



Macroecological patterns of amphibian assemblages in the Western Palearctic: Implications for conservation



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ABSTRACT

Unveiling the patterns of amphibian phylogenetic diversity across broad spatial scales is extremely timely, given the need to optimize conservation strategies for this group. Here we analyzed the distributions of 51 amphibians in the Western Palearctic, and we explored the variation in phylogenetic structure and beta diversity across space. We predicted that the incidence of phylogenetic clustering in local assemblages would follow a latitudinal gradient, since only a few families would be able to occupy most of the available climate space whereas many families would be restricted to the mid-latitudinal range. For the same reason, we predicted that we would observe a latitudinal pattern in the relative contributions of turnover and nestedness, the two components of overall beta diversity. We observed a decline in species richness at both geographic extremes, with these areas presenting relatively higher levels of phylogenetic clustering. As expected, a few families (Bufonidae, Ranidae, and Salamandridae) occupied one or both extremes, whereas the rest were confined to the mesothermal belt. Also as predicted, the nestedness mechanism prevailed in explaining overall beta diversity in both the northern and southernmost regions of the ecozone, but not in the temperate regions. We therefore illuminate a conservation challenge: in northern Europe and the arid regions of Northern Africa, the relatively high contribution of nestedness to overall beta diversity allows conservation efforts to prioritize the few areas with the greatest species richness. However, this pattern does not hold in southern Europe and the mesic regions of Northern Africa, where conservation efforts should be focused on identifying phylogenetically-diverse areas rather than focusing on species-rich sites.

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1. Introduction

Understanding and predicting the composition of communities of interacting organisms across broad geographic areas is a major aim of ecology. Several studies have revealed that the phylogenetic structure of a local community is governed by several processes operating at different spatio-temporal scales (Aragón et al., 2010; Gomez et al., 2010; Helmus et al., 2007). On the regional scale, these processes are mainly determined by the climate space occupied by a species (niche filtering), whereas at the local scale, habitat selection and species interactions tend to prevail (HilleRisLambers et al., 2012). Because phylogenetically related species show similar adaptive traits and tend to occupy similar niches, the existence of niche filtering over evolutionary periods has favoured the diversification of a few well-adapted phenotypes, promoting phylogenetic clustering. In contrast, its absence has

favoured the existence of competitively structured assemblages, showing relatively higher levels of phylogenetic evenness (Cavender-Bares et al., 2009; Webb, 2000). Overall, phylogenetic diversity is considered a key component of biological diversity, and its study is crucial because it reflects rarity, endemism, multi-functionality, and evolutionary history and potential (Faith et al., 2004; Rosauer et al., 2009; Fritz and Rahbek, 2012). Although some recent works have addressed phylogenetic patterns at global or intercontinental spatial scales in freshwater fauna (e.g., Fritz and Rahbek, 2012; Ruhí et al., 2013), it is often difficult to adapt these general, macroecological patterns to useful guidelines for biodiversity conservation at the regional scale. A way to do this could be to test if there is congruence between metrics of phylogenetic structure and spatial dissimilarity, since the latter (e.g. beta diversity and its components), but not the former, are commonly employed to test and optimize strategies for conservation. Addressing this idea in amphibians would be particularly timely, given the high conservation interest of this group (Stuart et al., 2004).

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Latitude is associated with strong environmental filters that largely influence the compositions of plant and animal assemblages at the global scale (Pärtel, 2002; Willig and Lyons, 1998). This is also true for amphibians, which are known to decrease steeply in richness as latitude increases (Kiestler, 1971). Therefore, variations in the complexity of amphibian assemblages are expected to occur across any large-scale latitudinal gradient. In particular, complexity may depend on the water–energy balance (Qian et al., 2007), but also on some other factors such as historical climate stability (Provan and Bennett, 2008), which may explain why some poorly-dispersing lineages are confined near their glacial refugia (Tarkhnishvili et al., 2000). Within this context, phylogeography helps explaining how current species distributions –and thus variation in species richness across broad spatial patterns– are related to postglacial colonization routes (Taberlet et al., 1998). The Western Palearctic hosts an overall high, but unevenly distributed, amphibian diversity: whereas some areas show high diversity and endemism (e.g., the Iberian and Italian peninsulas), other areas are species poor (e.g., the outer margins of the Sahara and the Scandinavian peninsula; Ben Hassine and Nouira, 2012; Gasc et al., 1997). This is because amphibians have very narrow physiological requirements and a limited dispersal capability, being relatively more diverse in high-temperature and high-humidity areas (Duellman, 1988). However, some lineages show different speciation optima across this energy–water gradient (Smith et al., 2007), which in Europe is known to peak at intermediate latitudes (Araújo et al., 2008). Therefore, the reported coexistence of basal Anuran families of relatively limited ranges (palaeoendemic lineages) with more advanced families of worldwide distributions (e.g. Pramuk et al., 2008) is likely to be more common across the mid-latitudinal range than in the latitudinal extremes. This would explain the presence of phylogenetic clusters under intense environmental filters such as boreal and desert climates (Wiens, 2007), but not in southern Europe, where these clusters would be “complemented” with endemic and restricted-range lineages (e.g., Plethodontidae or Proteidae) that have no functional analogues in other regions.

Latitudinal variation in species ranges may also elicit distinct beta diversity patterns. We propose that under the hypothesized spatially-dependent phylogenetic structure, a predominance of species replacements (as opposed to nestedness) should be observed in temperate areas (after partitioning beta diversity following Baselga, 2010). This would be explained by the fact that in the latitudinal extremes, environmentally-filtered clustered assemblages would be relatively more similar one to another, hence differences in composition would be better explained by species additions or removals (i.e. nestedness mechanism) rather than by species replacements (i.e. turnover component). In contrast, the opposite would be true in southern Europe, given the relatively higher contribution of endemic and restricted-range taxa to the regional species pools. If this is true, it would suggest a potential association between the phylogenetic structures of amphibian assemblages across a broad area and the patterns in (spatial) turnover that emerge when comparing these assemblages. To our knowledge, this relationship has not been explored to date. Filling this knowledge gap could potentially facilitate the design of conservation strategies for amphibians, since studying beta diversity and its components (as opposed to metrics based on phylogenetic diversity) is relatively easy, and could be widely implemented by managers and practitioners basing on existing local and regional taxa lists.

