BIODIVERSITY RESEARCH

Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe

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ABSTRACT

Aim We investigate patterns of phylogenetic diversity in relation to species diversity for European birds, mammals and amphibians to evaluate their congruence and highlight areas of particular evolutionary history. We estimate the extent to which the European network of protected areas (PAs) network retains interesting evolutionary history areas for the three groups separately and simultaneously.

Location Europe

Methods Phylogenetic (QE_{PD}) and species diversity (SD) were estimated using the Rao's quadratic entropy at 10′ resolution. We determined the regional relationship between QE_{PD} and SD for each taxa with a spatial regression model and used the tails of the residuals (QE_{RES}) distribution to identify areas of higher and lower QE_{PD} than predicted. Spatial congruence of biodiversity between groups was assessed with Pearson correlation coefficient. A simple classification scheme allowed building a convergence map where a convergent pixel equalled to a QE_{RES} value of the same sign for the three groups. This convergence map was overlaid to the current PAs network to estimate the level of protection in convergent pixels and compared it to a null expectation built on 1000 randomization of PAs over the landscape.

Results QE_{RES} patterns across vertebrates show a strong spatial mismatch highlighting different evolutionary histories. Convergent areas represent only 2.7% of the Western Palearctic, with only 8.4% of these areas being covered by the current PAs network while a random distribution would retain 10.4% of them. QE_{RES} are unequally represented within PAs: areas with higher QE_{PD} than predicted are better covered than expected, while low QE_{PD} areas are undersampled.

Main conclusions Patterns of diversity strongly diverge between groups of vertebrates in Europe. Although Europe has the world's most extensive PAs network, evolutionary history of terrestrial vertebrates is unequally protected. The challenge is now to reconcile effective conservation planning with a contemporary view of biodiversity integrating multiple facets.

Keywords

Europe, phylogenetic diversity, protected areas, spatial biodiversity congruence, species diversity, terrestrial vertebrates.

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INTRODUCTION

Species distributions, and ultimately biodiversity patterns, are shaped by the interplay of evolutionary, biological and anthropogenic processes (Ricklefs, 1987). With the rise of available distributional data, the last decades have seen an upsurge of studies exploring biodiversity patterns from local to broad geographical scales (Gaston, 2000), most of them focused on species richness (Currie & Paquin, 1987; Davies & Buckley, 2011) or species evenness (i.e. abundance

distribution among species) (Hillebrand *et al.*, 2008). Species richness has been the main focus of macro-ecological studies and is still widely used, mainly because of the easiness to quantify and interpret the data (Cadotte & Davies, 2010). In particular, conservation planning has traditionally used richness information combined to different irreplaceability measures (e.g. endemism or rarity) to prioritize some regions over others (e.g. 'Biodiversity Hotspots', Myers, 1988). However, focusing on species richness ignores the differences between species in terms of functional or evolutionary characteristics (Vane-Wright *et al.*, 1991; Faith, 1992; Petchey & Gaston, 2002). To account for these other aspects of diversity, measures of phylogenetic and functional diversity have recently been developed (Pavoine & Bonsall, 2011 for a review). Both the increasing availability of molecular data in public databases (e.g. GenBank) and the advances in phylogenetic methods (Roquet *et al.*, 2013) have enhanced the use of phylogenetic diversity measure (i.e. the amount of evolutionary history) as a powerful tool for featuring biodiversity. For instance, phylogenetic diversity measures are now widely used to understanding the diversity of current species distributions (e.g. Davies & Buckley, 2011) or the potential functioning of ecosystems (Lavergne *et al.*, 2010; Mouquet *et al.*, 2012). Although most phylogenetic diversity measures show a positive and monotonic link with species richness (Fig. 1) (Faith, 1992; Morlon *et al.*, 2011; Rodrigues *et al.*, 2011), this relationship can vary spatially (e.g. Forest *et al.*, 2007) and this deviation can inform about the processes (speciation, extinction, lineage filtering, competition and migration) partly responsible for the current biodiversity patterns at large spatial scale (Davies & Buckley, 2011; Fritz & Rahbek, 2012). For instance, a region with high species richness and endemism but a low phylogenetic diversity (Fig. 1, bottom right corner) might indicate areas where recent adaptive radiations have occurred (e.g. Cape Floristic Region of South Africa, Slingsby & Verboom, 2006).

Assuming that closely related species have more chances to share common features (e.g. ecological niches, functional traits, Faith, 1992, 1994) than randomly chosen species in the phylogeny, phylogenetic diversity could also serve as a proxy for functional diversity if traits related to these functions were highly conserved along the phylogeny (Webb *et al.*, 2002). Under this assumption, prioritizing phylogenetic diversity in protected area (PA) networks would lead at the same time to the maximization of evolutionary history of Earth's biota (Forest *et al.*, 2007; Cadotte & Davies, 2010) and functional diversity.

