

Phylogenetic signals in the climatic niches of the world's amphibians

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The question of whether closely related species share similar ecological requirements has attracted increasing attention, because of its importance for understanding global diversity gradients and the impacts of climate change on species distributions. In fact, the assumption that related species are also ecologically similar has often been made, although the prevalence of such a phylogenetic signal in ecological niches remains heavily debated. Here, we provide a global analysis of phylogenetic niche relatedness for the world's amphibians. In particular, we assess which proportion of the variance in the realised climatic niches is explained on higher taxonomic levels, and whether the climatic niches of species within a given taxonomic group are more similar than between taxonomic groups. We found evidence for phylogenetic signals in realised climatic niches although the strength of the signal varied among amphibian orders and across biogeographical regions. To our knowledge, this is the first study providing a comprehensive analysis of the phylogenetic signal in species climatic niches for an entire clade across the world. Even though our results do not provide a strong test of the niche conservatism hypothesis, they question the alternative hypothesis that niches evolve independently of phylogenetic influences.

The question of whether related species are also ecologically similar is as old as modern biology (Darwin 1859). Recently, the question has gained increased interest (Losos 2008a, b, Wiens 2008, Vieites et al. 2009a, Dormann et al. 2010), partly because of its implications for understanding global biodiversity gradients (Wiens and Donoghue 2004), and partly because it helps in comprehending how species might adapt to ongoing climate changes (Botkin et al. 2007). Understanding the extent to which there is a phylogenetic signal in ecological niches (the tendency for related species to resemble each other's ecological characteristics more than species randomly drawn from a phylogeny; Blomberg and Garland 2002, Losos 2008a) helps to formulate hypothesis about niche evolution. This is particularly true if one adopts the view that estimation of the signal strength in climatic niches may serve as a surrogate measure for the rate of climatic niche evolution (Garland 1992, Blomberg et al. 2003, Rheindt et al. 2004, but see Revell et al. 2008, Ackerly 2009). It needs to be added, though, that establishing such a phylogenetic signal does not demonstrate the existence of phylogenetic niche conservatism, which is the tendency of related species' niches to be even more similar than expected given their phylogeny (Losos 2008a). However, the existence of strong signals in climatic niches do challenge the alternative

hypothesis that niches evolve quickly (Broennimann et al. 2007) and independently of phylogeny (Dormann et al. 2010).

Despite the relevance of the climatic niche concept to contemporary ecology (Araújo and Guisan 2006, Soberón 2007), quantitative analyses on the strength of the phylogenetic signal in climatic niche similarities are scarce (but see, e.g. Prinzing et al. 2001). As pointed out by Losos (2008a), most studies investigating phylogenetic signals in ecological niches only include few species at rather small geographic extents. Thus, the need for taxonomically and geographically comprehensive analyses on phylogenetic signals in climatic niches is timely. Here, we provide the first of such analyses and test for the existence and strength of phylogenetic signals in climatic niches for an entire class of organisms, the amphibians, on a global scale. Ideally, one would test hypotheses about niche evolution using measures of the fundamental niche (*sensu* Hutchinson 1957), since the fundamental niche is the product of the genetics, morphology and physiology of the species, thus being the "feature" which evolves. In a climatic context, the fundamental niche would be the range of combinations of climatic variables in which the species could potentially exist (Austin et al. 1990, Soberón 2007). Unfortunately, estimates of the fundamental climatic niches for large

numbers of species are difficult to obtain. Therefore we have to rely on surrogates estimated with the climate envelope of species, i.e. the combination of climatic variables (e.g. means and extremes of precipitation and temperature) that best describes a species' geographical range. This characterisation can, however, at best represent the realised climatic niche of a species, and will never entirely portray the fundamental climatic niche (see discussion in Araújo and Guisan 2006, Colwell and Rangel 2009, Soberón and Nakamura 2009).

Here, we first used a family-level phylogeny of the world's amphibians to test for the existence of phylogenetic signals in species climate niches. Then we tested for the existence of phylogenetic signals and measured their strength separately for the three orders of amphibians and for each one of seven biogeographical regions.

Material and methods

We used distributions for 5527 amphibian species from all three amphibian orders (Anura, Caudata, Gymnophiona, see Supplementary material Table S1 for an overview of the numbers of species included in the dataset). Distribution data were compiled from the "Global Amphibian Assessment" (IUCN 2004). This dataset comprises distribution maps (extent of occurrence polygons) for each species based on documented records and expert knowledge. Although it is the most comprehensive global dataset available for amphibian distributions, many species are listed as "data deficient", due to a lack of knowledge on their real distributions. Climatic data (originally 19 bioclimatic variables at 10' resolution) were compiled from the WorldClim database (Hijmans et al. 2005). Distribution and climate data were resampled to a 2×2 degree latitude-longitude grid including 5017 terrestrial cells.

A taxonomic topology for genus, subfamily, family and higher taxonomic levels was compiled from the "Amphibian Tree of Life" (Frost et al. 2006) and the online database "Amphibian Species of the World" (ASW; Frost 2007). The taxonomic nomenclature of this database is based on a phylogenetic super tree considering the most recent studies of amphibian phylogeny and is thus building upon direct inferences of the evolutionary history of the species. Despite criticism on several aspects of the original "Amphibian Tree of Life" phylogeny (Wiens 2007), the ASW taxonomy is the most comprehensive taxonomic database for amphibians to date and is being used frequently in conservation and evolutionary studies (Blackburn 2008, Corey and Waite 2008, Santos et al. 2009).

