Environmental and historical constraints on global patterns of amphibian richness

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Our knowledge of the broad-scale ecology of vertebrate ectotherms remains very limited. Despite ongoing declines and sensitivity to environmental change, amphibian distributions are particularly poorly understood. We present a global analysis of contemporary environmental and historical constraints on amphibian richness, the first for an ectotherm clade at this scale. Amphibians are presumed to experience environmental constraints distinct from those of better studied endothermic taxa due to their stringent water requirements and the temperature dependence of their energetic costs and performance. Single environmental predictors set upper bounds on, but do not exclusively determine, amphibian richness. Accounting for differing regional histories of speciation and extinction helps resolve triangular or scattered relationships between core environmental predictors and amphibian richness, as the relationships' intercepts or slopes can vary regionally. While the magnitude of richness is strongly determined by regional history, within-region patterns are consistently jointly driven by water and temperature. This confirms that ecophysiological constraints extend to the broad scale. This coupling suggests that shifts in climatic regimes will probably have dramatic consequences for amphibians. Our results illustrate how the environmental and historical explanations of species richness gradients can be reconciled and how the perspectives are complements for understanding broad-scale patterns of diversity.

Keywords: amphibians; biogeography; climate change; diversity gradient; historical contingency; water–temperature hypothesis

1. INTRODUCTION

Amphibians have been declining worldwide for many years (Houlahan *et al.* 2000; Stuart *et al.* 2004). Yet we lack even a basic understanding of the drivers of amphibian distributions and diversity at broad spatial scales. Amphibians' peculiar physiological constraints are well documented and suggest strong sensitivity to environmental conditions (Feder & Burggren 1992). Consequently, amphibians have repeatedly been used as an indicator group for environmental change (Pounds *et al.* 1999, 2006). Here, we quantify for the first time how the environment determines amphibian species richness at the global scale, enabled by recently compiled distribution maps for nearly all of the approximately 6000 known amphibian species (IUCN *et al.* 2006).

Despite the fact that the majority of species are ectothermic, our knowledge of broad-scale ecology is primarily based on endothermic vertebrates. This study seeks general insights into how vertebrate ectotherms' differential responses to environmental temperatures and resource availability affect broad-scale ecological patterns. We investigate the following factors that have been purported to drive gradients of diversity: temperature, water, energy, habitat heterogeneity, and history (Hawkins *et al.* 2003a; Currie *et al.* 2004). Determinants of species richness may vary regionally, often shifting from

water to energy among endothermic vertebrates with movement away from the equator (Hawkins *et al.* 2003a).

While our analysis seeks general insights into constraints on vertebrate ectotherms, amphibians' traits may lead to particularly strong constraints. Water is a crucial constraint and resource for amphibians due to their highly water-permeable skin and water requirements for reproduction (Feder & Burggren 1992). In ectotherms, environmental temperatures influence rates of energy use and assimilation as well as performance in gathering resources and interacting with other organisms (Bennett 1990). Behavioural thermoregulation buffers changes in environmental temperature and subsequently energy use. However, the capacity for amphibian behavioural thermoregulation is limited because the cooling effect of evaporative water loss from skin counteracts heat gain by basking (Hutchinson & Dupe 1992). Environmental temperature is thus probably a strong constraint on mobility and energy acquisition in amphibians (Bennett 1990). Water and temperature act together in determining net primary productivity, which, as the amount of energy that can be gathered from the environment, may restrict the number of species that can coexist (Wright 1983; Jetz & Rahbek 2002; Hawkins *et al.* 2003a). However, energetic costs that are up to 10 times lower than those of endotherms sometimes enable ectotherms to live in environments with low productivity (Pough 1980). Habitat and topographic heterogeneity can influence the number of available ecological niches and speciation rates (Kerr *et al.* 2001; Rahbek & Graves 2001; Jetz & Rahbek 2002). Histories of speciation and extinction determine

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regional species pools (Jablonski & Bottjer 1991; Smith *et al.* 2005) and are both caused by (Dynesius & Jansson 2000) and result in (Ricklefs 2004) differential responses to climate. We demonstrate the interplay of environmental and historical constraints on amphibian richness.