Beyond the recent call to adopt a multifaceted approach to better understand and protect biodiversity as a whole (Devictor *et al.*, 2010), there are still few large-scale studies analysing patterns of phylogenetic diversity in relation to species richness and often limited to single taxonomic groups (e.g. plants, Forest *et al.*, 2007; mammals, Davies & Buckley, 2011 and Safi *et al.*, 2011; birds, Devictor *et al.*, 2010; fishes, Mouillot *et al.*, 2011; and amphibians, Fritz & Rahbek, 2012). In this perspective, understanding how phylogenetic
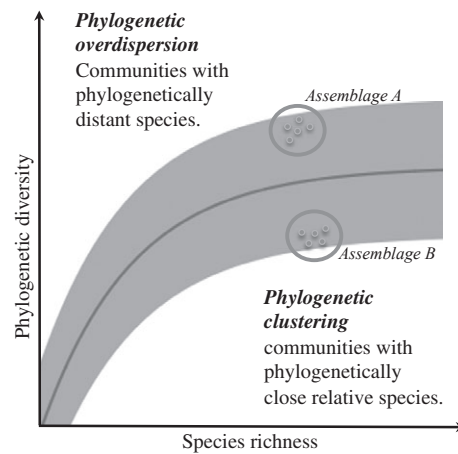

Figure 1 Hypothetical relationship between phylogenetic diversity and species richness (SR) of species assemblages. The grey region corresponds to the possible interval of phylogenetic diversity values for a given number of species while the darker line indicates the theoretical expected values of phylogenetic diversity. For an assemblage of few species, we would expect that the addition of one species will lead to a sharp increase in phylogenetic diversity value, this new species being likely to add new phylogenetic information, whereas at high level of SR, all the combinations of phylogenetic diversity have already been sampled and the addition of a new species does not influence the value of phylogenetic diversity for the region. As an example, region A shows an assemblage where phylogenetic diversity is higher than expected by its common relationship with SR. This type of assemblage would probably include phylogenetically distant species, reflecting thus a low level of diversification. On the contrary, assemblage B presents lower phylogenetic diversity than expected and thus it will mostly contain phylogenetically close species, for example resulting from events of massive diversification in the recent history.

diversity and species richness relate across multiple taxa is of interest, not only to further infer the processes generating biodiversity patterns but also to be able to maximize the efficient use of limited conservation resources (Margules & Pressey, 2000) to preserve all biodiversity facets. Although the real impact of considering phylogenetic diversity in current conservation planning is still debated (Winter *et al.*, 2013a), we miss large-scale studies on the congruence or mismatch between diversity facets of potential conservation interest across groups.

A limiting factor in conservation assessments is the lack of relevant data on spatial information (e.g. biodiversity distribution) upon which the effectiveness of conservation planning depends (Margules & Pressey, 2000). Consequently, conservationists often focus on a given group and use surrogates for which data can be obtained and assume that biodiversity features explicitly targeted in conservation efforts will also be effective in capturing unmapped biodiversity (Rodrigues & Brooks, 2007). Taxonomic surrogacy (whether one taxon is a good surrogate for another taxon when targeting species representation) has received substantial attention (Rodrigues & Brooks, 2007). Rodrigues *et al.* (2011) also

explored whether taxonomic diversity is a good surrogate for phylogenetic diversity as measured with Faith's phylogenetic diversity metric (Faith, 1992). However, the question of whether targeting a phylogenetic diversity measure for a group of organisms would also cover the one for another group has not been explored so far. Here, we propose a comparative approach to investigate spatial patterns of a phylogenetic diversity and species diversity (SD, combined measure of richness and evenness) for mammals, birds and amphibians over Europe while accounting for species habitat preferences within pixels. Using updated phylogenies and the Rao's quadratic entropy to measure phylogenetic diversity (Rao, 1982) (hereafter referred as QE_{PD}) and SD, we study their spatial distribution for each group separately and determine which regions show higher or lower phylogenetic diversity than expected. Finally, we undertake an assessment of the biodiversity coverage of the European network of PAs and estimate whether and to which extent the current PAs network covers areas of higher/lower phylogenetic diversity than expected for these three groups of species simultaneously.

METHODS

Extent of the study area and spatial dataset

The study area includes the entire European subcontinent including Turkey (part of Asian continent) to have a complete picture of the Mediterranean coast. We used data on the spatial distribution of 275 mammals, 429 birds and 102 amphibians. These datasets were compiled from Maiorano *et al.*, 2013 (see Appendix S1 in supporting information). For mammals and amphibians, the primary data were extent of occurrences (EOOs) collected from the IUCN Global Mammal Assessment and Global Amphibian Assessment (IUCN, 2013). For bird species, EOO were obtained in combining data available from Hagemeijer & Blair (1997) with those available from the BWP*i*2.0.1 DVD-ROM (Birds of the Western Palearctic Interactive 2006, version 2.0.1). For all species, habitat requirements were collected from expert opinion and published literature (Maiorano *et al.*, 2013, Appendix S1). The collected data were used to assign a suitability score (0, unsuitable; 1, secondary habitat; and 2, primary habitat) to each of the 46 GlobCover land use/land cover classes (300 m resolution). Scores were used to remove unsuitable cells (scored 0) and refine EOOs (no presence data were added, only false presence data were removed). Species distribution data were scaled up to a 10′ resolution. For each 10′ grid cell and for each species considered, we kept the percentage of suitable habitat by summing the 300 m pixels corresponding to primary or secondary habitat and we refer to this percentage as 'potential suitable area' hereafter.

Phylogenetic data

Phylogenetic data for mammals were based on the updated super tree of Fritz *et al.* (2009). We used 100 fully resolved

phylogenetic trees, where polytomies were randomly resolved applying a birth–death model to simulate branch lengths (Kuhn *et al.*, 2011). For birds, we extracted the 100 dated and fully dichotomous phylogenetic trees from Thuiller *et al.* (2011) and retained the 10 best ones as the variation between the trees was very low.