Quantifying climatic niches

Climatic niches were characterised using an ordination approach termed "outlying mean index" (OMI; Dolédec et al. 2000). In contrast to other ordination techniques, OMI does not make assumptions about the shape of the species' response curves to the environment and gives equal weight to sites independent of their species richness. OMI gives the species average position ("niche position") within environmental space, which represents a measure of the

distance between the environmental conditions used by the species and the mean environmental conditions of the study area. It also quantifies the variability of environmental conditions used by each species ("niche breadth"), given by the standard deviation along the respective OMI axes (for more details, see Dolédec et al. 2000, as well as Thuiller et al. 2004 for a case study using OMI). Here, environmental conditions were measured as a function of eight climatic variables: mean diurnal range of temperature, minimum temperature of the coldest month, annual range of temperature, mean temperature of the warmest quarter, annual precipitation, precipitation seasonality, precipitation of the driest quarter, and precipitation of the warmest quarter (for a detailed description of the derivation of these variables, see Hijmans et al. 2005). These variables include a range of climatic factors (temperature extremes, amount and seasonality of precipitation) which are known to impose constraints on the occurrence and survival of amphibians (Carey and Alexander 2003, Wells 2007), and are often used to model the geographical distributions of individual species (Araújo et al. 2006) and species richness (Araújo et al. 2008). In the OMI analysis, we used the first and second axes of the ordination since they explained 82 to 96% of the total inertia (Supplementary material Table S2). OMI analyses were performed using the *ade4* package in R (Chessel et al. 2004, R Development Core Team 2008). A randomisation test was performed to examine if niche positions along climate gradients could have arisen by chance (Dolédec et al. 2000); one thousand permutations were obtained for testing niche positions of each species occurring in each one of the biogeographical regions (see below). From the OMI analysis, we also obtained measures of niche breadth along the first and second OMI axes (for more details, see Dolédec et al. 2000, Thuiller et al. 2004).

Species may share ecological traits because of their shared evolutionary history, but also because they occur in similar places (see Freckleton and Jetz 2009, and references therein). For practical reasons, to account for possible confounding effects arising from spatial autocorrelation in niche characteristics and to explore the potential geographic variation in phylogenetic signal strength, all analyses except the one for the family-level phylogeny (see below) were performed separately for each amphibian order and biogeographical realm. Biogeographical realms were classified following the divisions of Sclater (1858) and Wallace (1876), later renamed by Olson et al. (2001): Afrotropics, Australasia, Indo-Malay, Nearctic, Neotropics, Palearctic, Antarctica, and Oceania (referred to here as "regions"; see Supplementary material Table S1 for an overview of the numbers of species for each species set). Because there are no amphibians in Antarctica and only a few across the scattered islands of Oceania, these regions were removed from the analyses. Madagascar harbours a rich amphibian fauna that is quite distinct from the Afrotropical fauna (Duellman 1999, Vieites et al. 2009b); therefore, we added Madagascar as a seventh region. Nevertheless, we are aware that the spatial extent of the regions is still too large to completely rule out any confounding spatial influence on niche similarity. However, the geographic and phylogenetic resolution of our data

does not allow for more sophisticated approaches (as recently proposed by Freckleton and Jetz 2009).

Testing for phylogenetic signals in climatic niche similarity

To test for phylogenetic signals in climatic niche similarity, we used Blomberg's randomisation test and K statistic, variance component analyses (VCA), analysis of similarity (ANOSIM) and Wilcoxon rank sum tests. Blomberg's randomisation test for phylogenetic signal assesses whether a given phylogenetic tree (including topology and branch lengths) better fits a set of data assigned to the tree tips (climatic niche positions in our case) as compared with the fit obtained when the data have been randomly permuted across the tree tips (Blomberg et al. 2003). The K statistic indicates the strength of phylogenetic signal, as compared with an expectation based on the tree structure and assuming Brownian motion character evolution. K values equal to 1 indicate a phylogenetic signal resembling the Brownian motion evolution model, values of $K > 1$ or < 1 indicate a stronger or weaker signal than the one expected by the Brownian motion model of character evolution (Blomberg et al. 2003). Since no complete phylogeny is yet available for the world's amphibians, we used the global family-level phylogeny from Roelants et al. (2007). Blomberg's randomisation and K analyses were performed using the picante package within R, with 1000 randomisations to assess significance (Kembel et al. 2009).

With VCA we quantified how much of the niche variance on the species level (among-species variance) can be explained at different taxonomic levels (Venables and Ripley 1999, Prinzing et al. 2001). As taxonomic levels we used the genus, subfamily and family grouping as well as the higher taxonomic categories above the family level as given by Frost et al. (2006). A large proportion of the among-species variance in niche position explained at higher taxonomic levels would indicate a phylogenetic signal in climatic niche similarity. On the other hand, all the variance localised among the species would indicate the absence of a phylogenetic signal. We applied VCA with a restricted maximum likelihood approach, using the functions `lme` and `varcomp` in the `ape` package within R (Paradis et al. 2004). We also performed null models to assess if the results of the VCA could be produced by chance alone. The null models simulate the case of no phylogenetic signal – running VCA based on a randomised phylogeny. To generate the null models, we randomised the taxonomic assignments of the species and calculated the variance components as the mean of one thousand randomisations. Again, we ran this analysis separately for the three amphibian orders within each region.