The overarching aim of this study was to examine amphibian community patterns across a broad latitudinal gradient in the Western Palearctic, combining analyses of phylogenetic structure and beta diversity partitioning (Fig. S1). We aimed at testing the following predictions: (i) phylogenetic structure will be spatially

dependent, with a relatively higher proportion of phylogenetically clustered assemblages at latitudinal extremes (because of the harsher environmental conditions) and with overdispersion prevailing in the mid-latitude range (because of the milder environmental conditions); (ii) this pattern will be explained by the fact that just a few families may occupy one or both climatic extremes, whereas most of the amphibian families may be restricted to the mesothermal belt; and (iii) due to the abovementioned latitudinal pattern in phylogenetic structure, an analogous pattern in the relative importance of the components of beta diversity will also emerge, with nestedness prevailing at the latitudinal extremes (Fig. 1A and C) and turnover being relatively more important in temperate areas (Fig. 1B and D). If these hypotheses are supported, we suggest the existence of the following conservation challenge: In areas where low environmental constraints have allowed phylogenetic diversity to be high, the spatial turnover component of beta diversity is likely to be more important than the nestedness component. Therefore, protecting just a few species-rich sites to preserve the regional species pool (which could be ideally achieved under a perfectly nested structure) may be useful at latitudinal extremes (predicted scenario: Fig. 1A) but not across the mid-latitudinal range (predicted scenario: Fig. 1D). Across these temperate regions, focusing on species-rich sites would probably neglect a substantial proportion of the regional species pool, particularly omitting restricted-range species of high conservation interest.

2. Study area

The study area covered part of the Western Palearctic ecozone, between latitudes 30°N and 71.5°N, excluding Eastern Europe and the Apennine and Balkan Peninsulas. This area constitutes an important climatic gradient, from the southern subtropical deserts to the northern subarctic areas. In this region, nine families and 51 species of amphibians have been described (Table 1 and Table S1; after Frost, 2013). Although several species of invasive frogs have breeding populations in Europe (Escoriza and Boix, 2012; Faraone et al., 2008; Schmeller et al., 2007), these species were excluded from the analyses because they can alter the assemblage patterns independently of historical environmental gradients.

3. Methods

3.1. Amphibian occurrence and climatic data

Data on the distributions of amphibians were obtained from the IUCN database, a source that has been widely used in biogeographic studies of vertebrates (e.g., Cooper et al., 2011; Dobrovolski et al., 2012; Sodhi et al., 2008). This database provides polygons that enclose the known range of each species, so the presence of a species is probable within the polygon, although it is not uniform. With the data extracted from these polygons, we built binary (presence–absence) matrices with cells at a spatial resolution of 0.1° and 2500 km².

Amphibian assemblage compositions are known to correlate with three main environmental controls: temperature, water availability, and primary productivity (Whittaker et al., 2007). Therefore, in our analyses, we included variables that describe these gradients: annual mean temperature, aridity index (a proxy for water availability), and biomass carbon density (a proxy for primary productivity). The aridity index is a measure of the water–energy balance (mean annual precipitation/mean annual potential evapotranspiration), with values ranging from 0–0.03 (hyper-arid) to >0.65 (humid; Trabucco and Zomer, 2009). Biomass–Carbon density is measured in m³ C ha⁻¹, ranging from <20 m³ C ha⁻¹ (steppes and deserts) to 200 m³ C ha⁻¹ (rainforests;

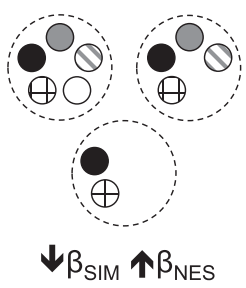
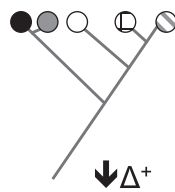
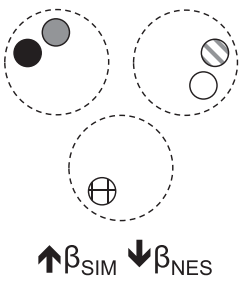
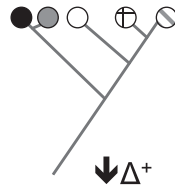
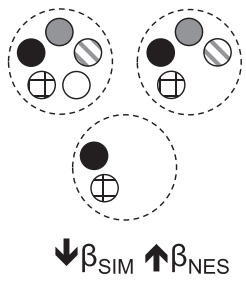
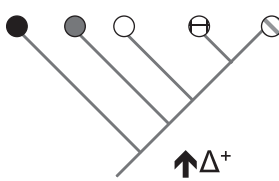
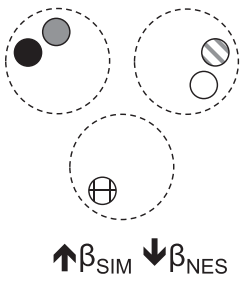
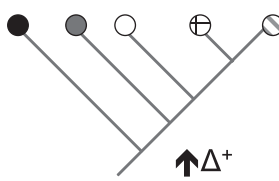
	Beta diversity pattern	Phylogenetic structure	Best conservation strategy
A	 <p>$\downarrow \beta_{SIM}$ $\uparrow \beta_{NES}$</p>	 <p>$\downarrow \Delta^+$</p>	<p>Protect a low number of species-rich areas</p> <p><i>Rationale:</i> Phylogenetic clustering and high relative contribution of nestedness to beta diversity ensure that most of the species and phylogenetic diversity will be preserved in these areas, since there is a single, ecologically-similar, species pool.</p>
B	 <p>$\uparrow \beta_{SIM}$ $\downarrow \beta_{NES}$</p>	 <p>$\downarrow \Delta^+$</p>	<p>Protect a high number of areas, regardless of their richness</p> <p><i>Rationale:</i> Despite phylogenetic clustering (i.e., ecologically-similar pool of species), the high relative contribution of turnover to beta diversity makes it difficult to preserve the regional pool of amphibians unless a large number of local communities are protected.</p>
C	 <p>$\downarrow \beta_{SIM}$ $\uparrow \beta_{NES}$</p>	 <p>$\uparrow \Delta^+$</p>	<p>Protect a low number of habitat-heterogeneous, species-rich areas</p> <p><i>Rationale:</i> Despite phylogenetic overdispersion (i.e., an ecologically-diverse pool), the high relative contribution of nestedness to beta diversity implies that the regional pool may be preserved by protecting a few species-rich, habitat-diverse areas.</p>
D	 <p>$\uparrow \beta_{SIM}$ $\downarrow \beta_{NES}$</p>	 <p>$\uparrow \Delta^+$</p>	<p>Protect a high number of habitat-heterogeneous areas, regardless of their richness</p> <p><i>Rationale:</i> Phylogenetic overdispersion and the high relative contribution of turnover to beta diversity implies phylogenetic diversity can only be preserved by protecting the many areas that cover the wide range of ecological requirements of the species pool.</p>