For amphibians, we conducted phylogenetic inference analyses based on DNA sequences extracted from GenBank (Appendix S2; Roquet *et al.*, 2013). The phylogenetic analysis, conducted with RAxML (Stamatakis, 2006), included a search for 100 suboptimal trees, which yield identical topologies and similar branch lengths. The 100 phylogenies were transformed into cophenetic distance matrices and compared with Mantel tests. There were all highly correlated (correlation > 0.99). Because of that, we run all subsequent amphibian analyses using the best maximum likelihood tree (available on TreeBASE, accession number: S13561). This tree was dated with penalized likelihood as implemented in r8s (Sanderson, 2003), using several fossil data to constrain certain nodes (Appendix S2). This is to our knowledge the most up-to-date phylogenetic tree for European amphibian species.

Diversity measures

To measure both species and phylogenetic diversity, we used the Rao's quadratic entropy (QE; Rao, 1982), a within-assemblage diversity measure (so-called alpha diversity) defined as the extent of dissimilarity between species in an assemblage (de Bello *et al.*, 2010). For a given site (a 10′ cell), QE is defined as:

$$QE = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j$$

where d_{ij} is the dissimilarity between each pair of species i and j. p_i and p_j are the respective proportion of the species i and j, and can be expressed as any measure of relative species abundances (de Bello *et al.*, 2010). In our study, p_i and p_j are taken from the 'potential suitable area' estimated for each species. For measuring phylogenetic diversity (QE_{PD} hereafter), d_{ij} was calculated as the patristic distance between species i and j derived from the phylogenetic trees. For species diversity (SD), d_{ij} was set to either 1 (when $i \neq j$) or 0 (when $i = j$) and in this particular case, QE equates to the Gini–Simpson index (de Bello *et al.*, 2010). To make sure our indices were directly comparable, we transformed QE_{PD} and SD values into equivalent number (Jost, 2007; Chao *et al.*, 2010). The analyses were performed on 100 trees for mammals and 10 trees for birds to account for phylogenetic uncertainty. The results shown are median QE_{PD} over the trees.

Phylogenetic diversity was originally estimated using the sum of the branch length of the species present in the assemblage (Faith, 1992), but since then several alternatives have been proposed (Pavoine & Bonsall, 2011). Here, we used

QE_{PD} because it allows incorporating our measure of 'potential suitable area'. In particular, it makes sure that pixels with equal number of species but very different proportion of suitable habitat for the respective species are distinguished. Practically, it allows a fine mapping, and this is also particularly interesting for a conservation perspective, because it allows distinguishing sites to prioritize based on the potential population size of species (i.e. assuming that area is linked to population size).

Species diversity against phylogenetic diversity

Instead of using a null model to remove the effect size of QE_{PD} as usually done in community ecology to detect under- or over-dispersion (e.g. Cavender-Bares *et al.*, 2004), we used a model-based approach. The reason was twofold: first, standardized effect size estimations require a Gaussian distribution of phylogenetic distances, which was not the case here, and second, most of large-scale analyses have used a model-based approach, which facilitates comparisons (Davies & Buckley, 2011; Fritz & Rahbek, 2012). To analyse the spatial pattern of discrepancy between QE_{PD} and SD in Europe, we built a spatial regression model between QE_{PD} and SD for each vertebrate group. As the relationships between QE_{PD} and SD were visually between linear and quadratic, (Fig. S2), we tested both linear and quadratic terms. To account for spatial autocorrelation, we included geographic coordinates as a smooth factor (Wood, 2006). We chose this simplistic approach because models that account for a geographic correlation structure (e.g. generalized least squared regression) or more complex autocovariate (e.g. Eigen vector mapping, Peres-Neto & Legendre, 2010) were too data and time demanding to run at such resolution.

Pixels that deviated from the expected QE_{PD}/SD relationship were thought to be the signature of particular evolutionary histories (Fig. 1, Fritz & Rahbek, 2012). To identify them, we used extreme positive and negative residuals depicting, respectively, areas with higher and lower QE_{PD} than expected from the European QE_{PD}/SD relationship. These residuals are called QE_{RES} hereafter. All models have been calibrated using the 'mgcv' package within R.2.12.1 (R Development Core Team, 2013).

Spatial covariation of phylogenetic diversity across vertebrate groups

To examine how QE_{PD} covaried in space for the three taxonomic groups, we regressed QE_{RES} of each group against the other two. To evaluate congruency between the spatial distribution patterns of the different taxonomic groups, we classified QE_{RES} for each taxa within each cell as follow: values larger than 75% quantile were classified as 1, values lower than 25% quantile were classified as -1 and values falling in between were assigned a 0 value (we used this classification because we wanted to have the distribution tails of the residuals values). We then combined the values for the three

taxonomic groups obtaining 27 codes (e.g. 1 for mammals, 0 for birds, 1 for amphibian results in the code 101). We referred the combinations '-1-1-1' and '111' as *negative* and *positive convergence,* respectively, whereas '000' was called *neutral convergence.* The combinations differing in all three digits were referred to as *divergent,* whereas the remaining codes were noted as *others*. This classification allowed calculating the proportion of areas that show congruency (i.e. convergent sites) or mismatch (i.e. divergent and 'others' sites) between the three taxonomic groups and was further used in the PAs assessment analysis (see next section). This classification might be seen as subjective but is close to hot-spot definition based on species–area relationships (Guilhaumon *et al.*, 2008). Here, it allows us to highlight the pixels where the three vertebrate groups have strikingly lower or higher than expected phylogenetic diversity.

