SPECIAL PAPER

Global patterns of amphibian phylogenetic diversity

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ABSTRACT

Aim Phylogenetic diversity can provide insight into how evolutionary processes may have shaped contemporary patterns of species richness. Here, we aim to test for the influence of phylogenetic history on global patterns of amphibian species richness, and to identify areas where macroevolutionary processes such as diversification and dispersal have left strong signatures on contemporary species richness.

Location Global; equal-area grid cells of approximately 10,000 km^2.

Methods We generated an amphibian global supertree (6111 species) and repeated analyses with the largest available molecular phylogeny (2792 species). We combined each tree with global species distributions to map four indices of phylogenetic diversity. To investigate congruence between global spatial patterns of amphibian species richness and phylogenetic diversity, we selected Faith's phylogenetic diversity (PD) index and the total taxonomic distinctness (TTD) index, because we found that the variance of the other two indices we examined (average taxonomic distinctness and mean root distance) strongly depended on species richness. We then identified regions with unusually high or low phylogenetic diversity given the underlying level of species richness by using the residuals from the global relationship of species richness and phylogenetic diversity.

Results Phylogenetic diversity as measured by either Faith's PD or TTD was strongly correlated with species richness globally, while the other two indices showed very different patterns. When either Faith's PD or TTD was tested against species richness, residuals were strongly spatially structured. Areas with unusually low phylogenetic diversity for their associated species richness were mostly on islands, indicating large radiations of few lineages that have successfully colonized these archipelagos. Areas with unusually high phylogenetic diversity were located around biogeographic contact zones in Central America and southern China, and seem to have experienced high immigration or *in situ* diversification rates, combined with local persistence of old lineages.

Main conclusions We show spatial structure in the residuals of the relationship between species richness and phylogenetic diversity, which together with the positive relationship itself indicates strong signatures of evolutionary history on contemporary global patterns of amphibian species richness. Areas with unusually low and high phylogenetic diversity for their associated richness demonstrate the importance of biogeographic barriers to dispersal, colonization and diversification processes.

Keywords

Amphibians, biogeography, global species richness, mean root distance, phylogenetic diversity, taxonomic distinctness.

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INTRODUCTION

It is increasingly recognized that macroevolutionary processes, such as diversification and dispersal, may leave a detectable signal in contemporary large-scale patterns of species richness beyond the signal given by contemporary processes (Ricklefs, 2004; Wiens & Donoghue, 2004). Proxy measures of contemporary processes, for example available environmental energy, have been shown to correlate well statistically with patterns of species richness (Hawkins et al., 2003). However, such correlative models typically leave huge regions as statistical outliers, in most cases tropical mountains with exceptionally high richness (Rahbek & Graves, 2001) and/or regions containing many small-ranged species (Jetz & Rahbek, 2002). The considerable amount of variation in species richness which is left unexplained by contemporary factors has been attributed to effects of phylogenetic history, i.e. to effects of macroevolutionary processes such as diversification and dispersal (Rahbek & Graves, 2001; Currie et al., 2004; Rahbek et al., 2007). Whereas evidence for the influence of post-glacial dispersal limitation on current species ranges is mounting (e.g. Normand et al., 2011), effects of regionally differing speciation and extinction rates on contemporary richness patterns are more contentious (Ricklefs, 2006; Weir & Schluter, 2007; Rabosky, 2009).

Phylogenetic diversity can provide information about the diversification history and past dispersal events which may have shaped contemporary species assemblages (Faith, 1992; Fjeldså & Rahbek, 2006; Davies et al., 2007; Davies & Buckley, 2011). For example, if the phylogenetic diversity within an assemblage reflects the number of phylogenetic lineages present, then species-rich areas exhibiting low underlying phylogenetic diversity apparently consist of large radiations of few lineages. This pattern suggests that diversity in these assemblages was generated by in situ diversification after few initial immigration events, and that other lineages from the same taxon have not successfully colonized. Conversely, if a species-rich assemblage contains high phylogenetic diversity due to the presence of many phylogenetic lineages, either high in situ diversification of multiple lineages or immigration of multiple lineages (probably in conjunction with high diversification) has maintained this diversity over time. If phylogenetic diversity is based on a phylogeny with divergence times and reflects not just the number of lineages but also their age, then inferences may even be made about speciation and extinction rates separately instead of net diversification (Davies et al., 2007; Davies & Buckley, 2011).