Fig. 1. Conceptual schematization of the possible scenarios (A to D) of beta diversity patterns and dominant phylogenetic structure in a given meta-community, and their implications for conservation. With regards to beta diversity patterns, overall spatial dissimilarity across a meta-community (beta diversity, β_{SOR}) may be explained by a combination of two mechanisms, namely nestedness (β_{NES}) and turnover (β_{SIM}). If nestedness dominates in explaining overall beta diversity (scenarios A and C), composition differences across local communities (dashed circles) may be explained by species gains and losses, with the richest local community hosting all or most of the species that are present in poorer habitats (each species is represented by a different small circle). In contrast, if turnover prevails (scenarios B and D), relatively richer local communities are not pools of the species that are present in species-poor habitats, but simply different draws from a non-shared species pool (after Baselga, 2010). However, the dominant phylogenetic structure of local communities (i.e., clustered, random, overdispersed) may be also relevant when optimizing conservation strategies. Local communities with members more closely related in the Linnean tree than would be expected by chance (phylogenetic clustering, A and B) usually reflect the effects of environmental filtering, whereas those hosting species significantly unrelated (phylogenetic overdispersion, C and D) usually reflect a relatively stronger biotic filtering. Therefore, whereas in scenarios A and B the protection of different habitat types (within each area) would be potentially unnecessary, due to the similarities in ecological niches across species within the same assemblage, in scenarios C and D this guideline would be crucial to integrate the wide range of ecological niches present in a local assemblage. Overall, we propose that each combination of possibilities, with regards to both beta diversity and phylogenetic structure patterns (scenarios A to D), allows for a different optimal conservation strategy.

Ruesch and Gibbs, 2008). These bioclimatic variables were obtained from the WorldClim database (Hijmans et al., 2005), the Consortium for Spatial Information (Trabucco and Zomer, 2009) and the Carbon Dioxide Information Analysis Center (2013).

3.2. Data analysis

3.2.1. Assemblage structure across regions

First, we aimed at determining whether the phylogenetic structure of the analyzed assemblages followed the hypothesized spa-

Table 1

Species richness and geographical distribution of the amphibian families reported in the study region (Western Palearctic). Plethodontidae (*) shows a very limited occurrence in the region and was excluded from the analyses.

Family	Species richness	Latitudinal range (°N)
Alytidae	7	30.3–52.3
Bombinatoridae	2	44.3–55.7
Pelobatidae	3	32.5–57.6
Pelodytidae	2	36.0–50.9
Bufoidea	6	30.0–67.7
Hylidae	3	30.0–56.4
Ranidae	8	30.0–71.0
Plethodontidae	1	43.0*
Salamandridae	19	31.4–67.1

tial-climatic gradients. We used taxonomy as a surrogate for phylogeny, since molecular data was not readily available for all pairs of the considered taxa. Although we accept this is not ideal and may potentially influence results, good correlations between taxonomy and phylogenetic relationships have been described for amphibians (Pyron and Wiens, 2011). Furthermore, some studies have concluded that using taxonomic ranks as a surrogate of phylogenetic distances may only slightly affect the estimates of phylogenetic distinctness between sites (Hardy and Senterre, 2007). In particular, taxonomic distinctness as a surrogate for phylogenetic structure has successfully been used in similar studies examining broad-scale patterns of marine (Carranza et al., 2011) and freshwater assemblages (Ruhí et al., 2013, 2014). Therefore, we used the SPECDIST routine to obtain a taxonomic distance matrix, with distance values representing lengths of paths connecting species pairs, traced across a standard Linnean tree that considered seven taxonomic levels (i.e., species, genus, subfamily, family, suborder, order, and class; after Frost, 2013). We subsequently computed *average taxonomic distinctness* (Δ^+ ; Clarke and Warwick, 1998) to characterize the structure of assemblages. This parameter describes if species within an assemblage (a “sample”) are taxonomically close (low Δ^+) or distant (high Δ^+). However, since this parameter is potentially influenced by species richness, a null model was needed to test if the observed Δ^+ values were as expected (or conversely, higher- or lower-than-expected) according to the species richness of each assemblage. To this end we used the TAXDTEST routine (Clarke et al., 2008), a null model that tests if the observed Δ^+ values can be obtained by drawing random subsets of species from the “regional” pool (after 999 permutations). Samples (i.e., assemblages) falling outside the interval obtained with the 95 % of the simulated values would have a higher- or lower-than-expected taxonomic relatedness: a higher-than-expected taxonomic relatedness would imply having a taxonomically clustered assemblage, whereas a lower-than-expected relatedness would represent a taxonomically-overdispersed assemblage. We focused on the significance of Δ^+ (hereafter $\% \Delta^+$), which indicates the probability that an assemblage falls within the simulated funnel, i.e., the higher $\% \Delta^+$, the more likely is the assemblage to show a random phylogenetic structure (i.e., neither clustering nor overdispersion; after Clarke and Warwick, 1998).