Spatial congruence between protected areas and phylogenetic diversity patterns

We evaluated the current representation of each convergence-divergence category within three nested protected area (PA) networks. We first conducted the analyses on the complete list of PAs available from the World Database on Protected Area (WDPA, http://protectedplanet.net/) for our study area. To account for the broad range of PAs in WDPA that vary in terms of conservation action, we conducted analyses on a second network including only PAs with the most stringent conservation legislation (i.e. PAs belonging to IUCN category I and II). Finally, the third network concerned only Natura 2000 sites (http://www.eea.europa.eu/) and was reduced to European Union countries only. We first estimated the percentage of protection of each 10′ grid cell (N_{PROT}). To assess the representation (R) of each convergence-divergence categories within the PAs, we calculated the overlap between N_{PROT} and the cells of each category ($Ncat_{PROT}$) and we then divided $Ncat_{PROT}$ by the total number of cells of each category ($Ncat_{TOT}$).

To test the effectiveness of PAs network, we spatially randomized the distribution of N_{PROT} (1000 times) and recalculated R of each category for each run, obtaining with this procedure a null distribution to be compared with the observed R for each category. This randomization scheme explicitly tested whether the sites of QE_{PD} convergence versus divergence between species groups were more or less protected than under a random distribution of PAs.

RESULTS

The relationship between species diversity (SD) and phylogenetic diversity (QE_{PD}) was nonlinear (Fig. S2). For mammals and amphibians, a quadratic model had a better fit ($R^2 = 0.93$, $P < 0.001$ and $R^2 = 0.83$, $P < 0.001$, respectively, Table S1) than any linear alternatives (mammals, $R^2 = 0.87$, $P < 0.001$ and amphibians $R^2 = 0.82$, $P < 0.001$, Table S2). For birds, the difference between a linear and a quadratic fit

was null (equal $R^2 = 0.59$, $P < 0.001$, Tables S1 and S2). To have consistent relationships for the three groups, the results presented hereafter refer to the quadratic models. The QE_{PD}/SD relationships were linear for low and moderate levels of SD (i.e. the addition of a given species increased QE_{PD}) and then became saturated for high SD values. In other words, when reaching a certain level of SD, QE_{PD} cannot increase anymore, the overall tree of life for a given group being already entirely sampled.

Comparing spatial patterns of SD, QE_{PD} and QE_{RES} provided complementary results within and among the three groups of vertebrates. In particular, the distribution of QE_{PD} for both mammals and birds showed a north-eastward increase with highest values in the Russian plains and Turkey for mammals, whereas this pattern was not found for amphibians (Fig. 2), which concentrate high QE_{PD} values in south-west of Europe, particularly in the Po valley (Italy) and in Galicia (Spain). However, while the values of QE_{RES} for birds were negative in the major European mountain ranges (Alps, Carpathians, Apennins, Turkey mountains and Pyrenees), the opposite pattern was shown for mammals and amphibians (Fig. 2). In other words, the visible high QE_{PD} for mammals and amphibians in European mountains was not only an effect of SD. Birds also showed areas of QE_{PD} higher than expected from SD in regions associated with rivers (e.g. Volga Delta in Russia, Dniester and Dnieper estuary in Ukraine, Danube Delta in Romania) and lakes (e.g. Lacha lake in Russia, Värnen in Sweden, lake Van and Tuz in Turquey) (Fig. 2). There were also very diverging patterns in Cyprus and Corsica and in Mediterranean Basin across the different groups; whereas QE_{PD} of birds was generally high in those areas, there was correspondingly lower QE_{PD} than expected with respect to SD for mammals (Fig. 2).

The covariation of SD between taxonomic groups was positive with a high correlation between mammals and amphibians (Table 1a, Fig. S3). Species-rich areas for one taxonomic group tended also, to some extent, to be rich areas for the other two groups. However, this apparent congruency did not hold for QE_{PD}: as expected from the apparent mismatch of QE_{PD} spatial distributions (Fig. 2), the strength of covariation between the three groups did not show any kind of relationship for both QE_{PD} and QE_{RES} (Table 1b,c, Figs S4 and S5). Moreover, strong spatial patterns emerged when comparing extreme values of QE_{RES} (Fig. 3). Only 1% of Europe (Fig. S6, Appendix S3) shows areas of positive convergence for the three taxonomic groups (i.e. areas with higher QE_{PD} than expected for each group) and 1.6% of negative convergence (i.e. areas with lower QE_{PD} than expected for each group), whereas 17% of the territory diverges completely between mammals, birds and amphibians (i.e. areas where QE_{RES} is positive for one taxa, negative for the second and null for the last one).