With ANOSIM – a non-parametric test analogous to ANOVA – we tested if niche similarities within groups were larger than between groups (Clarke 1993). The procedure started with a calculation of within- and between-group niche dissimilarities, as follows. Euclidean distances between niche positions were calculated for pairwise combinations of all possible pairs of species. The Euclidean distances – reflecting niche dissimilarity between pairs of species – were then compared within and between

taxonomic groups aggregated at the genus and family levels. When the mean within-group niche dissimilarity is smaller than between-group niche dissimilarity, this is interpreted as indicating the presence of a phylogenetic signal in climatic niche similarity; when the mean is larger, it means the phylogenetic signal is lost. Based on 999 permutations, we tested whether within- and between-group niche dissimilarities were more different than expected by chance. ANOSIM was run with the `vegan` package of R (Oksanen et al. 2009), again separately for each one of the biogeographical regions (see also Supplementary material Fig. S1 for an illustration of the procedure, and Fig. S2 for examples of two species sets).

We also calculated the amount of niche overlap along the first and second OMI axis within and between groups (families and genera). To do so, according to the protocol of the ANOSIM analysis, we calculated the pairwise niche overlap for all possible species pairs, again separately for each order and biogeographical region. Species occurring in only one grid cell have by definition a niche breadth of zero and are therefore excluded from the overlap analyses. We then grouped the pairwise niche overlap values into a within-taxon and between-taxon group (the taxon being the family or genus). For each dataset (amphibian order per region), the within- and between-group separation was done 1) for the entire species pool and 2) separately for each taxon (see also Table 2 for details). Wilcoxon rank sum tests (Hollander and Wolfe 1999) were used to test if within-group overlap was larger than between-group overlap, which would indicate a phylogenetic signal.

By applying different methods to test for phylogenetic signal we try to decrease the risk that the outcomes are biased by the uncertainties or problems of a certain method. Results indicating the same tendency for different methods (although not quantitatively comparable) would strengthen the general value of results and support stronger inference. To ensure that the results were not systematically biased by species with niche characterisations that could have arisen by chance, VCA and ANOSIM analyses were performed 1) including all species and 2) including only species with climatic niches significantly better characterised by OMI than expected by chance.

Results

In the global analyses on the family level, we found a phylogenetic signal in climatic niches for the first and second OMI axes ($p = 0.001$ and $p = 0.026$, respectively). Signal strength differed considerably among the two axes, the first axis showing a signal stronger than expected from a Brownian motion evolution model ($K = 1.45$), the second axis showing a signal lower than that ($K = 0.44$).

The analysis conducted with VCA showed that a high proportion of among-species variance in climatic niche position is explained at higher taxonomic levels (Fig. 1). Results were consistent independently of whether the whole set of species or the sub-set with significant OMI values was considered. In most cases, the analyses of the species for which climatic influences were significant showed an even stronger phylogenetic signal (Supplementary material Fig. S3); this indicates that there were no biases arising from

