably supports these high diversity levels. Similarly, the northwest of France is also a region of strong congruence, but of low diversities which is probably related to the

strong landscape homogeneity of that region (mostly farmlands).

We further investigated how FD and PD were distributed beyond the spatial variation in TD by mapping their residuals on TD. These maps directly highlight regions of high and low 'net' FD or PD. As shown in Fig. 4, these residuals were not distributed randomly in space. The functional and phylogenetic residuals were also congruent in some areas (e.g. in the southeast and around the Mediterranean region) but non-congruent in others (e.g. in the northeast part of France).

These patterns of congruence or non-congruence suggest that species occurring locally may derive from regional species pools with similar as well as different biogeographical and evolutionary histories (Webb *et al*. 2002; Losos 2008; Prinzing *et al*. 2008; Cumming & Child 2009). Moreover, for a given regional pool, species may respond to environmental gradients in different ways affecting the spatial distribution of FD and PD and generating spatial mismatch between taxonomic, functional and phylogenetic diversities (Prinzing *et al*. 2008).

Concerning beta-diversities, we found high correlations and high spatial congruence between all diversity facets (Figs 2d–f and 3d–f). Changes in species functional or phylogenetic composition between two plots were therefore often proportional to the change in species identity between these plots and mapping beta-diversities revealed coherent transitional zones between regions with different pools of species, functional or phylogenetic compositions. Our results suggest that a beta diversity analysis (even only based on beta-TD) could therefore help to identify and delimit ecological boundaries around areas of particular interest. On its own, beta-diversity is however silent on the amount of diversity of a given region. For instance, high beta-diversity can be obtained in highly fragmented landscapes with low gamma diversities if few species (or little functional or phylogenetic diversities) are included in these landscapes. This is remarkably visible in the highly disturbed and fragmented surrounding of Paris (Fig. 3) where high beta but low gamma diversities are concentrated (mostly human dwellers and generalist species can thrive in these landscapes). Therefore, mapping both gamma and beta diversities offer interesting emergent perspectives that cannot be highlighted if only one or the other aspect of diversity is considered.

In fact, as for gamma diversity, patterns of congruence between the different beta-diversity facets are also driven by different ecological processes as well as by the relatedness between species. In particular, changes between environmental conditions among plots should cause turnover in species composition between these plots. Taxonomic beta-diversity should thus mainly be influenced by the steepness of environmental gradients (Gaston *et al*. 2007). But for a given change in species composition, environmental gradients may independently affect the phylogenetic and functional turnover, depending on the strength of environmental filtering, the particular traits affected, and the phylogenetic relatedness of the species considered (Webb *et al*. 2002). In this respect, we found a strong correlation and spatial congruence between functional and phylogenetic beta-diversity, a relationship presumably driven by the tendency of species to retain ancestral ecological characteristics, so-called niche conservatism (Wiens & Graham 2005).

When abundance was not included (i.e. equal weights were given to common and rare species), we still found similar qualitative results (Figure S3). This suggests that large-scale patterns of mismatch and congruence between diversity facets mainly result from changes in species composition rather than only from variations in species abundances. Interestingly, each given facet of diversity calculated with abundance was only weakly correlated to the same facet calculated without abundances (correlations between metrics with and without abundance ranged from $r^2 = 0.42 - 0.52$). This raises the question of the relevance of accounting for abundance or not when estimating diversity facets. Obviously, answering this question is again a matter of objective, scale and data availability. For instance, integrating abundance is of little importance if one is interested in complementing an existing collection of species, traits or phylogenetic branches already included in protected areas. Conversely, when looking for maintaining high diversity within and between species assemblages present in the field, accounting for the effective differences in abundance structures in these assemblages can be relevant. Overall, including abundance does not necessarily provide better metrics but rather offers the possibility to add a new view on what and where diversity is.