The percentage of QE_{PD} representation in European PAs was not equal between the different PA networks (Fig. 4) with a higher representation of the QE_{PD} congruency catego-

ries in Natura 2000 compared to the global world's protected area network (WDPA) and the world's protected area network with only IUCN categories I and II considered (WDPA I, II). This is not surprizing as Natura 2000 covers more surface (17.7%) of Europe than the others do (10.4% for WDPA and 2.3% for WDPA I, II). In average, any PAs network tended to retain less QE_{PD} than expected for birds and mammals while for amphibians PAs retained more QE_{PD} than random (Table S4, Appendix S3). Regarding the areas of higher/lower QE_{PD} relative to SD, results show an uneven protection: areas of high QE_{PD} relative to SD tend to be well represented in PAs compared to random for any taxa and any PA network analysed, but areas of low QE_{PD} relative to SD tend to be underrepresented (Table S5, Appendix S3, significant for all taxa except for mammals). The representation of each category is consistent among PAs networks meaning that when one category is well represented by one network it is also the case in the other network. Sites with positive, negative and neutral convergence (PC, NC and NeC) are always less represented in PAs than random (Fig. 4; only significant for PC in WDPA, $P < 0.01$, for NC in WDPA I, II, $P < 0.001$ and for NeC for Natura 2000, $P < 0.001$). For instance, only 8.54%, 1.63% and 16.41% of the total PC cells are covered by WDPA, WDPA I, II and Natura 2000, respectively (Fig. 4 and Table S3, Appendix S3), when a random distribution of those PAs networks will cover these cells category better (10.43% ± 0.94 for WDPA, 2.26% ± 0.51 for WDPA I, II and 17.70% ± 1.68 for Natura 2000). On the contrary, divergent sites (D, Fig. 4 and Table S3, Appendix S3) are better covered by any PAs network than a random distribution of PAs would. Indeed, 11.3%, 3.03% and 20.8% of D cells are covered by WDPA, WDPA I, II and Natura 2000, respectively, whereas only 10.41% (± 0.21), 2.28% (± 0.11) and 17.75% (± 0.37) of D cells would be captured if WDPA, WDPA I, II and Natura 2000, respectively, were randomly distributed.

DISCUSSION

Patterns of spatial mismatch between the phylogenetic diversity of European vertebrates

Surrogate taxa are often used in conservation exercises due to the urgency in decision-making and the lack of comprehensive data for the majority of taxa (Rodrigues & Brooks, 2007). Such approaches assume that maximizing the diversity of one clade could lead to the maximization of overall biodiversity (e.g. other taxa). In our study, we showed positive covariation of SD across vertebrates in Europe with highest correlation observed between mammals and amphibians compared to birds. Similar patterns have also been found at global (Grenyer *et al.*, 2006; Lamoreux *et al.*, 2006; Fritz & Rahbek, 2012), continental (Araújo *et al.*, 2004) and national levels (Xu *et al.*, 2008). This supports the idea that a species-rich region for one taxonomic group might be also expected, to some extent, to be rich for other
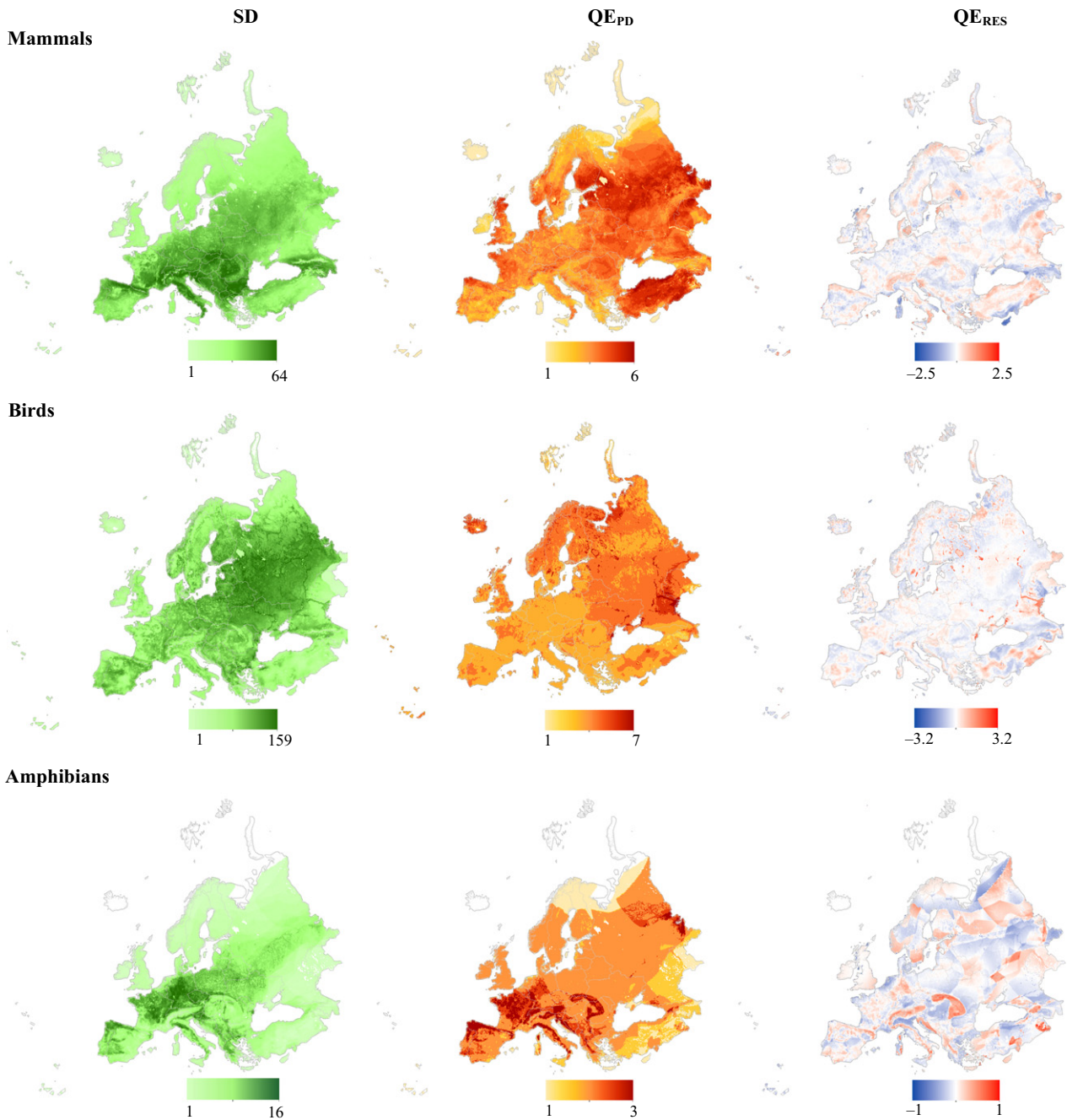
Figure 2 Spatial distribution patterns of species diversity (SD, left column), phylogenetic diversity (QE_{PD}, middle column) and the residuals (QE_{RES}, right column) from the spatial regression between QE_{PD} and SD for mammals (upper line), birds (middle line) and amphibians (lower line). For SD, low to high values are represented by a green colour gradient from soft to dark green, the QE_{PD} follows a yellow to red gradient for increasing values of QE_{PD} and for QE_{RES} values, the blue colours depict negative values of residuals (lower diversity than expected by the relationship between QE_{PD} and SD) while the red colours depict positive residuals (higher QE_{PD} than expected).