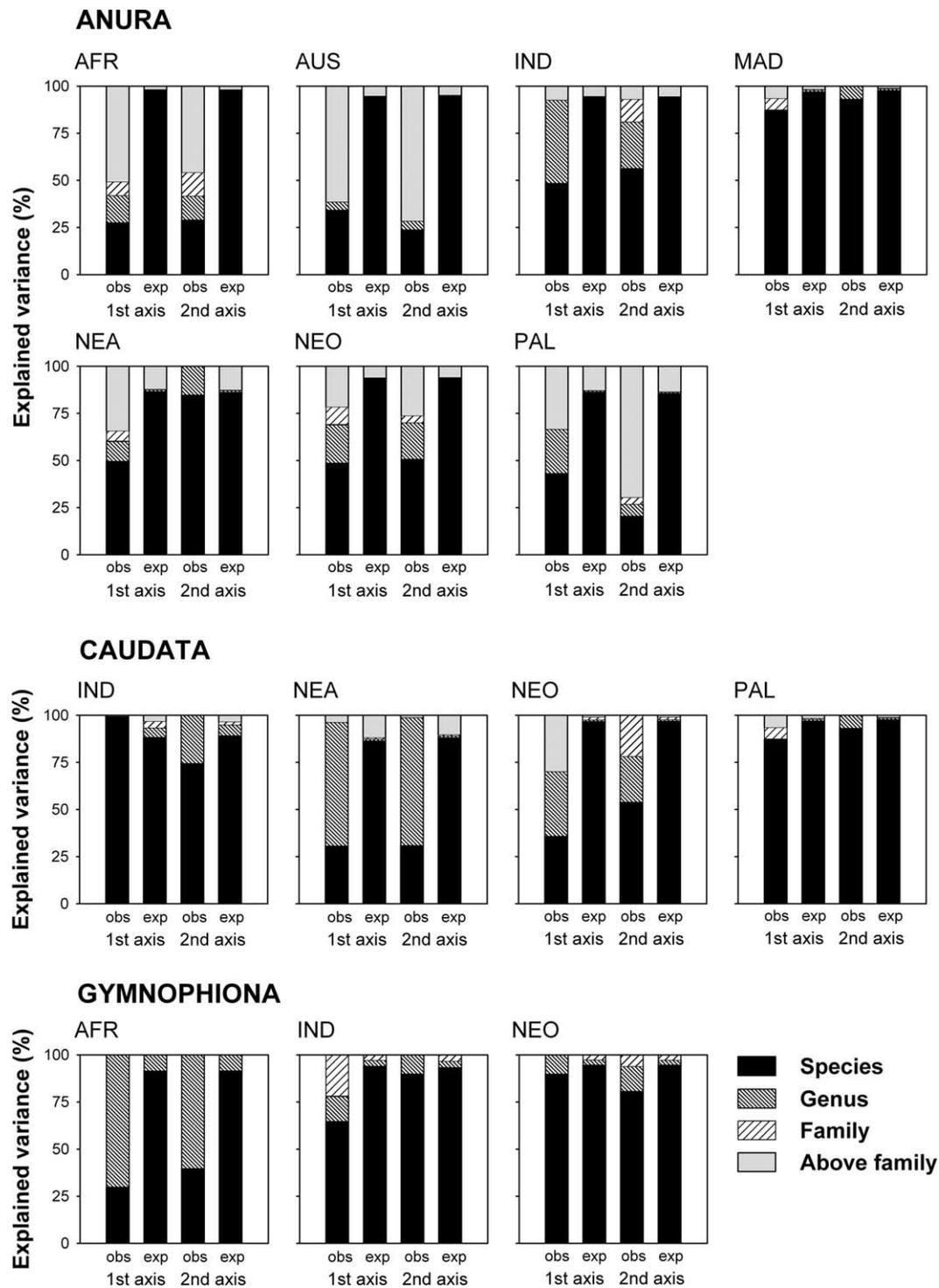


Figure 1. Results of the variance component analyses (VCA). Variance components are calculated as the proportion of among-species variance in climatic niche positions that is explained at different taxonomic levels (species, genus, family, above-family; see key). The bars are organised from lower (species) to higher (above-family) taxonomic levels. A completely black bar indicates that all variance lies at the species-level, and none is explained at higher taxonomic levels. The analyses were performed separately for the three orders and each of the biogeographical regions (AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palearctic). Within one species set (represented by a box), the first and third bars give the observed (obs) values (for the first or second OMI axis, respectively), and the second and fourth bars give the values for the according null model (exp). Null models were conducted by randomising the phylogenetic assignment for the species pool, thus representing the null expectation of no phylogenetic signal in climatic niche similarity (see text for further details).

Table 1. Climatic niche distances for amphibians on the family and genus levels within different biogeographical regions.

	n	Mean niche distance*				ANOSIM†	
		Within	SD	Between	SD	r _{ANOSIM}	p
Families							
Anura							
AFR	16	2.04	1.18	2.37	1.35	0.14	< 0.001
AUS	9	2.03	1.64	3.18	1.87	0.35	< 0.001
IND	12	2.42	1.42	2.50	1.39	0.034	< 0.001
MAD	3	1.65	0.94	1.83	1.03	0.10	0.003
NEA	8	2.31	1.41	2.35	1.35	0.022	0.143
NEO	19	2.08	1.41	2.37	1.54	0.11	< 0.001
PAL	11	2.37	1.47	2.73	1.57	0.14	< 0.001
Caudata							
IND	2	1.53	0.89	1.37	0.79	−0.10	0.785
NEA	7	2.46	1.73	2.40	1.56	−0.0045	0.522
NEO	3	2.13	1.48	2.87	1.77	0.25	< 0.001
PAL	4	2.92	1.88	3.61	2.02	0.21	< 0.001
Gymnophiona							
AFR	–	–	–	–	–	–	–
IND	2	2.58	1.55	2.56	1.51	−0.0040	0.44
NEO	2	2.14	1.26	2.24	1.50	0.0012	0.462
Genera							
Anura							
AFR	50	1.96	1.12	2.35	1.34	0.16	< 0.001
AUS	37	2.69	1.84	2.92	1.88	0.074	0.002
IND	67	2.04	1.43	2.50	1.39	0.19	< 0.001
MAD	16	1.62	0.94	1.74	0.99	0.069	0.02
NEA	17	2.37	1.51	2.34	1.35	−0.0042	0.454
NEO	126	1.98	1.51	2.33	1.52	0.16	< 0.001
PAL	41	2.08	1.50	2.69	1.56	0.25	< 0.001
Caudata							
IND	6	1.43	0.78	1.47	0.87	0.0089	0.445
NEA	20	1.37	1.22	2.57	1.66	0.44	< 0.001
NEO	9	1.69	1.31	2.38	1.57	0.28	< 0.001
PAL	17	2.31	1.78	3.42	1.99	0.35	< 0.001
Gymnophiona							
AFR	7	1.12	1.17	2.90	1.67	0.62	< 0.001
IND	4	2.66	1.61	2.51	1.49	−0.052	0.725
NEO	10	2.12	1.32	2.17	1.31	0.029	0.321

*Mean distances were calculated by averaging all Euclidean distances in niche positions in climatic space between species pairs within a family or genus (Within) or between species pairs that do not share the same family or genus (Between). Furthermore, we give the respective standard deviations (SD) and the number of families or genera (n) within each region used in the analysis. For further details on how the distance values were calculated, see Supplementary material Fig. S1.

†The ANOSIM statistic (r_{ANOSIM}) and the associated p values give estimations on the likelihood that the observed differences were significantly different from 0. (For more details, see text.) Values are given separately for the three amphibian orders and for each biogeographical region. ANOSIM values showing significantly larger niche distances for between-group than for within-group species pairs are indicated in bold. Note that the analyses could not be conducted on the family level for Afrotropical Gymnophiona, as all species occurring there belong to the same family.

AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palaeartic.

potentially unreliable niche characterisations. Therefore, results for the full analyses are presented. The observed proportions of explained variance at higher taxonomic levels were consistently larger than those yielded by the null models, which simulated the case of no phylogenetic signal (the only exception were Indo-Malayan Caudata). However, when comparing different regions and orders, we found considerable variation (Fig. 1): for Anura, variance explained above the species level ranged from 7% (Madagascar) up to 76% (Australasia), with most values exceeding the mean value of 49% (averaged across all regions and both OMI ordination axes). For Caudata, values ranged from 0% (Indo-Malay) to 87% (Palaeartic), and the mean was 50%. For Gymnophiona, extreme values for niche variance explained above the species level were

10% (Indo-Malay and Neotropics) and 70% (Afrotropics), with a mean of 34%.