Here, we use the relationship between species richness and phylogenetic diversity together with the spatial pattern of the residuals of this relationship to test the hypothesis that phylogenetic history has left a detectable signature on patterns of contemporary species richness. Species richness and phylogenetic diversity are usually positively correlated (e.g. Rodrigues & Gaston, 2002; Faith, 2008; Morlon et al., 2011). However, this correlation arises at least partly from the way most indices of phylogenetic diversity are calculated, so a simple correlation of phylogenetic history and species richness does not imply a causal relationship. Instead, we aim to investigate the global spatial pattern of the residuals of this relationship between species richness and phylogenetic diversity (Forest et al., 2007; Davies et al., 2008). If residuals are spatially random, then phylogenetic history either perfectly explains patterns of species richness, or it does not influence patterns of richness at all. These cases can be distinguished by the congruence between spatial patterns of species richness and phylogenetic diversity. On the contrary, a non-random spatial pattern of the residuals would indicate some influence of spatially heterogeneous phylogenetic history on contemporary patterns of species richness, with areas of unusually high and low phylogenetic diversity where diversification and dispersal have differed from a global norm.

We assess global congruence between species richness and phylogenetic diversity for approximately 95% of all amphibian species, and test whether residuals from the relationship of species richness and phylogenetic diversity show strong spatial patterning. These ideas have not been explicitly tested for amphibians, although their species richness patterns have been argued to depend on contemporary environment as well as on historical processes such as diversification or Quaternary climate change (Buckley & Jetz, 2007; Araújo et al., 2008). Previous studies of global patterns of phylogenetic or taxonomic diversity have focused on mammals (Davies et al., 2008; Fritz & Purvis, 2010; Safi et al., 2011) or birds (Davies et al., 2007; Thomas et al., 2008). However, amphibian species richness patterns may be more likely to preserve signals of macroevolutionary processes because amphibian species have on average smaller ranges than other vertebrates (Grenyer et al., 2006) and are therefore thought to be slower dispersers in general. Amphibian phylogenetic history has been discussed recently, in particular with reference to the latitudinal diversity gradient and phylogenetic signal in climatic niches (Wiens, 2007; Algar et al., 2009; Hof et al., 2010; Olalla-Tárraga et al., 2011).

We assembled a global amphibian phylogeny from taxonomic information and molecular studies by hand, but additionally performed all analyses with the most comprehensive molecular phylogeny of amphibians available (Pyron & Wiens, 2011). These phylogenies were combined with a global species distribution dataset (IUCN, 2008) to compare global patterns of species richness with global patterns for each of the four indices of phylogenetic diversity. Because many indices of phylogenetic diversity with different properties are available (Helmus et al., 2007; Schweiger et al., 2008), we explored four which represent different aspects of phylogenetic diversity.

The aim of our study was to test whether there is a global correlation between species richness and phylogenetic diversity, and, more importantly, whether residuals from this relationship show spatial structure. The identification of areas which contain unusually high or low phylogenetic diversity for their underlying species richness would indicate that macroevolutionary processes as expressed by phylogenetic history have left a detectable signal in contemporary patterns of global amphibian species richness.

MATERIALS AND METHODS

We adjusted the amphibian distribution maps published by the Global Amphibian Assessment (IUCN, 2008) to the global taxonomy of Frost (2009), excluding 'incertae sedis', 'klepton', and undescribed taxa and ranges classified as 'introduced' or 'uncertain/introduced'. The final distribution dataset contained 6111 species distributions and was sampled into a global equal-area grid (cell size approximately 100 km × 100 km; see also Orme et al., 2005). We defined land grid cells as those containing > 25% land, which resulted in a global grid of 16,685 land cells. All statistical analyses were performed in R 2.10.1 (R Development Core Team, 2009), utilizing functions in the CAIC package (Orme et al., 2009).