The need for a combined ecological and phylogenetic framework to explain large scale patterns is now accepted (Wiens & Donoghue 2004). We suggest that mapping phylogenetic and functional gamma-diversity and turnover simultaneously will also improve our understanding of the relationships between species diversity and FD at the biogeographical scale. Indeed, for a given change in species composition between locations within a given region, high turnover in FD (or PD) will reveal the functional (or phylogenetic) uniqueness of species within the region. Losing few species in these areas could in turn potentially affect ecosystem functioning over large scales even in species-rich ecosystems (Taylor *et al*. 2006). The simultaneous mapping of several diversity facets may also help to integrate phylogeny and functional traits to mechanisms involved in community ecology. For instance, once mismatch between biodiversity facets have been highlighted, one could try to identify major processes driving the observed patterns by adding information on which traits are

conserved across the phylogeny. For traits highly conserved, strong regional environmental filters on these traits should be accompanied by low PD in this region whereas high competition between species sharing these traits should drive high PD in the same region (Webb *et al.* 2002). Using metrics of trait evolution could thus help to refine our findings regarding the sources of mismatches between FD and PD. In particular, testing for the niche conservatism in each functional trait could indicate which traits mostly contribute to differences in gamma (or beta) PD and FD.

Spatial patterns of species richness and species turnover depend strongly on scale (Lennon *et al.* 2001). The relationships between FD or PD and TD and between their respective turnovers are also likely to be scale dependent. Indeed, increasing the size of the region considered would enclose more heterogeneous habitats and/or contrasting biogeographical zones which should result in regions composed of species with more contrasting functional traits and/or phylogenetic histories. Accordingly, we found that as we increased the size of the window (using 25, 50, 100, 150 and 200 km windows with 5, 10, 20, 30 and 40 plots) the relationships between gamma and beta diversities became stronger (Figure S4a). Regardless the spatial scale considered, we however still found only partial correlations between diversity facets (Figure S4b). Therefore, areas of mismatch and areas of congruence between diversity facets can be delineated at any scale. However, exploring how the relationships between diversity facets vary at different spatial scales should provide complementary information about the mechanisms generating the distribution of these facets, as well as about the locations of areas of conservation interest (Lennon *et al.* 2001).

Implications for conservation strategies

The spatial mismatches among diversity components have widespread implications for environmental management and protected area design (Forest *et al.* 2007; Naidoo *et al.* 2008; Cumming & Child 2009). Areas of high conservation interest are traditionally defined as biodiversity hotspots based upon arbitrary threshold criteria. Moreover, variations among species abundance are generally ignored when calculating PD and FD or when optimizing reserve design. Here, we used a more continuous approach in which each level of diversity was considered. We also explicitly integrated variations in species abundance in TD, PD and FD. This method allows a more systematic assessment without arbitrary criteria and reflects finer variations in community structure and composition. We found that windows with high TD are generally better-represented than for PD and FD. We further showed that windows with the highest values of FD were systematically under-represented within French protected areas.

Interestingly, working with beta-diversity revealed different results: beta-TD and PD were generally better protected than expected while the protection of beta-FD did not differ from what was expected by chance. These results mirror the uneven location of protected areas around particular landscapes and habitats. In particular, French National Parks and nature reserves are often delineated around wetlands and mountain areas, leading to high beta-diversities in these regions which may or may not coincide with areas with high gamma diversities.

Overall, our results raise the dilemma of which and how diversity component should be favoured in large-scale conservation strategies. Although PD should be maintained to preserve the Tree of Life in the long run (Mace *et al.* 2003), land-use intensification is currently reducing FD, which may negatively affect ecosystem goods and services (Díaz *et al.* 2006; Knapp *et al.* 2008; Flynn *et al.* 2009). We suggest that implementing and assessing conservation strategies using a given diversity component as a cure-all should be avoided (Brooks *et al.* 2006; Flynn *et al.* 2009). Instead, biodiversity assessment should benefit from integrative approaches connecting biogeography, evolutionary and functional ecology (Wiens & Graham 2005; Johnson & Stinchcombe 2007). To complement traditional strategies focusing on biodiversity hotspots, we suggest that our approach could help to improve the protection of each biodiversity component and to embrace the multifaceted nature of biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Functional dendrogram based on species coordinates along eight axes of a multivariate analysis.

Figure S2 Spatial distribution of taxonomic, phylogenetic and functional diversity and of their relative turnover obtained with an alternative phylogeny.

Figure S3 Spatial distribution of taxonomic, phylogenetic and functional diversity and of their relative turnover obtained using presence–absence data instead of abundance.

Figure S4 Relationships between diversity facets at different spatial scales. (a) Relationships between gamma and beta diversities and (b) between gamma and beta TD, FD and PD.

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

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