taxonomic groups. However, these correlations are usually weak and sometimes simply explained by latitudinal gradients in diversity (Flather *et al.*, 1997). Comparatively, the covariation of QE_{PD} patterns is weak between mammals and amphibians and almost null between birds and the two others taxonomic groups, meaning that high QE_{PD} areas for one group is not at all representative of the QE_{PD} level of the other groups. This suggests that in Europe and while accounting for species potential suitable area in the estimation of diversity, the surrogate's principle cannot hold for other biodiversity facets than species richness, here phylogenetic diversity.

Table 1 Cross-taxon correlations (Pearson correlation coefficient) across birds, mammals and amphibians for (a) species diversity (SD), (b) phylogenetic diversity (QE$_{PD}$) and (c) residuals (QE$_{RES}$).

	Mammals			Birds		
	Correlation coefficient	t_{value}	P_{value}	Correlation coefficient	t_{value}	P_{value}
(a)						
Birds	0.44	116.09	< 0.001	/	/	/
Amphibians	0.75	265.12	< 0.001	0.46	120.08	< 0.001
(b)						
Birds	0.0024	0.56	0.576	/	/	/
Amphibians	0.33	81.08	< 0.001	−0.33	−80.87	< 0.001
(c)						
Birds	−0.06	−11.82	< 0.001	/	/	/
Amphibians	0.09	21.51	< 0.001	−0.12	−28.96	< 0.001
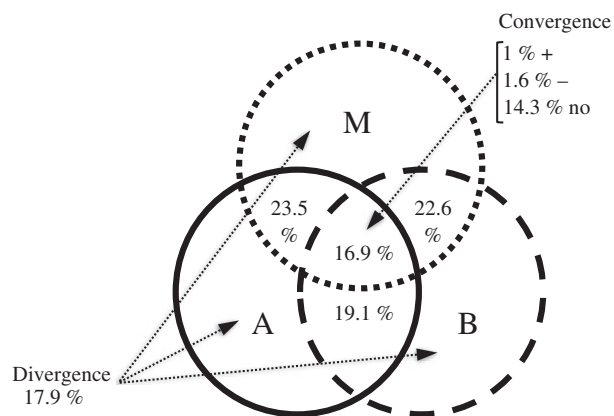
Figure 3 Venn diagram showing the congruence (in number of sites out of the total study area) in phylogenetic diversity (QE$_{PD}$) patterns between mammals (M), birds (B) and amphibians (A). Divergence represents areas where the residuals (QE$_{RES}$) for the three groups of vertebrates mismatch completely in space. Convergence encompasses areas where the three groups show higher values of QE$_{PD}$ than expected (+), lower values than expected (−) and finally areas where QE$_{RES}$ was equal to 0 (no) for the three groups.

Potential mechanisms explaining biodiversity patterns

Disentangling the processes governing biodiversity patterns is not trivial (Gaston, 2000). Behavioural and ecological variation between the different groups of species might partly explain the observed patterns (Mittelbach *et al.*, 2007). We showed that mammals have high SD in mountains, while this pattern is not found for amphibians and birds. Mammals are endotherm species and can stand in harsh climates (Mittelbach *et al.*, 2007) while amphibians have difficulties to cope with values below zero (Araújo *et al.*, 2006) and will tend to avoid extreme environments. Birds are also endotherm but might be more capable to avoid stressful environment due to their high dispersal ability or migration strategies (Mittelbach *et al.*, 2007). But behavioural and ecological characters are probably not the only drivers of biodiversity.