Our supertree phylogeny was compiled by hand from taxonomic information and molecular phylogenetic studies to genus level; details are described in Appendix S1 (see Supporting Information). The family backbone followed Frost et al. (2006) with many changes and updates, and we followed a range of published phylogenies for genus relationships within families (Table S1 in Appendix S1). The final phylogeny was an undated genus-level topology which conformed to Frost's (2009) taxonomy and was 85% resolved (509 genera; Fig. S1 in Appendix S2). Species were then appended as within-genus polytomies, assuming genus monophyly (Appendix S1). The final species-level tree contained all 6111 amphibian species which were in our distribution dataset, and was 13% resolved. Despite the overall low resolution, our phylogeny contained 434 nodes above the genus level. It was therefore much more informative than the classic systematic categories (three orders, 59 families), which have previously been used for the investigation of historical components of diversity (e.g. Thomas et al., 2008).

In order to compare results of our supertree with those using a phylogeny estimated directly from one molecular dataset, we reran analyses with a recently published large-scale phylogeny (Pyron & Wiens, 2011). This phylogeny (hereafter referred to as the Pyron & Wiens tree) contained 2792 amphibian species that we had distribution data for, i.e. 46% of the species in our supertree. We ran analyses with the two trees because both have different strengths: global patterns with our supertree of all species are not compromised by uneven spatial sampling, while the Pyron & Wiens tree contains higher phylogenetic resolution (the best maximum likelihood tree from Pyron & Wiens we used contained no polytomies).

All branch lengths were set to one for the analyses (see discussion and Humphries et al., 1995). For each land cell, we calculated four indices of phylogenetic diversity for each of the two phylogenies because the different indices reflect different aspects of phylogenetic diversity: (1) phylogenetic diversity following Faith (1992), hereafter termed Faith's PD, i.e. the total sum of phylogenetic branch lengths representing the species occurring within an area, or the length of the minimum spanning tree; (2) average taxonomic distinctness (AvTD), the average of the phylogenetic distances between all species pairs within an area (Clarke & Warwick, 1998); (3) total taxonomic distinctness (TTD), the sum of these pairwise distances (Clarke & Warwick, 1998; Williams, 1998); and (4) mean root distance (MRD), the average of the inverse phylogenetic distances measured between each species and the most recent common ancestor for the whole taxon, i.e. between each tip and the root of the global phylogeny (Williams, 1998).

Schweiger et al. (2008) compared the first three of these indices in a simulation study, and concluded that Faith's PD and TTD are highly dependent on species richness, but they do not increase if species are lost or decrease if species are added, all else being equal. On the contrary, AvTD and MRD are independent of species richness due to averaging of calculated quantities across species, but they change if species are lost or added, all else being equal. The simulation study recommended TTD and AvTD for their high sensitivity to changes in community composition (Schweiger et al., 2008), but Faith's PD is the most widely known and used index of phylogenetic diversity, and it may reflect the number of lineages best (e.g. Rodrigues & Gaston, 2002; Faith, 2008; Morlon et al., 2011). We also included MRD here because on a phylogeny with equal branch lengths it is thought to represent a rough approximation of the average age of assemblages or 'derivedness' of their lineages (Williams, 1998; Hawkins et al., 2006). Because we were interested in the phylogenetic diversity contained just by the species in each cell, Faith's PD as calculated here did not include the branch length from the most recent common ancestor of all species in the cell back to the root of all amphibians (see Rodrigues & Gaston, 2002 for discussion). Instead, we only included the immediate stem branch leading to the most recent common ancestor of all species in the cell (unless this ancestor was the root of the global amphibian phylogeny).

We used Pearson correlation coefficients to assess spatial congruence among global patterns of the different phylogenetic diversity indices, and with species richness across grid cells. Due to spatial autocorrelation, an inherent feature of such biogeographic patterns, we do not report P-values for these coefficients (Legendre, 1993; Rahbek & Graves, 2000). In order to model the respective relationships of the different measures of phylogenetic diversity with species richness, we used local regression with nonparametric smoothing techniques (Forest et al., 2007) as implemented by the LOESS function in R. For Faith's PD and TTD, we identified areas with unusual phylogenetic diversity given the global relationship between phylogenetic diversity and species richness, by selecting cells for which the residual value from these regressions was within the top or bottom 5% of all residuals. This is akin to using the global relationship between species richness and phylogenetic diversity as a simple null model, in order to account for sampling effects arising from different levels of species richness among grid cells. This approach is arbitrary in the selection of the cut-off, but it avoids taking decisions about species pools that are necessary for more elaborate null models, which do not currently exist and which we deemed overly complex for our comparison among spatial patterns of different diversity measures.