Tests of niche differences with ANOSIM revealed that within-group niche distances were significantly smaller than between-group distances in the vast majority of cases (Table 1). This outcome matches the findings of the VCA, also indicating the presence of a phylogenetic signal in climatic niches at both the genus and the family levels for most regions and taxa. Again, running the analyses with all species or using only those species for which OMI performed significantly well rendered highly consistent results (Supplementary material Table S3). Despite the consistent trend of within-group niche distances being smaller than between-group distances, we found a small number of cases deviating from the overall pattern. At the

Table 2. Climatic niche overlap analyses for amphibians on the family and genus levels, along the first and second OMI axes (OMI1 and OMI2), within different biogeographical regions.

	n*	OMI1 Pooled†	n _{W>B} ‡	n _{W<B} ‡	OMI2 Pooled	n _{W>B}	n _{W<B}
Families							
Anura							
AFR	15 (2)	W > B***	10 (0)	0 (5)	W > B***	6 (4)	1 (4)
AUS	9 (0)	W > B***	7 (1)	0 (1)	W > B***	6 (2)	0 (1)
IND	12 (1)	W > B***	7 (1)	2 (2)	W > B***	7 (1)	1 (3)
MAD	3 (2)	W < B (n.s.)	0 (0)	0 (3)	W > B***	1 (1)	1 (0)
NEA	8 (3)	W > B**	1 (2)	0 (5)	W > B (n.s.)	0 (3)	0 (5)
NEO	19 (1)	W > B***	8 (3)	3 (5)	W > B (n.s.)	9 (1)	3 (6)
PAL	11 (3)	W > B (n.s.)	3 (4)	1 (3)	W > B**	4 (2)	3 (2)
Caudata							
IND	2 (1)	W > B*	1 (1)	0 (0)	W > B (n.s.)	0 (1)	0 (1)
NEA	7 (1)	W < B***	2 (3)	1 (1)	W < B***	3 (2)	1 (1)
NEO	2 (1)	W > B***	2 (0)	0 (0)	W < B (n.s.)	0 (1)	0 (1)
PAL	4 (1)	W > B*	1 (1)	0 (2)	W > B***	2 (0)	0 (2)
Gymnophiona							
IND	1 (1)	W < B (n.s.)	0 (0)	0 (1)	W < B (n.s.)	0 (0)	0 (1)
NEO	2 (0)	W > B (n.s.)	0 (1)	0 (1)	W > B***	1 (0)	0 (1)
Genera							
Anura							
AFR	47 (34)	W > B***	16 (18)	0 (13)	W > B***	12 (10)	2 (23)
AUS	34 (17)	W > B***	17 (7)	1 (9)	W > B***	9 (11)	1 (13)
IND	60 (32)	W > B***	22 (21)	0 (17)	W > B***	25 (17)	4 (14)
MAD	16 (8)	W > B (n.s.)	3 (2)	2 (9)	W > B***	3 (3)	1 (9)
NEA	15 (15)	W > B*	2 (6)	0 (7)	W > B (n.s.)	4 (2)	0 (9)
NEO	112 (52)	W > B***	39 (27)	4 (42)	W > B***	32 (34)	5 (41)
PAL	38 (18)	W > B***	5 (19)	0 (14)	W > B***	8 (13)	1 (16)
Caudata							
IND	5 (2)	W > B (n.s.)	0 (3)	0 (2)	W > B (n.s.)	0 (3)	0 (2)
NEA	18 (7)	W > B***	4 (6)	1 (7)	W < B*	6 (3)	1 (8)
NEO	7 (6)	W > B***	5 (0)	0 (2)	W > B*	0 (4)	0 (3)
PAL	16 (13)	W > B***	4 (2)	0 (10)	W > B***	4 (1)	0 (11)
Gymnophiona							
AFR	4 (7)	W > B (n.s.)	0 (2)	0 (2)	W < B (n.s.)	0 (0)	0 (4)
IND	2 (3)	W < B (n.s.)	1 (0)	0 (1)	W > B (n.s.)	1 (1)	0 (0)
NEO	9 (7)	W > B***	1 (1)	0 (7)	W > B***	2 (2)	0 (5)

*Number of groups (families or genera, respectively) included in the overlap analyses. Values in brackets give the number of groups for which tests could not be performed (e.g. groups that included a single species only or that only consisted of species occurring in a single grid cell).

†For the pooled comparisons, all within- (W) and all between-group (B) values of niche overlap (families or genera, respectively) were pooled and then compared using Wilcoxon rank sum tests. “W > B” indicates that within-group overlap was larger than between-group overlap (which would indicate a phylogenetic signal). Asterisks indicate significance levels, ***p < 0.001, **p < 0.01, *p < 0.05, n.s., not significant.

‡Numbers of groups (families or genera) showing within-group niche overlap being larger or smaller than between-group overlap (numbers in brackets indicate the number of within- or between-group comparisons that were not significant).

AFR, Afrotropics; AUS, Australasia; IND, Indo-Malay; MAD, Madagascar; NEA, Nearctic; NEO, Neotropics; PAL, Palearctic.

family level, 3 out of 13 analyses showed larger within-group distances than between-group distances. At the genus level, within-group distances were larger than between-group distances only for 2 out of 14 data sets (see Table 2 for details).