Our approach to depict areas of higher and lower QE$_{PD}$ than expected for a given SD highlights regions with particularly rich or poor phylogenetic assemblages. Areas of positive residuals might reflect areas where the speciation rate has been low through time and lineages present in such region are likely to be old and suspend only few evolutionary distinct species (Isaac *et al.*, 2007). Such sites might also be the mirror of ancient diversification or migration events but could also reflect high extinction rates (Davies & Buckley, 2011). Comparatively, assemblages with high SD but low QE$_{PD}$ can reflect a massive and recent diversification event only for some clades with a low extinction rate. We showed for mammals that islands (e.g. Corsica and Cyprus) present lower QE$_{PD}$ than expected; this could be explained partly by isolation from the main continent, with a species pools generated mostly by in situ radiation through sympatric speciation resulting in assemblages composed of closely related species (Losos & Ricklefs, 2009).

Besides the ecological and historical drivers of species distribution, we cannot disregard the effects of anthropogenic influence (Mittelbach *et al.*, 2007) and past climate change events (Araújo *et al.*, 2006). Mammals, birds and amphibians are highly sensitive to human disturbance (Stuart *et al.*, 2004; Schipper *et al.*, 2008; Visconti *et al.*, 2011). Anthropogenic forces are likely to have impacted species range and distributions by forcing species to migrate from their original habitat to new places. Such events (migration, introduction, extinction or range contraction) are likely to have modified the composition of assemblages and ultimately influenced phylogenetic diversity patterns differently for each groups, for instance, we may lose large body size species first (Fritz *et al.*, 2009).

Accounting for phylogenetically rich assemblages in conservation planning

We showed that areas characterized by either high or low QE$_{PD}$ for the three vertebrate groups simultaneously (i.e. convergent sites) are few in Europe and not better captured by PAs network than random. However, when taxonomic

Figure 4 Percentage of representation of congruency categories within protected areas. PC, *positive convergence*, NC, *negative convergence*, NeC, *neutral convergence* and D, *divergence*. The black crosses are the observed percentage of protection while the boxes represent the mean percentage of protected cells (relative to the total number of cell within the given category) over 1000 randomizations. The stars are the two-sided p_{values} of the test comparing the observed and expected value. ***$P < 0.001$, **$P < 0.005$.
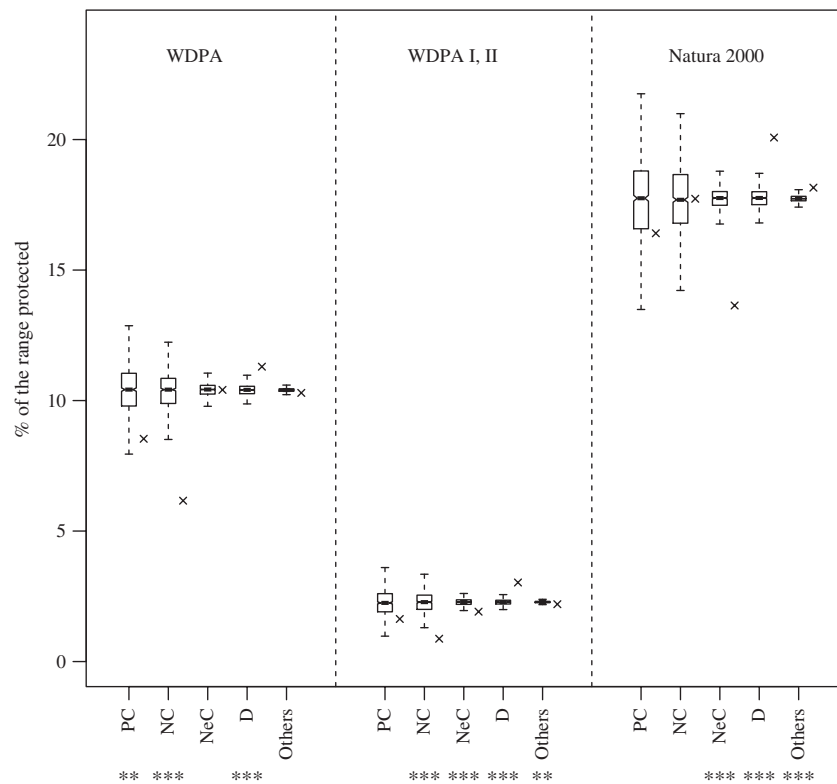
groups are analysed separately, areas of higher QE_{PD} than predicted are better represented than random for any taxa, and for any PAs network. Such areas can be considered important to preserve because they are likely to contain profound nodes (great evolutionary history). Additionally, if we assume that assemblages with phylogenetically distinct species reflect assemblages of functionally different species, the protection of such areas would potentially maximize the preservation of ecosystem functioning (Cadotte *et al.*, 2008; Cardinale *et al.*, 2012). However, whether phylogenetic relatedness is a good proxy for functional similarity is controversial, and recent analyses have shown that the assumption does not always hold (Lavergne *et al.*, 2010; Mouquet *et al.*, 2012). To verify such assumption, functional diversity, as measured directly from functional trait data, should be compared to phylogenetic diversity. Areas of lower phylogenetic diversity than expected could also be of conservation interest because they could potentially contribute to future evolutionary radiations under the hypothesis that they will continue to evolve at similar rates as in the past (Forest *et al.*, 2007). In Europe, these sites tend to be underrepresented in the PAs network.