After obtaining these assemblage descriptors, we investigated the variation in species richness (S), Δ^+ and $\% \Delta^+$ across the described climatic gradients. To do this, we first classified the amphibian composition samples using K-means Cluster Analysis (CA). The optimal number of clusters was obtained by v-fold cross validation, after 100 iterations, setting a minimum of 2 clusters and a maximum of 25. After identifying broad groups of samples, we tested whether the amphibian composition differed significantly among these groups. To this end, we performed a permutational analysis of variance (PERMANOVA, one fixed effect: region) using Sørensen similarity index, including 5% randomly selected

locations, because of the computation limits imposed by permutation analyses. We classified the samples into six groups according to the results of the CA: North Africa (NAF), Iberian Peninsula (IP), France (F), southern Germany (SG), northern Germany, Denmark and the Netherlands (NG) and Scandinavian Peninsula (SP) (Fig. 2). Because amphibian assemblages may be spatially autocorrelated (Dobrovolski et al., 2012), we assessed this effect with permutation tests (Dormann et al., 2007; Koenig, 1999). We computed Euclidean distance matrices for each of the variables, and the relationships between these matrices were quantified with Mantel-type tests (999 permutations). Aridity and vegetation cover were correlated, but could explain different gradients in species occurrence (Thuiller et al., 2004). For this reason, we calculated the relationship between assemblage descriptors and biomass carbon density while holding the aridity index constant. Permutation analyses are computationally intensive. For this reason, Mantel correlations were estimated with a randomly selected 10% of the locations. These environmental matrices were also related to spatial distances to explore the existence of autocorrelated structures. SPECDIST, TAXDTEST and PERMANOVA analyses were performed using Primer-E (PRIMER-E Ltd.); K-means cluster analysis, with Statistica v.7 (STATSOFT Inc.), and Mantel tests, using the ‘vegan’ package (Oksanen et al., 2012) in R (R Development Core Team, 2013).

3.2.2. Niche width of the main lineages

Second, we determined whether the families studied differed in their niche widths, which could help to explain their phylogenetic patterns. To do this, we estimated the niche widths from two climatic variables (log mean annual temperature and log aridity index), and calculated Bayesian posterior estimates of the standard ellipse area (SEA). This method has been widely used to estimate bivariate niche widths (Layman and Allgeier, 2011) and was suitable in our case because it provides a metric that is unbiased by differences in sample size (Jackson et al., 2011). Statistical significance was achieved after 10,000 iterations when calculating the

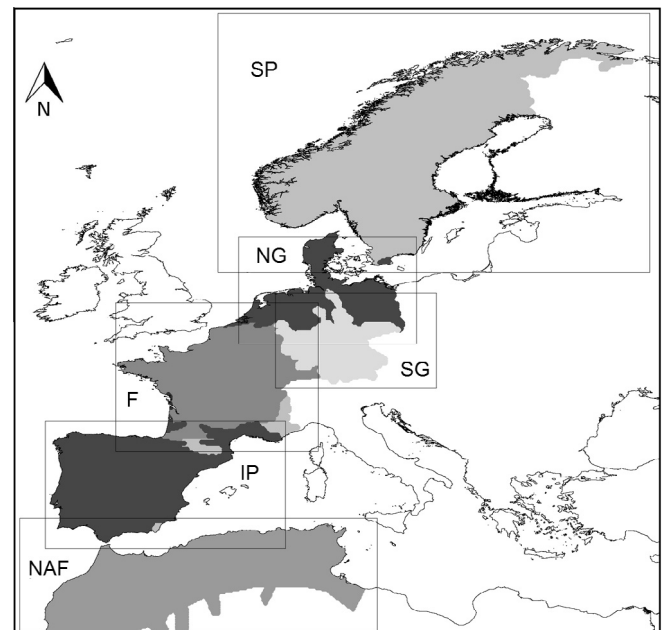


Fig. 2. Optimal number of clusters of the amphibian assemblage cells, obtained using K-means Cluster Analysis. (NAF) North Africa; (IP) Iberian Peninsula; (F) France; (SG) Southern Germany; (NG) Northern Germany, the Netherlands and Denmark and (SP) Scandinavian Peninsula.

mean and 95% credible limits of the posterior distribution. A single family (Plethodontidae) was excluded from the analysis because its distribution was highly restricted (Salvidio, 2013). These analyses were performed with the package 'siar' (Parnell and Jackson, 2013) for R (R Development Core Team, 2013).

3.2.3. Relationship between assemblage structure and beta diversity

Third and finally, we wished to explore which components best explained the spatial variation in species composition among assemblages. When comparing communities from different sites, many matrix configurations are possible (Almeida-Neto et al., 2008). However, all situations in which communities differ can be described by a combination of two mechanisms, species replacement (i.e., turnover) and species gain or loss (i.e., nestedness; Baselga, 2010). To determine the relative contributions of turnover and nestedness to overall beta diversity, it is necessary to compare different matrices of assemblages. We also needed to keep size equal across the compared areas, so we divided the former gradient into 18 discrete regions, with each region being delimited by a "latitudinal" rectangle of 250,000 km². This was achieved by maintaining the latitudinal distance constant and adjusting the longitudinal sides of each rectangle (after Sastre et al., 2009). A grid of 2500 km² cells was then superimposed onto the study area, and latitudinal rectangles containing ≤ 30 cells with data were excluded. The remaining latitudinal rectangles (i.e. those containing at least 30 cells with amphibian assemblage data) were included in the analyses. To control for differences in the numbers of cells among latitudinal rectangles, 30 cells per rectangle were resampled 100 times, which allowed us to obtain the mean values for the beta diversity components. We calculated three measures of beta diversity: Simpson dissimilarity (indicating species turnover across space; β_{SIM}), nestedness (indicating species gain or loss across space, β_{NES}), and Sørensen dissimilarity (β_{SOR} ; an overall measure of beta diversity), described as the sum of the first two components ($\beta_{SOR} = \beta_{SIM} + \beta_{NES}$; Baselga, 2010). Despite some controversy around this partitioning method (Almeida-Neto et al., 2012), in our case its use was well justified, since we were not interested in assessing nestedness or turnover *per se*, but the contribution of this mechanism to overall composition dissimilarities. This method was also appropriate because it was based on multiple-site relationships. Pairwise dissimilarities do not account for patterns of co-occurrence among more than two sites, and thus fail to properly quantify overall heterogeneity and its components (Baselga, 2013). The average values of the environmental variables were also obtained for each discrete region. The correlation between latitude, climate, and assemblage descriptors (i.e., S, Δ^+ and $\% \Delta^+$) and the beta diversity components was tested with linear models (LM). Because amphibian species richness is known to be higher at intermediate latitudes, the relationship between these variables was expected to follow a unimodal function. Therefore, we analyzed these relationships with first- and second-order LMs. The existence of significant differences in accuracy between both LM types was assessed running an ANOVA test. LM, ANOVA and beta diversity analyses (betapart package, Baselga et al., 2013) were run in R (R Development Core Team, 2013).