Niche overlap analyses showed that in the majority of cases within-group overlap was larger than between-group overlap (Table 2). In the comparison of pooled within- and between groups, within-family overlap was significantly larger than between-family overlap in 8 out of 13 datasets along the first OMI axis and in 7 out of 13 datasets along the second OMI axis. On the genus level, within-group overlap was significantly larger than between-group overlap in 10 out of 14 datasets along the first OMI axis and in 9 out of 14 datasets along the second OMI axis. Comparing within- and between-group overlap separately for each family or genus per region, still the majority of datasets

showed the overall pattern. As for the other analyses, the results varied considerably among regions, taxa, and the two OMI axes.

Discussion

Our analyses provide evidence in support of the idea that phylogenetically related species have similar realised climatic niches, even though the strength of the phylogenetic signal varied considerably across amphibian orders and biogeographical regions. To our knowledge, this is the first study investigating phylogenetic niche signals across an entire class of organisms on a global scale, nevertheless accounting for regional variation. Thus it provides a starting point to address questions related to evolutionary niche dynamics of amphibians.

Overall, we found a phylogenetic signal in amphibians' realised climatic niches, as was first shown at the family level by Blomberg's randomisation test and K statistic. However, the strength of the signal differed considerably for the two niche axes. Both the VCA and the niche overlap analyses, which were done separately for the different regions and orders, supported the existence of a phylogenetic niche signal among amphibians in the majority of the datasets. Applying a different methodology (ANOSIM) again supported the general finding of a phylogenetic signal. Admittedly, the values for the ANOSIM statistic (r_{ANOSIM} , Table 1) are relatively low in many cases, even though the p values indicated statistical significance. These low values may often be attributable to the high species numbers in some regions (e.g. Neotropical or Indo-Malayan Anura), resulting in high significance levels even though the differences might be weak. However, the general tendency confirmed by four different methods and across the majority of the species sets analysed supports the conclusion that the trend is robust.

Only a few studies have measured phylogenetic niche signals of clades at large geographical scales. For European plants, Prinzing et al. (2001) found that 28–75% of among-species niche variance (niche positions along environmental gradients) was explained at higher taxonomic levels. This result is roughly concordant with our findings. For central European spiders, 20–40% of the variance in niche position in shading and moisture was explained at higher taxonomic levels (Entling et al. 2007). However, the spiders' phylogenetic signal in ecological traits was consistently lower than in morphological traits (>70% of morphological variance explained above the species level). For dietary niches of European birds, Brändle et al. (2002) found that about 70% of the variance was explained at higher taxonomic levels. Even though there are a limited number of studies to compare our results with, our findings are consistent with results previously reported for phylogenetic signals in climatic niches, and also with those in morphological traits or dietary niches.

Despite an overall and robust trend of detection of phylogenetic signals in climatic niches, we found considerable variation in the strength of the signal among biogeographical regions and the three amphibian orders. Further analyses are needed to examine such variation in detail. In the context of this study we can only discuss some of the limitations of the analysis and some of the most striking findings.

As mentioned before our analyses are based on characterizations of species realised climatic niches. Such niches are incomplete representations of species' true limits of tolerance to climate variables and so cannot entirely portray fundamental climatic niches (Soberón 2007). Obviously the possibility of existence of strong mismatches between the observed realised and the fundamental niches decrease the likelihood of detecting a phylogenetic (i.e. evolutionary) signal and it is impossible to rule out that such mismatches may have caused weak phylogenetic signal in some of our data sets. Nevertheless, given 1) this conceptual mismatch between realised and fundamental climatic niches, and 2) that except for the global family-level analysis we use a

taxonomy (albeit based on recent phylogenies) that introduced further uncertainties (see below), one could expect that any phylogenetic signal would be obscured. Given this potential for ambiguity, identifying a consistent pattern across most of the regions even with the data and methods used rather strengthens the conclusion that a phylogenetic signal exists in amphibian climatic niches.

However, the coarse spatial resolution of the data may on the other hand weaken the information content of the results. Many of the grid cells (which cover areas of almost 50 000 km² at the equator) contain strong climatic gradients and exceed the range of many species. Assigning closely related species within one grid cell to the same climatic niche although they actually have very different climatic preferences could inflate the phylogenetic signal. In fact, within areas of rather small extent, closely related species may show strong tendencies of niche divergence (Graham et al. 2004, Knouft et al. 2006, Kozak and Wiens 2007). However, an inflation of the phylogenetic signal should not occur if such species with different niches within the same grid cell belong to different genera or families – assigning them to the same niche position would in this case rather weaken the phylogenetic signal in our analyses. In any case, we cannot fully discard the potential inflation of the phylogenetic signal's strength here, but we emphasize that with our analyses we do not and cannot unravel complex evolutionary mechanisms such as speciation (Kozak and Wiens 2006) or the phylogenetic structuring of local or regional communities (Webb et al. 2002), all of which require data at a much finer spatial and phylogenetic resolution.

Besides methodological factors, geographic, taxonomic and climatic idiosyncrasies contribute to the observed variation in the strength of the phylogenetic signal. For Anura, e.g. only Nearctic genera showed a result contradictory to the overall pattern of the ANOSIM analysis, the within-group similarity being slightly lower than the between-group similarity. This result was driven by the low niche similarity within the genus *Lithobates*, which is the largest genus in the Nearctic Anura (30 species). An examination of the different species reveals that some are widely distributed (e.g. *L. sylvatica*, *L. catesbeiana*), but others (e.g. *L. dunni*, *L. onca*, *L. sevosus*) have small ranges located in very different regions within the Nearctic and thus have very different climatic niches. This combination of high species richness and a high within-genus variety of climatic niches may have contributed to the low phylogenetic signal in the Nearctic Anuran genera. Furthermore, taxonomic misclassifications may also influence the failure of detection of a phylogenetic signal (Blomberg et al. 2003). This is a general issue for our analyses, of course, but may be particularly important for Nearctic Anura, as classification of *Lithobates* as a genus remains controversial (Hillis and Wilcox 2005, Frost et al. 2006, Che et al. 2007).