However, we do not recommend targeting only the areas mentioned above as conservation priorities, because such a prioritization scheme would overlook species complementarity and cost-efficiency (Margules & Pressey, 2000). Indeed, two sites or regions having the same values of diversity (SD or QE_{PD}) can reflect either similar or completely different species to the regional diversity and pools, meaning that in the maps presented here, there is no

information on the redundancy between sites. A way to avoid redundancy between sites would be to not only maximize a set of high diversity sites (α-diversity) but also take into account the β-diversity (spatial turnover). This would tell us how much a site contributes to the regional diversity (γ-diversity) and the degree of compositional difference between sites. In any case, we believe that mapping the residuals as done here provides conservationists with a simple tool to contrast regions of high/medium/low congruencies between groups.

Underlying uncertainties

Although we used the best information available at European scale (Maiorano *et al.*, 2013), it is evident that the resolution used in this study is too rough for practical management. We have partially addressed this problem by accounting for the amount of potential suitable area within pixel in the calculation of the phylogenetic diversity measure. However, the size of PAs in Europe still far exceeds the resolution of the distribution data, and our estimated percentage of protection should not be taken as exact quantitative estimates. Regional assessments with higher-quality data should then follow such large-scale studies to accurately test the efficiency of PAs at protecting feature diversity.

Phylogenetic diversity in conservation: perspectives

Recent literature has questioned the rationale behind conserving phylogenetic diversity as well as the likelihood of

adding this component in real conservation plans (Winter *et al.*, 2013a,b; Rosauer & Mooers, 2013). Several reasons can justify the difficulty to use phylogenetic diversity as a relevant component for conservation. Obviously, one reason is ethical and does not need any biological justification: maximizing evolutionary history would preserve the 'immense history of Earth' as a valuable dimension of biodiversity per se (Cadotte *et al.*, 2010). The ecological reasons (i.e. phylogenetic diversity as a proxy for ecological processes, evolutionary potential and ecosystem services) are less clear because many of the hypothesis behind cannot be taken for granted but need to be proved for each case considered. Moreover, adding a biodiversity component such as phylogenetic diversity to the one already used and accepted by conservation practitioners and policy makers is not an easy task. In this respect, species will probably still be considered as a simple and amenable currency for setting conservation action. However, when it comes that species are not representative of biodiversity as a whole, phylogenetic diversity offers an interesting alternative and is more or less already used in existing programs (e.g. CITES or EDGE). The growing availability of phylogenies for several groups and the development of handy softwares to estimate different indices of phylogenetic diversity (e.g. package *picante* in R, Kembel *et al.*, 2010; Phylocom, Webb *et al.*, 2008) help to produce maps, which are interesting tools for increasing the scope of conservation biogeography (Margules & Pressey, 2000). Beyond these technical aspects, conservationists might communicate efficiently on the importance and meaning of phylogenetic diversity. A possible way of doing so could be to alert people on the natural heritage that phylogenetic diversity brings.

CONCLUSION

While global pattern of richness, threat and endemism have been widely investigated, still little is known on the distribution of other diversity facets among multiple taxa. In our study, we offer a simple approach to identify areas of convergence of phylogenetic diversity for the three main groups of European terrestrial vertebrates. We show that phylogenetic diversity patterns strongly mismatch in space between groups and highlight that the diversity of one taxonomic group is not representative of the diversity of other groups. Moreover, we show that the current protected area network largely misses the few convergent regions and that protecting simultaneously several taxa and facets of diversity is challenging. Finally, we suggest that further research should be conducted on surrogate analyses, both to investigate other groups of taxa and to explore other facets of biodiversity (e.g. functional diversity) at different scales.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary information on the acquisition and compilation of species distribution data.

Appendix S2 Amphibian phylogenetic data acquisition, phylogenetic tree calibration and accession number for sequence retrieved in GenBank.

Figure S1 Maximum likelihood tree with highest likelihood for the European amphibians.

Table S1 Parameter estimates for the quadratic relationship between the species diversity (SD) and the phylogenetic diversity (QE_{PD}) for the three taxonomic groups.

Table S2 Parameter estimates for the linear relationship between the species diversity (SD) and the phylogenetic diversity (QE_{PD}) for the three taxonomic groups.

Figure S2 Relationship between phylogenetic diversity (QE_{PD}) and species diversity (SD) for the three groups of vertebrate.

Figure S3 Covariation of the species diversity (SD) among mammals, birds and amphibians.

Figure S4 Covariation of phylogenetic diversity (QE_{PD}) among mammals, birds and amphibians.

Figure S5 Covariation of the residuals (QE_{RES}) of the quadratic relationship between the species diversity (SD) and the

phylogenetic diversity (QE_{PD}) among mammals birds and amphibians.

Appendix S3 Supplementary analyses and details on the PAs assessment.

Table S3 Mean observed and expected percentage of representation of each convergence category (PC, positive convergence, NC, negative convergence, NeC, neutral convergence, D, divergence) within the 3 different protected area network. Standard deviation is indicated in the brackets.

Table S4 Mean observed value of QE_{PD} within and outside PAs compared to the mean expected value of QE_{PD} when PAs are randomly distributed (1000 randomisations).

Table S5 Observed mean percent of representation of each residuals category for mammals, birds and amphibians within the three different PAs networks.

Figure S6 Area of convergence and divergence across the 3 groups of vertebrates in Europe.

BIOSKETCH

Laure Zupan interests lie at the interface between macroecology and biological conservation. Her focus has been on understanding global patterns of biodiversity for different groups of species to develop novel spatial conservation planning approaches to account for evolutionary history and ecosystem functioning.

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