RESULTS

When using the global dataset and our supertree, spatial patterns for amphibian species richness were highly similar to those for two indices of phylogenetic diversity, Faith's PD and TTD (Fig. 1a–c). Phylogenetic diversity as measured by either Faith's PD or TTD was strongly correlated with species richness on a global scale (Table 1; Fig. 1f–g; LOESS regressions with 11940.9 equivalent d.f.: Faith's PD, residual sum of squares = 309.7; TTD, residual sum of squares = 6730.5). The residuals from local regression models of Faith's PD or TTD against species richness showed noticeable spatial pattern (Fig. 2a,c). Residual patterns for Faith's PD and TTD were moderately correlated with each other (Pearson correlation coefficient $r = 0.716$). Our 5% cut-off identified some areas with consistently low or high phylogenetic diversity using either Faith's PD or TTD, but also areas with values beyond our cut-off for only one of these two indices [Fig. 2b,d; 600 of 1189 cells (50%) were identified with both indices].

The other two indices of phylogenetic diversity, AvTD and MRD, each reflected very different aspects of diversity as they were only weakly correlated with any of the other indices, including species richness (Fig. 1d–e & h–i, Table 1). AvTD was the only phylogenetic diversity index to have a negative relationship with species richness. For both AvTD and MRD, the variance was much higher when species richness was low than when species richness was high (Fig. 1h–i).

All results were highly similar when using the Pyron & Wiens tree (Table 1, Appendix S3). Spatial patterns of species richness for the subset of species in the Pyron & Wiens tree reflected patterns using the global dataset quite well ($r = 0.984$; compare Fig. 1a with Fig. S2a in Appendix S3). Correlations of the different indices for phylogenetic diversity with global species richness and with each other were also similar for the two phylogenies, except for MRD (Table 1, Fig. S3 in Appendix S3). All spatial patterns except those for MRD were highly correlated between the two phylogenies (Table 1, Appendix S3).

DISCUSSION

Our comparison of global patterns of amphibian phylogenetic diversity and species richness showed that macroevolutionary processes, as inferred from phylogenies, have left a visible signal in the contemporary distribution of amphibian species richness across the globe. Global patterns of Faith's PD and TTD were similar to the species richness pattern with both phylogenies used, so these indices seem to measure the 'lineage richness' aspect of phylogenetic diversity well. From the construction of these two indices, areas with many species are also expected to

contain many phylogenetic lineages, simply due to a hierarchical sampling effect (Rodrigues & Gaston, 2002; Faith, 2008; Morlon et al., 2011), which makes it difficult to disentangle the influence of phylogenetic history on contemporary richness patterns. Our study shows that some areas have unusually high or low residuals from the relationship between species richness and phylogenetic diversity as measured by either TTD or Faith's PD, implying a strong signature of evolutionary history on contemporary amphibian diversity patterns.

Maps of the other two indices of phylogenetic diversity, AvTD and MRD, differed considerably from the global species richness pattern. They might therefore seem more desirable as indices for phylogenetic diversity, if the aim is measuring a diversity aspect complementary to species richness (Schweiger et al., 2008). These indices do not correlate well with species richness because their values are averages across species in a cell (which is also the reason why we did not look at spatial patterns of residuals for these two indices). In fact, AvTD is related to the phylogenetic species variability measure proposed by Helmus et al. (2007) and to the net relatedness index by Webb et al. (2002), and both of these have previously been shown to measure aspects of diversity which differ from species richness and Faith's PD (Helmus et al., 2007).

In our study, the variance of AvTD and MRD values varied systematically with species richness, so that more extreme values were common when relatively few species were present. Especially for AvTD, it seems that very high values could hardly be achieved by assemblages with > 30 species (Fig. 1h), leading to a negative correlation of AvTD and species richness. Possibly also due to this issue, previous studies have often reported extreme MRD values in relatively species-poor regions (e.g. Fjeldså & Rahbek, 2006; Hawkins et al., 2006). However, we conclude from our results that a meaningful comparison of AvTD or MRD values between assemblages of differing richness is rendered virtually impossible. Depending on the research question, these indices may be useful if an appropriate null model simulation is used (Webb et al., 2002), but we would not recommend the use of these indices for direct, large-scale comparisons of diversity patterns across regions as performed in this study.