A rather weak phylogenetic signal was also detected at the family level of Nearctic Caudata as indicated by the VCA and the niche overlap analysis (Fig. 1, Table 2). Here, the family Plethodontidae comprises more than three times as many species as the other families combined (143 vs 43 species). The highly diverse Plethodontid salamanders

occupy a great variety of niches (Vieites et al. 2007), whereas the niches of species within each Plethodontid genus are very similar (e.g. for *Hydromantes*, *Desmognathus*, or *Batrachoseps*). Indo-Malayan Caudata showed no clear pattern, possibly because of the low species richness of Caudata in this region (25 species) and because for many species the distributions used represent only a small part of their entire distribution. Thus, this species set is rather negligible. However, we stress that in the vast majority of cases, the total ranges of species are contained within one biogeographical region.

Some authors question whether establishing the existence of a phylogenetic signal is a useful pursuit (Wiens and Graham 2005, Wiens 2008). In parallel, calls for “further research into the extent and occurrence of PNC [phylogenetic niche conservatism], and phylogenetic signal more generally” (Losos 2008a, p. 1001) are also common. Testing for the existence of a phylogenetic signal is important as the assumption underlies several types of studies, such as the investigation of diversity gradients and the building of species distribution models for climate change prediction, and because its generality is still under debate.

Although the aim of our study was to test for a phylogenetic signal in climatic niches, our analyses provide a baseline for further investigations on climatic niche conservatism in amphibians. Phylogenetic niche conservatism can be defined as the tendency of closely related species to be more similar than expected based on phylogenetic relationships (Losos 2008a); put more broadly, it is the temporal constancy of the ecological niche (Pearman et al. 2008, Nogués-Bravo 2009). Niche conservatism is a topic of recent growing interest (Peterson et al. 1999, Prinzing et al. 2001, Wiens 2004, Wiens and Graham 2005, Kozak and Wiens 2006, Freckleton and Jetz 2009, Vieites et al. 2009a, Dormann et al. 2010). Overall, its generality or even existence remains a matter of controversial debate (Losos 2008a, Pearman et al. 2008). Based on our findings, we can draw two conclusions with regard to phylogenetic niche conservatism and temporal niche constancy in amphibians. First, as recently pointed out by Losos (2008a, p. 997), a “lack of phylogenetic signal is sufficient to indicate that PNC does not occur.” Thus, based on our detection of a phylogenetic signal in climatic niches, the niche conservatism hypothesis cannot be rejected. Second, for several regions, we found high values of among-species niche variance explained above the family level (Afrotropical and Palearctic Anura: >30%, Australasian Anura: >60%). This result lends support to the suggestion of the existence of considerable constancy in climatic niches for a period of time that reaches back to the late Cretaceous or even earlier (>65 Mya ago), when many of the above-family splits took place (Roelants et al. 2007). However, further studies are needed using finely resolved phylogenetic and climatic data to test for the occurrence and strength of phylogenetic conservatism in amphibian climatic niches.

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References

- Ackerly, D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. – *Proc. Nat. Acad. Sci. USA* 106: 19699–19706.
- Araújo, M. B. and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. – *J. Biogeogr.* 33: 1677–1688.
- Araújo, M. B. et al. 2006. Climate warming and the decline of amphibians and reptiles in Europe. – *J. Biogeogr.* 33: 1712–1728.
- Araújo, M. B. et al. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. – *Ecography* 31: 8–15.
- Austin, M. P. et al. 1990. Measurement of the realized qualitative niche – environmental niches of 5 *Eucalyptus* species. – *Ecol. Monogr.* 60: 161–177.
- Blackburn, D. C. 2008. Biogeography and evolution of body size and life history of African frogs: phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. – *Mol. Phylogenet. Evol.* 49: 806–826.
- Blomberg, S. P. and Garland, T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. – *J. Evol. Biol.* 15: 899–910.
- Blomberg, S. P. et al. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. – *Evolution* 57: 717–745.
- Botkin, D. B. et al. 2007. Forecasting the effects of global warming on biodiversity. – *Bioscience* 57: 227–236.
- Brändle, M. et al. 2002. Dietary niche breadth for central European birds: correlations with species-specific traits. – *Evol. Ecol. Res.* 4: 643–657.
- Broennimann, O. et al. 2007. Evidence of climatic niche shift during biological invasion. – *Ecol. Lett.* 10: 701–709.
- Carey, C. and Alexander, M. A. 2003. Climate change and amphibian declines: is there a link? – *Divers. Distrib.* 9: 111–121.
- Che, J. et al. 2007. Phylogeny of Raninae (Anura: Ranidae) inferred from mitochondrial and nuclear sequences. – *Mol. Phylogenet. Evol.* 43: 1–13.
- Chessel, D. et al. 2004. The ade4 package – I – one-table methods. – *R News* 4: 5–10.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. – *Aust. J. Ecol.* 18: 117–143.
- Colwell, R. K. and Rangel, T. F. 2009. Hutchinson’s duality: the once and future niche. – *Proc. Nat. Acad. Sci. USA* 106: 19651–19658.
- Corey, S. J. and Waite, T. A. 2008. Phylogenetic autocorrelation of extinction threat in globally imperilled amphibians. – *Divers. Distrib.* 14: 614–629.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. – John Murray.
- Dolédéc, S. et al. 2000. Niche separation in community analysis: a new method. – *Ecology* 81: 2914–2927.
- Dormann, C. F. et al. 2010. Evolution of climate niches in European mammals? – *Biol. Lett.* 6: 229–232.