4. Results

4.1. Assemblage structure across regions

As predicted, species richness peaked in the intermediate latitudes (Table 2 and Fig. 3A). Δ^+ showed a different but still unimodal pattern across the latitudinal gradient (Table 2 and Fig. 3B), suggesting that taxonomic trees in the mid-latitudinal range were

not only relatively richer, but also more complex than in the other ranges. In turn, the phylogenetic structure was lower at high latitudes, with random structures generally increasing with latitude (up to >90% random structures above the 65°N parallel, Table 2 and Fig. 3C).

PERMANOVA tests confirmed that the six regions (NAF, IP, F, SG, NG and SP) differed significantly in their species composition (*Pseudo-F*_{2,179} = 1246, *P* = 0.001). When the regions were compared, most of the assemblages fell within the 95% confidence limits of the null distributions (TAXDTEST), indicating a random phylogenetic structure. However, we identified some areas where Δ^+ was higher or lower than expected by chance. In particular, in NAF, 11% of the localities showed taxonomic clustering and none showed taxonomic repulsion; in IP, no location showed taxonomic clustering and 1.6% of the localities showed taxonomic repulsion; and in SP, 0.2% of the localities showed taxonomic clustering and none showed taxonomic repulsion.

Mantel tests revealed a highly significant spatial autocorrelation among sites (for all tests, *P* < 0.05), justifying the subsequent use of permutation tests in our analyses. The gradients of S, Δ^+ and $\% \Delta^+$ were explained by different variables in each of the six regions: aridity was the environmental variable that best explained assemblage compositions in the southern regions (NAF and IP), while temperature explained assemblage patterns more consistently in the north (SP and NG regions). At intermediate latitudes (i.e., F and SG), we did not detect strong environmental gradients in assemblage composition (Table 3). Plant biomass showed lower to no explanatory power in any region.

4.2. Niche width of the main lineages

Our results showed a variety of niche widths, with some families (namely Bufonidae, Ranidae, and Salamandridae) presenting distinctly wider niches than the rest of the families (Fig. 4). Therefore, this result supported our prediction that some families would occupy most of the available regional climate space, whereas the majority of them (5 out of 8) would not.

4.3. Relationship between assemblage structure and beta diversity

Analysis of the beta diversity patterns showed that the overall observed beta diversity (β_{SOR}) did not follow any significant spatial or environmental pattern. In contrast, species turnover (β_{SIM}) and nestedness (β_{NES}) related significantly to S, Δ^+ , $\% \Delta^+$ and the selected spatial and climatic variables (Table 4 and Fig. 5). Therefore, these results supported the predicted relationship between phylogenetic structure and beta diversity. In particular, we confirmed that under harsh climatic conditions, phylogenetic clustering elicited a higher contribution of nestedness in explaining overall composition dissimilarities (beta diversity).

5. Discussion

5.1. Macroecological patterns in assemblage structure

We observed some clear spatial patterns in the phylogenetic structure of amphibian assemblages, supporting the hypothesis that under relatively harsh climatic conditions, amphibian assemblages are more homogeneous. The regional clusters we observed showed a high congruence with those previously described in Europe for amphibians and reptiles using coarser resolutions (Rueda et al., 2010). This suggests the existence of some common drivers structuring the distribution of low-dispersal vertebrates (i.e., current and historical climate conditions and geographical barriers). These clusters are well-defined climatically, but also correspond

Table 2

Descriptive statistics of the analyzed assemblages. p25–p75, percentile ranges; S, species richness; Δ^+ , average taxonomic distinctness; $\% \Delta^+$, probability of random phylogenetic structure; NAF, North Africa; IP, Iberian Peninsula; F, France; SG, southern Germany; NG, Northern Germany, the Netherlands and Denmark; SP, Scandinavian Peninsula; AMT: annual mean temperature ($^{\circ}\text{C}$); Biomass, Biomass-Carbon density ($\text{m}^3\text{C ha}^{-1}$).

Region		S	Δ^+	$\% \Delta^+$	AMT	Aridity index	Biomass
NAF	Mean	4.0	48.9	21.9	17.3	0.23	9.8
	p25–p75	3–5	47.6–59.5	8.4–26.6	15.2–19.5	0.08–0.33	1.1–11.3
IP	Mean	10.0	70.7	42.5	13.4	0.63	33.2
	p25–p75	8–12	70.1–71.9	26.4–54.3	11.7–15.5	0.42–0.76	10.9–52.4
F	Mean	12.5	69.5	46.9	10.1	1.0	18.8
	p25–p75	11–14	68.9–70.1	23.8–73.5	9.4–11.0	0.84–1.1	5.1–28.5
SG	Mean	13.4	68.4	53.4	8.2	0.98	27.2
	p25–p75	13–14	67.6–69.2	37.2–72.5	7.8–8.8	0.86–1.1	12.2–39.0
NG	Mean	10.1	66.9	74.9	8.6	0.98	12.2
	p25–p75	8–12	66.3–68.0	62.1–91.9	8.2–9.1	0.80–1.2	5.7–13.3
SP	Mean	3.2	55.4	73.3	3.1	1.63	18.1
	p25–p75	2–4	42.9–76.2	54.9–99.3	–0.2 to 6.0	1.11–1.83	4.5–29.6