The phylogenetic history behind amphibian species richness patterns

Residuals of both Faith's PD and TTD against species richness highlighted many islands and archipelagos (e.g. Madagascar, New Guinea, the Caribbean) and the comparatively isolated continent of Australia as containing low phylogenetic diversity for the number of species present, which signifies the presence of

Figure 1 Global maps of (a) amphibian species richness and (b–e) four indices of amphibian phylogenetic diversity calculated on our global phylogeny, and graphs (f–i) of the relationship of each phylogenetic diversity index with species richness across grid cells. Phylogenetic diversity indices were: (b,f) Faith's (1992) phylogenetic diversity (Faith's PD); (c,g) total taxonomic diversity (TTD); (d,h) average taxonomic diversity (AvTD); and (e,i) mean root distance (MRD). Red lines in (f–i) were fitted to the data by local regression models with nonparametric smoothing. Colour scales in (a–e) are based on 30 equal-interval categories labelled with median values; the first and last categories are larger and labelled with the minimum and maximum value. Maps use the Behrmann projection.
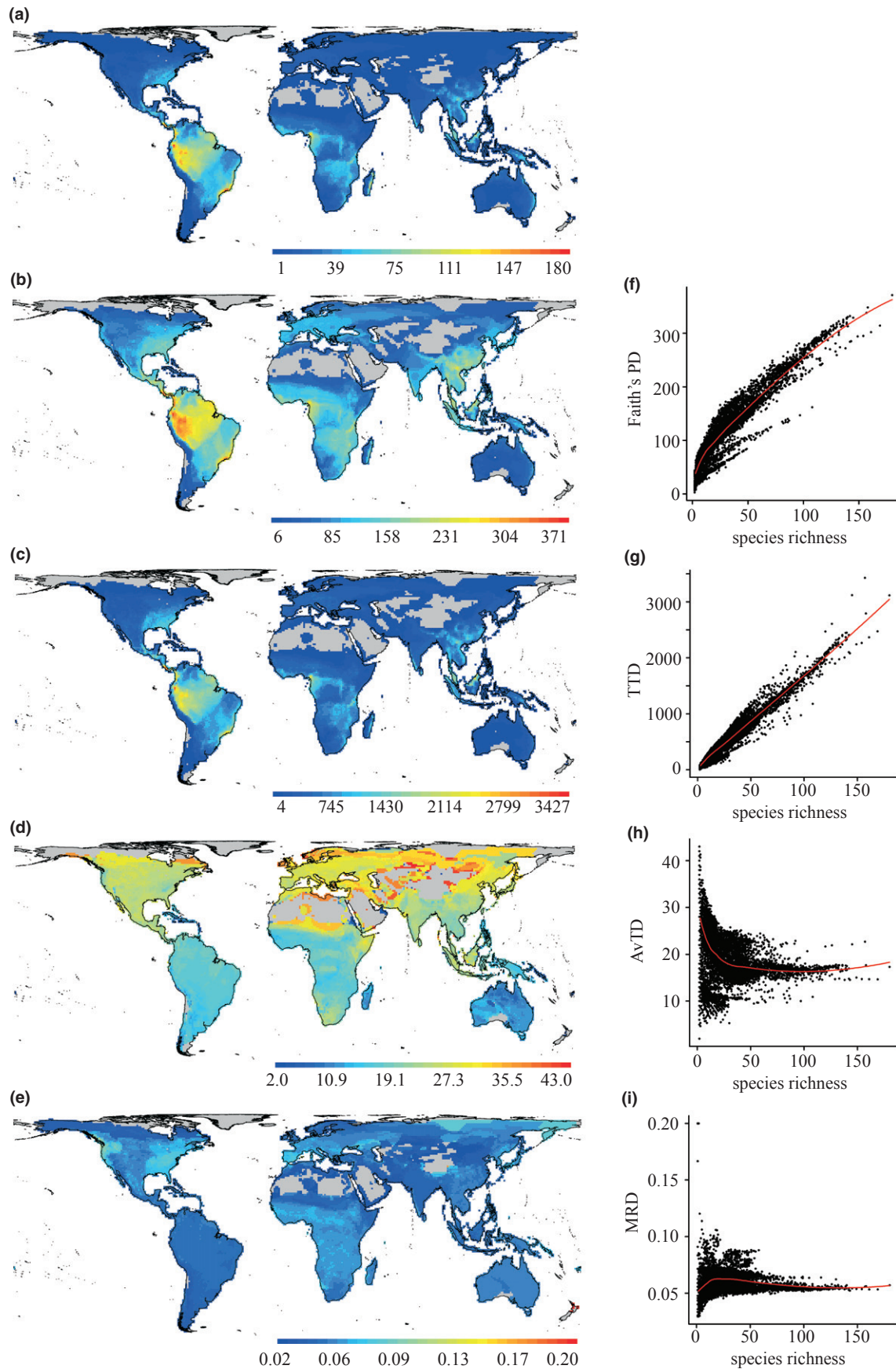
Table 1 Pearson correlation coefficients for global amphibian species richness and four indices of phylogenetic diversity, calculated for our phylogeny and the one published by Pyron & Wiens (2011).