- Duellman, W. E. 1999. Patterns of distribution of amphibians – a global perspective. – John Hopkins Univ. Press.
- Entling, W. et al. 2007. Niche properties of central European spiders: shading, moisture and the evolution of the habitat niche. – *Global Ecol. Biogeogr.* 16: 440–448.
- Freckleton, R. P. and Jetz, W. 2009. Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. – *Proc. R. Soc. B* 276: 21–30.
- Frost, D. R. 2007. Amphibian species of the world: an online reference. Version 5.1. – <<http://research.amnh.org/herpetology/amphibia/index.php>>.
- Frost, D. R. et al. 2006. The amphibian tree of life. – *Bull. Am. Mus. Nat. Hist.*, American Museum of Natural History.
- Garland, T. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. – *Am. Nat.* 140: 509–519.
- Graham, C. H. et al. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. – *Evolution* 58: 1781–1793.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Hillis, D. M. and Wilcox, T. P. 2005. Phylogeny of the New World true frogs (*Rana*). – *Mol. Phylogenet. Evol.* 34: 299–314.
- Hollander, M. and Wolfe, D. A. 1999. Nonparametric statistical methods. – Wiley.
- Hutchinson, G. E. 1957. Population studies – animal ecology and demography – concluding remarks. – *Cold Spring Harbor Symp. Quant. Biol.* 22: 415–427.
- IUCN 2004. Global amphibian assessment. – <www.globalamphibians.org/>.
- Kembel, S. W. et al. 2009. picante: R tools for integrating phylogenies and ecology. – R package ver. 0.7-0.
- Knouft, J. H. et al. 2006. Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. – *Ecology* 87: S29–S38.
- Kozak, K. H. and Wiens, J. J. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. – *Evolution* 60: 2604–2621.
- Kozak, K. H. and Wiens, J. J. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. – *Proc. R. Soc. B* 274: 2995–3003.
- Losos, J. B. 2008a. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. – *Ecol. Lett.* 11: 995–1003.
- Losos, J. B. 2008b. Rejoinder to Wiens (2008): phylogenetic niche conservatism, its occurrence and importance. – *Ecol. Lett.* 11: 1005–1007.
- Nogués-Bravo, D. 2009. Predicting the past distribution of species climatic niches. – *Global Ecol. Biogeogr.* 18: 521–531.
- Oksanen, J. et al. 2009. vegan: community ecology package. – R package ver. 1.15-2.
- Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. – *Bioscience* 51: 933–938.
- Paradis, E. et al. 2004. APE: analyses of phylogenetics and evolution in R language. – *Bioinformatics* 20: 289–290.
- Pearman, P. B. et al. 2008. Niche dynamics in space and time. – *Trends Ecol. Evol.* 23: 149–158.
- Peterson, A. T. et al. 1999. Conservatism of ecological niches in evolutionary time. – *Science* 285: 1265–1267.
- Prinzing, A. et al. 2001. The niche of higher plants: evidence for phylogenetic conservatism. – *Proc. R. Soc. B* 268: 2383–2389.
- R Development Core Team 2008. R: a language and environment for statistical computing. – R Foundation for Statistical Computing.
- Revell, L. J. et al. 2008. Phylogenetic signal, evolutionary process, and rate. – *Syst. Biol.* 57: 591–601.
- Rheindt, F. E. et al. 2004. Rapidly evolving traits and the comparative method: how important is testing for phylogenetic signal? – *Evol. Ecol. Res.* 6: 377–396.
- Roelants, K. et al. 2007. Global patterns of diversification in the history of modern amphibians. – *Proc. Nat. Acad. Sci. USA* 104: 887–892.
- Santos, J. C. et al. 2009. Amazonian amphibian diversity is primarily derived from Late Miocene Andean lineages. – *PLoS Biol.* 7: 448–461.
- Slater, P. L. 1858. On the general geographical distribution of the members of the class aves. – *J. Proc. Linn. Soc. (Zool.)* 2: 130–145.
- Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and assumptions. – *Proc. Nat. Acad. Sci. USA* 106: 19644–19650.
- Thuiller, W. et al. 2004. Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. – *Ecology* 85: 1688–1699.
- Venables, W. N. and Ripley, B. D. 1999. Modern applied statistics with S-Plus. – Springer.
- Veites, D. R. et al. 2007. Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. – *Proc. Nat. Acad. Sci. USA* 104: 19903–19907.
- Veites, D. R. et al. 2009a. Reconstruction of the climate envelopes of salamanders and their evolution through time. – *Proc. Nat. Acad. Sci. USA* 106: 19715–19722.
- Veites, D. R. et al. 2009b. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. – *Proc. Nat. Acad. Sci. USA* 106: 8267–8272.
- Wallace, A. R. 1876. The geographical distribution of animals. – Macmillan.
- Webb, C. O. et al. 2002. Phylogenies and community ecology. – *Annu. Rev. Ecol. Syst.* 33: 475–505.
- Wells, K. W. 2007. The ecology and behavior of Amphibians. – Univ. of Chicago Press.
- Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. – *Evolution* 58: 193–197.
- Wiens, J. J. 2007. The amphibian tree of life (book review). – *Q. Rev. Biol.* 82: 55–56.
- Wiens, J. J. 2008. Commentary on Losos (2008): niche conservatism déjà vu. – *Ecol. Lett.* 11: 1004–1005.
- Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – *Trends Ecol. Evol.* 19: 639–644.
- Wiens, J. J. and Graham, C. H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. – *Annu. Rev. Ecol. Evol. Syst.* 36: 519–539.

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