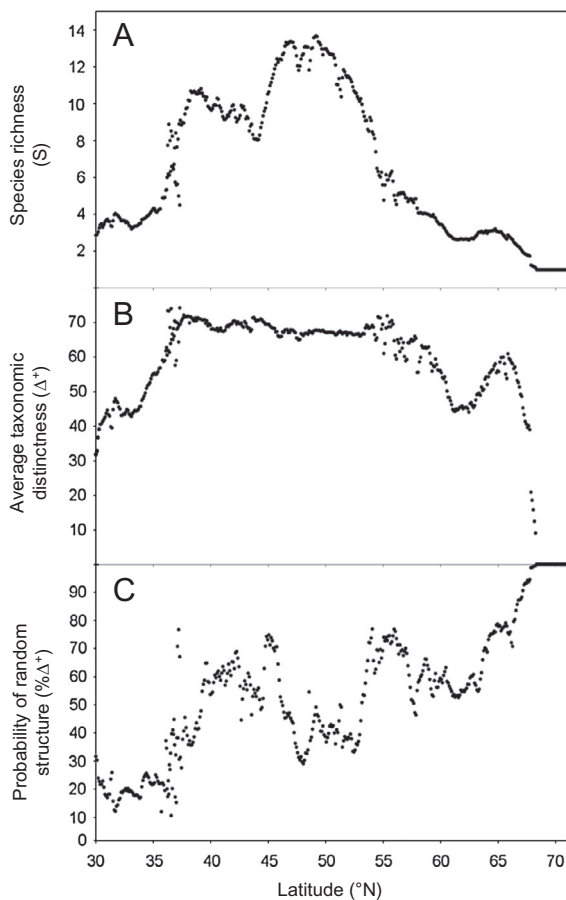


Fig. 3. Spatial patterns of assemblage descriptors. Each point represents the mean value obtained at every 0.1° of latitude. (A) species richness (S), (B) average taxonomic distinctness (Δ^+), and (C) probability of random phylogenetic structure ($\% \Delta^+$).

to different postglacial routes, as shown by the presence of some species with eastern–Europe refugia in NG–SG regions (e.g., *Bufo viridis* or *Bombina* species; Hofman et al., 2007; Stöck et al., 2006) that are largely absent everywhere else in the ecozone. Within this context, previous studies on amphibian phylogenetic diversity showed that areas with unusually low and high phylogenetic diversity (relative to their richness) reflect the importance of biogeographic barriers to dispersal, colonization and diversification processes (Fritz and Rahbek, 2012).

Table 3

Relationship between species richness (S), average taxonomic distinctness (Δ^+), probability of random phylogenetic structure ($\% \Delta^+$) and the studied environmental variables, obtained with Mantel tests. The table shows the statistic of correlation r ; significant results ($P < 0.05$) are bolded. NAF, North Africa; IP, Iberian Peninsula; F, France; SG, Southern Germany; NG, Northern Germany, the Netherlands and Denmark; SP, Scandinavian Peninsula; AMT, annual mean temperature ($^{\circ}\text{C}$); Biomass, Biomass-Carbon density ($\text{m}^3\text{C ha}^{-1}$).

	Region	AMT	Aridity index	Biomass
S	NAF	0.15	0.49	0.33
	IP	0.03	0.16	0.10
	F	0.13	0.08	0.07
	SG	–0.02	0.01	0.07
	NG	0.24	0.10	–0.02
	SP	0.38	0.00	0.36
Δ^+	NAF	0.21	0.48	0.01
	IP	0.08	–0.05	–0.03
	F	0.06	0.02	0.09
	SG	–0.03	0.01	–0.02
	NG	0.08	0.13	–0.02
	SP	0.17	0.10	0.02
$\% \Delta^+$	NAF	0.03	0.15	0.15
	IP	0.01	0.04	–0.00
	F	0.00	–0.02	0.03
	SG	0.02	0.01	0.01
	NG	0.15	0.07	–0.01
	SP	0.10	–0.00	0.15

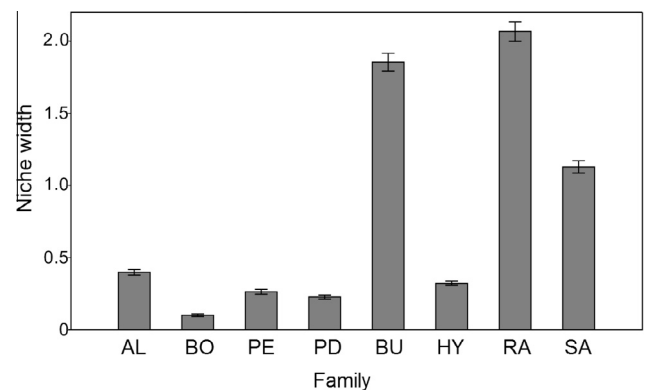


Fig. 4. Estimated niche widths of the studied amphibian families, computed using the climatic variables annual mean temperature and aridity index. The y-axis shows the area ellipse and the whisker bars of the 95% Bayesian credible intervals. AL: Alytidae; BO: Bombinatoridae; PE: Pelobatidae; PD: Pelodytidae; BU: Bufonidae; HY: Hylidae; RA: Ranidae; SA: Salamandridae.

In NAF, amphibian assemblages showed a progressive reduction of their complexity towards the pre-Saharan region, which was mainly explained by the increasing aridity. In Western Europe,

Table 4
Relationship between overall beta diversity (β_{SOR}) and its components (nestedness, β_{NES} ; turnover, β_{SIM}) with the spatial, climate and assemblage descriptors analyzed across the ecozone. The table shows the 1st and 2nd order linear model (LM) statistics and the improvement in the accuracy (1st LM vs 2nd LM ANOVA test). Significant results ($P < 0.05$) are bolded. LAT, Latitude; AMT, annual mean temperature ($^{\circ}\text{C}$); AI, Aridity index; S, species richness; Δ^+ , average taxonomic distinctness; $\%\Delta^+$, probability of phylogenetic random structure.