		Species richness	PD		TTD		AvTD		MRD
			Our tree	P&W tree	Our tree	P&W tree	Our tree	P&W tree	Our tree
PD	Our tree	0.925							
	P&W tree	0.923	0.976						
TTD	Our tree	0.978	0.967	0.954					
	P&W tree	0.945	0.944	0.978	0.971				
AvTD	Our tree	−0.403	−0.233	−0.262	−0.290	−0.293			
	P&W tree	−0.389	−0.253	−0.236	−0.287	−0.249	0.922		
MRD	Our tree	0.107	0.145	0.129	0.128	0.127	−0.196	−0.273	
	P&W tree	−0.080	−0.098	−0.104	−0.040	−0.055	0.074	−0.070	0.777

PD, Faith's (1992) phylogenetic diversity; TTD, total taxonomic diversity; AvTD, average taxonomic diversity; MRD, mean root distance; P&W tree, Pyron & Wiens' (2011) phylogeny.

large, isolated radiations. Our results suggest that these areas have been successfully colonized by relatively few amphibian lineages, which have then radiated to unusually high species richness: for example the eleutherodactylids in the Caribbean; asterophryine microhylids and pelodryadine hylids in Australasia; and the mantellids and cophyline and scaphiophrynine microhylids in Madagascar (Heinicke et al., 2007; van der Meijden et al., 2007; Vieites et al., 2009). Alternatively, areas may have retained those lineages by vicariance (Van Bocxlaer et al., 2006). In any case, due to the isolation of islands and archipelagos and the saltwater intolerance of amphibians, no or few potential competitors reached those areas while the lineages that were present radiated. The overall low phylogenetic diversity on islands we show here confirms the importance of biogeographic barriers to dispersal, colonization and diversification processes and their signature on contemporary amphibian species richness (Buckley & Jetz, 2007; Olalla-Tárraga et al., 2011).

At the other end of the spectrum, Central America and southern China contained unusually high phylogenetic diversity for the number of species present. Therefore, these areas may be species rich due to high immigration rates of multiple lineages, or they may be centres of diversification, where old lineages are still present and many new lineages have arisen. They roughly coincide with contact zones between the long-isolated faunas of North and South America, and between the Indo-Malay and Palaearctic biogeographic realms in southern China. High speciation rates have been postulated previously for ecotones or biogeographic contact zones (Schilthuizen, 2000). Alternatively, contact zones may contain high phylogenetic diversity if they can sustain assemblages from both biogeographic regions, implicating a role for dispersal rather than *in situ* diversification. For example, different hypotheses have been proposed to explain current amphibian diversity patterns in Central America, such as ancient dispersal events and subsequent radiation of southern American eleutherodactyline lineages (Heinicke et al., 2007), persistence of old hylid lineages in mountains in concert with high *in situ* diversification rates and a time-for-speciation effect (Smith et al., 2007), and temperature niche constraints on regional species pools but

not on species composition for hylid communities (Algar et al., 2009). However, if our highlighted areas contain outstanding phylogenetic diversity because they are contact zones, it is unclear why other contact zones have not produced outstanding amphibian diversity, for example the transitions between the Palaearctic and the Afrotropics or the Indo-Malay in Southwest Asia, or biome transitions such as the rain forest–savanna transitions in Africa. Although this needs to be tested with a more rigorous null model, the global patterns we found seem to fit with temperate or subtropical centres of diversification for the basal amphibian lineages, such as in China or the south-eastern USA, and tropical origins for the species-rich crown clades found among the anurans, such as in Central America (Vieites et al., 2007; Wiens, 2007; Wiens et al., 2009).

While being highly congruent overall, patterns for Faith's PD and TTD differed in some areas because they apparently reflect subtly different aspects of phylogenetic diversity. Due to the emphasis on pairwise distances between species in the TTD measure, these differences possibly arise particularly in assemblages with relatively few but very distantly related clades. In these assemblages, the distance between clades is counted only once in Faith's PD, but multiple times for TTD. For example, residuals from the TTD but not the Faith's PD analyses are higher than our arbitrary cut-off in the south-eastern USA, which is known for its high caudate diversity but also contains some derived anuran lineages. It is also noteworthy that some areas have positive residuals when using TTD but negative ones when using Faith's PD or vice versa, for example the African richness peaks in Mount Cameroon and the Eastern Arc Mountains. Finally, Faith's PD had a nonlinear relationship with species richness (Faith, 2008; Morlon et al., 2011), while TTD had a linear one.

Robustness of our approach

Our results were robust to which of the two phylogenies we used, despite the many differences: the topology of deep branches differed slightly in many places between the Pyron & Wiens tree and ours, our tree was much less resolved, and only about half the species were represented in the Pyron & Wiens
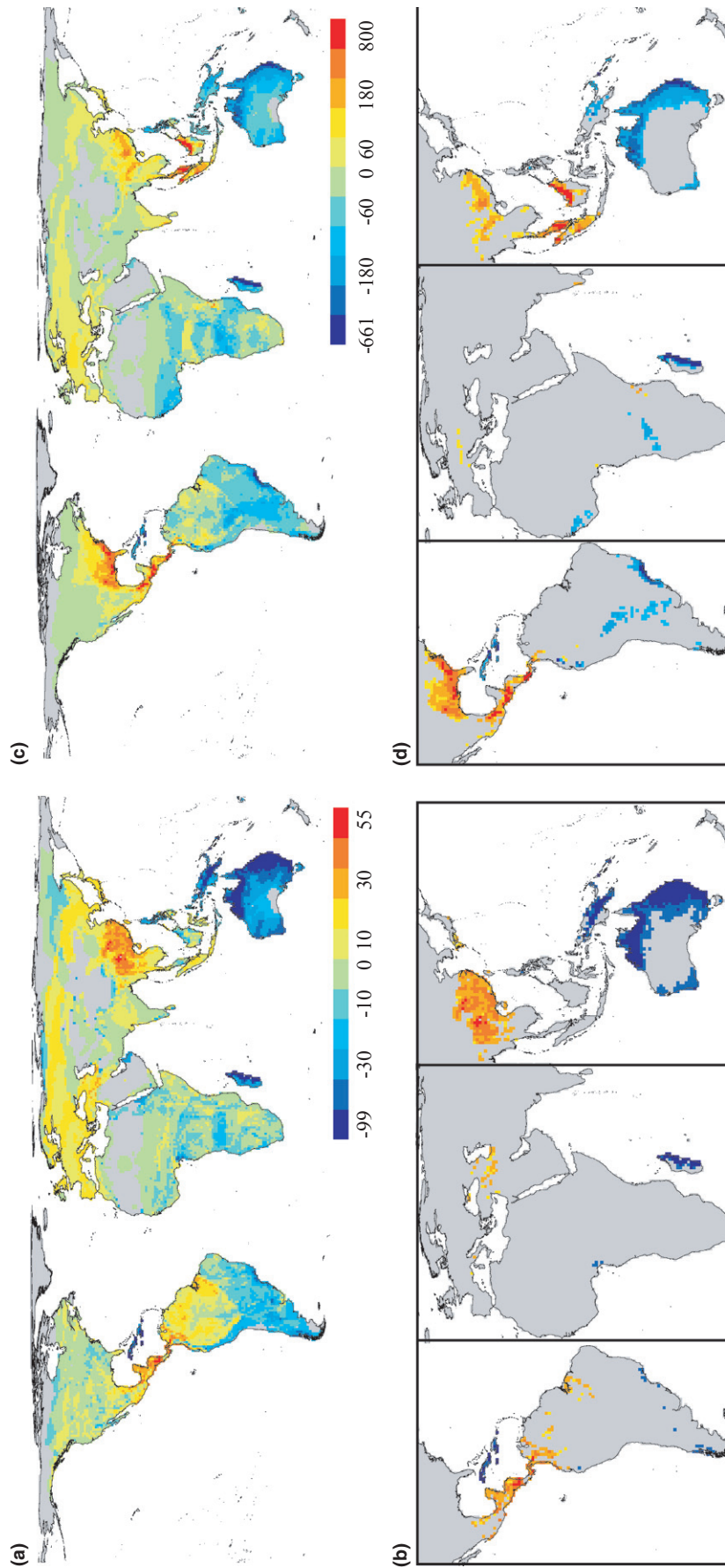
Figure 2 Global maps of residuals from a local regression model of (a, b) Faith's (1992) phylogenetic diversity (Faith's PD) and (c, d) total taxonomic diversity (TTD) against amphibian species richness, using the global supertree. In (a, c), all values and areas are shown; in (b, d), enlarged parts of the same maps are shown, with grid cells not in the top or bottom 5% of residuals masked in grey. Colour scales are based on equal-interval categories centred on zero and labelled with median values; the first and last categories are larger and labelled with the minimum and maximum value. Maps use the Behrmann projection.