			LAT	AMT	AI	S	Δ^+	$\%\Delta^+$
β_{SIM}	1st LM	r^2	0.04	0.01	0.06	0.44	0.48	0.00002
		P	0.40	0.66	0.31	0.002	0.001	0.98
	2nd LM	r^2	0.39	0.49	0.51	–	–	0.35
		P	0.02	0.01	0.01	–	–	0.04
	1st LM vs. 2nd LM	P	0.01	0.002	0.002	–	–	0.01
β_{NES}	1st LM	r^2	0.02	0.002	0.12	0.72	0.53	0.003
		P	0.62	0.86	0.16	0.00001	0.001	0.84
	2nd LM	r^2	0.52	0.66	0.74	–	–	0.38
		P	0.004	0.0003	0.00004	–	–	0.03
	1st LM vs. 2nd LM	P	0.001	0.00008	0.00002	–	–	0.01
β_{SOR}	1st LM	r^2	0.05	0.03	0.05	0.19	0.01	0.01
		P	0.39	0.49	0.37	0.07	0.77	0.63
	2nd LM	r^2	0.13	0.11	0.15	0.43	0.07	0.02
		P	0.36	0.43	0.31	0.02	0.58	0.89
	1st LM vs. 2nd LM	P	–	–	–	0.03	–	–

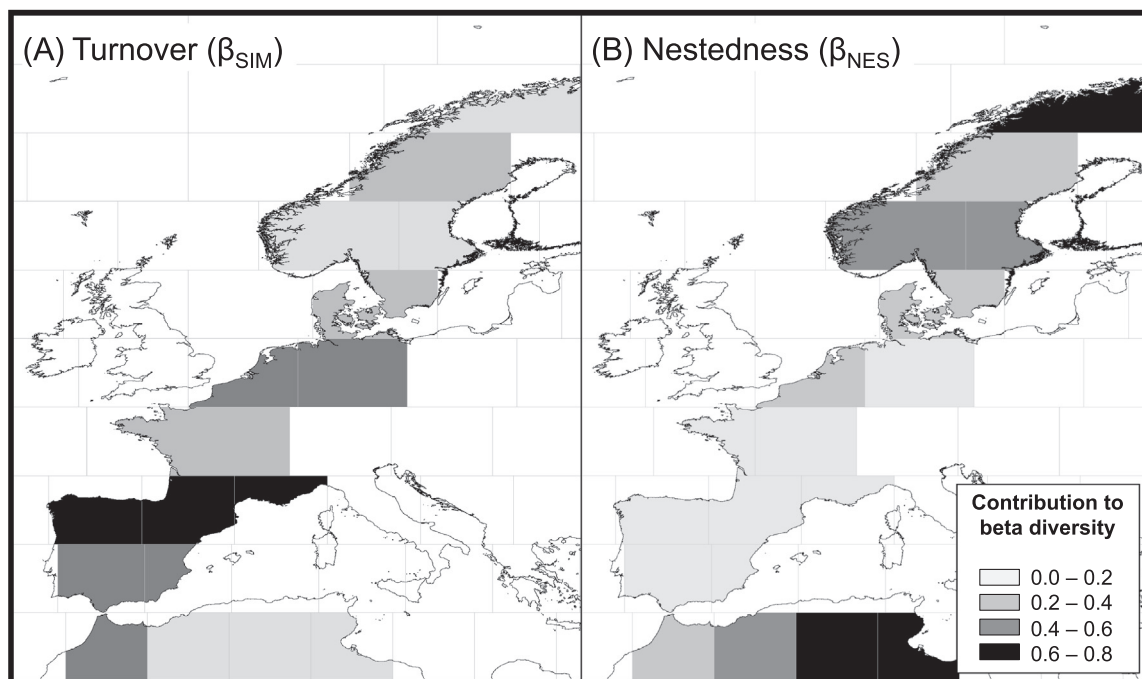


Fig. 5. Latitudinal variation in beta diversity patterns, estimated from two components: turnover (species replacements, β_{SIM} ; panel A) and nestedness (species gains and losses, β_{NES} ; panel B).

species richness was highest at the intermediate latitudes (F, SG and IP regions), where most of the assemblages lacked any non-random structure. This was already expected in an area that falls under the mesothermal climate, which has probably not promoted the prevalence of specialized phenotypes. Within this context, the only assemblages that displayed phylogenetic evenness were located in areas with relative historical climatic stability (i.e., IP), where many endemic lineages have persisted (Gómez and Lunt, 2007). These areas also showed a large spatial turnover, probably explained by the prevalence of allopatric speciation and niche specialists (Arntzen and Alexandrino, 2004; Martínez-Solano et al., 2004). In SP, assemblages showed nested patterns and were simpler, with their structure following a thermal gradient. This lower complexity is consistent with the described disappearance of boreal ecosystems during the Last Glacial Maximum (Hewitt, 1996).

Assemblages in this region consisted of species that have colonized the area within the last 10,000 years (Palo et al., 2004), with some of them being cold-tolerant species that had their glacial refugia in central-eastern Europe (Babik et al., 2004). Our results showed that a high proportion of amphibian assemblages in the subtropical deserts of the ecozone's southern edge are clustered phylogenetically. Therefore, aridity seems to impose stricter limits on amphibian diversification than does temperature. Arid regions are extreme environments for amphibians, mainly because this group has permeable skins and a water-dependent reproductive cycle. For these reasons, very few amphibian lineages have developed the necessary adaptations to colonize arid regions (Dayton and Fitzgerald, 2001). On the contrary, several families have diversified to reach subarctic regions (Kuzmin, 1999), where they have developed specific physiological adaptations to tolerate low temperatures

(Storey, 1990). Cold tolerance has evolved independently in several metazoan lineages (including mammals, birds, reptiles, amphibians, and arthropods) possibly in response to climatic fluctuations on evolutionary time scales (Araújo et al., 2013).

As predicted, we also found that most of the ecozone's climate space is occupied by a few lineages (Bufonidae, Ranidae, and Salamandridae) that comprise a large proportion of the global diversity of amphibians (65% of species richness). These lineages have diversified into one or both geographic extremes (Bons and Geniez, 1996; Gasc et al., 1997), whereas the rest are restricted to milder climates. This fact can be related, on the one hand, to their great dispersal capacity (e.g., in Bufonidae; Van Bocxlaer et al., 2010) that allowed them to quickly recolonize northern Europe after the regression of glaciers in the Holocene (Beebe and Rowe, 2000). On the other hand, the wide distribution of these groups can also be attributed to their cold tolerance, which allowed some species from these families to maintain stable populations in northern areas during the Last Glacial Maximum (Zeisset and Beebe, 2008).

5.2. Beta diversity patterns and implications for amphibian conservation in the Western Palearctic

Scientific research has recently addressed some knowledge gaps that may help preserving amphibian biodiversity, mainly in the fields of biomonitoring (Beebe and Griffiths, 2005), pollutant and pathogen effects on amphibian demography (Cheng et al., 2011), responses to habitat restoration (Lee et al., 2006), and captive breeding and reintroduction of some fragile species (Griffiths and Pavajeau, 2008). However, among the most effective measures there is site conservation, which requires the identification of Key Biodiversity Areas (KBA; after Eken et al., 2004). These areas are usually selected based on the number of threatened species they shelter (Silvano et al., 2007). Although in the studied area there are very few regions that concentrate amphibian species at risk (Cox et al., 2006), we believe our findings could be relevant to the establishment of a network of KBAs in the Western Palearctic. Overall, with the spatial analysis of phylogenetic structure and beta diversity components we identified two optimal scenarios with different implications for the identification of KBAs: in northern Europe and in the semi-arid areas of North Africa, conservation efforts would be optimized by focusing on the few areas that present the highest species richness (scenario A in Fig. 1). In contrast, in southern Europe it would be preferable to protect the largest possible number of sites, focusing on phylogenetic and functional diversity rather than on species richness (scenario D in Fig. 1).

We subsequently groundtruthed these scenarios by calculating the minimum number of cells that would be necessary to protect the 75%, 90%, and 100% of the amphibian species richness found in each of the latitudinal rectangles of 250,000 km² (Table 5). These results supported the previous inferences: the 90% of the amphibian species richness of Northern Africa's latitudinal rectangles could be included in just one or two 2500 km² cells, and only one area would be necessary in the latitudinal rectangles that cover from North-east France to Scandinavia. In contrast, between two and four 2500 km² cells would be needed to protect the same proportion of the amphibian richness in the case of the Iberian Peninsula. This latter region was as well the one that had the latitudinal rectangle with the "most challenging" situation if we were to protect the 100% of the amphibian richness, with up to six 2500 km² cells being needed in the North-eastern Iberian Peninsula latitudinal rectangle.

We believe these results present clear implications for amphibian conservation at large geographic scales. On the one hand, because some families display narrow niches, there could be an asymmetric loss of diversity under ongoing and future climate

Table 5

Minimum number of areas necessary to protect the 75%, 90%, and 100% of the species richness of each latitudinal rectangles of 250,000 km². Each area accumulates the maximum species richness of each region within a land surface of 2500 km².

Latitudinal rectangle	75%	90%	100%
Northern Morocco	1	2	3
North-Western Algeria	1	2	3
North-Eastern Algeria	1	1	1
Tunisia	1	1	1
South-Western Iberian Peninsula	1	2	3
South-Eastern Iberian Peninsula	1	3	4
North-Western Iberian Peninsula	1	2	3
North-Eastern Iberian Peninsula	2	4	6
South-Eastern France	2	2	3
North-Western France	1	2	3
North-Eastern France	1	1	2
Netherlands–Belgium	1	1	2
Germany	1	1	2
Denmark–Southern tip Scandinavian Peninsula	1	1	3
South-Western Scandinavian Peninsula	1	1	1
South-Eastern Scandinavian Peninsula	1	1	1
Central Scandinavian Peninsula	1	1	1
Northern Scandinavian Peninsula	1	1	1

change, as occurred previously in the region during the late Neogene. This period was characterized by a progressively increasing seasonality (Ródriguez-Sánchez and Arroyo, 2008) that elicited range contractions, species loss and, in some cases, the extinction of some ancient lineages (Hossini, 1993; Rage and Rocek, 2003). In contrast, other families experienced a diversification process during the same period (e.g., Ranidae, Veith et al., 2003), becoming the main components of the ecozone's amphibian fauna. Increasing effects of other anthropogenic factors related to global change (e.g., wetland destruction) are also likely to cause a decline in the connectivity of amphibian meta-communities, potentially disrupting migratory flows that could allow some species to find suitable refuges (Araújo et al., 2006). These cumulative effects are likely to cause an increased number of threatened amphibian species in the Western Palearctic in the coming decades (IUCN database, 2013). Therefore, designing strategies that optimize the preservation of amphibian diversity in this ecozone should be a priority. On the other hand, conservation strategies in the ecozone are focused on protecting critically endangered taxa (Council Directive 92/43/EEC) rather than areas of high species richness or phylogenetic diversity. Amphibians also often benefit (unintentionally) from the protection of areas of particular aesthetic value (Múgica and De Lucio, 1996), or from coexisting with larger vertebrates that act as umbrella species for conservation efforts (e.g., the European otter; Bifolchi and Lodé, 2005). However, contrasting to other groups (e.g. Albouy et al., 2012; Gossner et al., 2013), large-scale strategies directed towards the preservation of amphibian diversity have been missing thus far (Bombi et al., 2012).

Our study had some limitations, namely the use of taxonomic distinctness as a surrogate of phyletic distances, and the limited geographical scope (as we studied an important part, but not the totality, of the Western Palearctic ecozone). Nevertheless, we unveiled an undescribed relationship between the relative importance of beta diversity components and the dominant assemblage structure, which holds across the broad latitudinal gradient studied. We believe there is a need to bridge the macroecological patterns that have long been described by fundamental ecology at continental scales, with the spatial patterns that manifest at relatively smaller scales (i.e. region). The latter (but not the former) are the scales at which biodiversity conservation is managed, and hence even if the aim is to preserve as much as possible of the ecozone's biodiversity, conservation strategies are most relevant at regional scales. To our knowledge, this is the first study to fill this knowledge gap on amphibians. Therefore, these results should

help optimizing existing and future networks of amphibian KBAs in the Western Palearctic.

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Appendix A. Supplementary material

Supplementary information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.05.030>.

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