tree. Therefore, we take this as suggesting that large-scale global patterns of deep phylogenetic history are consistently captured by our residual approach, even with incomplete phylogenies or phylogenies like our supertree, which are unresolved below genus level. A condition for this conclusion is that species sampling in incomplete phylogenies is spatially random (the species richness pattern of species sampled in the Pyron & Wiens tree represented the global pattern well).

In both phylogenies, we set all branch lengths to one, so measures of phylogenetic diversity in our study reflect only topology, not divergence over time. Nevertheless, the consistency of the results with the two different phylogenies implies that just the topology already contains the information needed to address our hypothesis of signatures of phylogenetic history on contemporary species richness. In effect, we implicitly assumed a punctuational evolutionary model, where the number of nodes is correlated with morphological change (Humphries *et al.*, 1995). There is a long-standing debate whether phylogenetic diversity as measured by Faith's PD on dated molecular phylogenies, i.e. a measure scaled by neutral evolution, is a meaningful measure of feature diversity or morphological disparity (Faith, 1992, 2002; Owens & Bennett, 2000). As especially the phylogenetic nodes above genus level should constitute points of strong morphological divergence, the patterns of phylogenetic diversity we show may not reflect evolutionary history in terms of years, but should reflect evolutionary history in terms of morphological disparity (Faith, 1992; Humphries *et al.*, 1995).

CONCLUSIONS

In summary, our analyses showed that Faith's PD and TTD as indices of phylogenetic diversity exhibit a strong positive global relationship with species richness, which can be utilized to identify signatures of phylogenetic history on contemporary amphibian diversity in areas departing from this relationship. Our results indicate strong signals of evolutionary processes in contemporary amphibian richness patterns, but we cannot disentangle the effects of dispersal and diversification processes. Previous studies have built predictive frameworks about regional net diversification rates, or have even drawn inferences on speciation and extinction rates, from the residual approach (Davies *et al.*, 2007; Davies & Buckley, 2011). However, dispersal processes may mask the signal of *in situ* diversification mechanisms (Goldberg *et al.*, 2005), as these studies also point out. Given the complex dynamics of species ranges in space and through time, simulation models may offer a way to advance knowledge beyond pattern analyses such as ours (Gotelli *et al.*, 2009; Pigot *et al.*, 2010). Also, we note that the spatial residual pattern for mammals (Davies *et al.*, 2008) differs strongly from the one we present here for amphibians, whereas richness patterns are broadly congruent. An intriguing avenue for further study would be to investigate whether there are common rules underlying these different patterns, or whether phylogenetic history is played out in a unique way for each taxon.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Construction of the global amphibian phylogeny.

Appendix S2 Representation of the global amphibian genus-level phylogeny.

Appendix S3 Results of all analyses rerun with the global amphibian phylogeny from Pyron & Wiens (2011).

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Editor: Peter Linder