2. MATERIAL AND METHODS

Distribution maps (Global Amphibian Assessment; IUCN *et al.* 2006) for 5634 of the approximately 6000 known amphibian species were overlaid in ArcGIS to estimate amphibian richness. The extent of occurrence maps group the known occurrences with polygons and include multiple polygons when known range discontinuities exist. Distributions were peer reviewed by a global assemblage of scientists. We use an equal area cylindrical projection and equal area grid cells of 3091 km^2 (approx. equivalent to $0.5 \times 0.5°$ latitude–longitude near the equator) to examine amphibian richness patterns. We excluded cells that contained more than 50% water, leaving 41 792 cells for analysis. We additionally excluded cells containing exclusively islands, leaving 40 315 cells for analysis. We included cells with zero values of richness, but results were similar when they were excluded. We added 1 to species richness values to enable log10 transformation. We repeated all analyses using a grid resolution that was four times and eight times coarser (equivalent to 2 and 4° grid cells near the equator).

Environmental and geographical data for assessing hypothesized explanations of richness patterns were assembled and extracted in ArcGIS. All variables were log10 transformed. The temperature hypothesis states that the influence of energy on species richness is mediated by species' thermoregulatory needs (Currie 1991) or by higher rates of biological interaction or diversification (Rohde 1992). Often, the influence of temperature appears as a threshold below which species are unable to perform sufficiently to gather resources (Bennett 1990). We use mean annual temperature, mean annual diurnal temperature range and frost-day frequency to assess the effect of temperature (data from 1961 to 1990 with 10' resolution; New *et al.* 2002). We additionally consider potential evapotranspiration, which is strongly influenced by temperature (30' resolution; Ahn & Tateishi 1994). We use annual precipitation, mean precipitation of the driest three months, wet-day frequency and relative humidity to indicate water availability (data from 1961 to 1990 with 10' resolution; New *et al.* 2002). The water–temperature balance hypothesis postulates that water and energy dually constrain the species distributions (Andrews *et al.* 2002).

The energy hypothesis proposes that the number of coexisting species is determined by food availability (Wright 1983; Hawkins *et al.* 2003b). We use consensus net primary productivity (NPP) estimates from the Potsdam model to estimate energy availability (gCm^{-2}, 30' resolution; Cramer *et al.* 1999). We use both the annual mean NPP and the mean three-month minimum NPP (NPP$_{min}$), which indicates the annual bottleneck in energy availability. We use annual evapotranspiration (AET), which is closely tied to the water–temperature balance, as an alternative indicator of energy availability (mm, 30' resolution; Ahn & Tateishi 1994).

Habitat and topographic heterogeneity can influence the number of available ecological niches and speciation rates (Kerr *et al.* 2001; Rahbek & Graves 2001; Jetz & Rahbek 2002). We use the count of 300 m topographic bands within each quadrat (30' resolution, GTOPO30) and the number of vegetation classes according to the Olson global land-cover classification (USGS 2002) to indicate landscape heterogeneity. We investigate the influence of historical differences in speciation and extinction rates by partitioning data according to seven biogeographic realms (Udvardy 1975). While this representation of history is relatively crude, it does capture major known differential histories of amphibian speciation and extinction, such as those in the New and Old Worlds (Duellman 1999). We subsequently consider regional history and the environment together by both controlling for realm and examining whether the influence of the environment on species richness varies by realm.

Environmental variables that were examined and subsequently omitted owing to limited explanatory power (with AIC and r^2 values substantially weaker than those of other closely related environmental variables) include annual mean minimum temperature, DOLY model NPP (tCha^{-1}yr^{-1}), topographic relief and the number of global land cover vegetation classes. To account for potential hump-shaped relationships, we include squared terms in the generalized linear models when doing so improves the linear model's AIC value by at least 10%. We choose the 10% AIC threshold as most squared terms significantly improved the model fits (AIC) according to likelihood ratio tests due to the large sample size. We account for triangular relationships between environmental variables and amphibian richness using quantile regressions for the 10, 50 and 90% quantiles (R package quantreg). All coefficients are reported in the text with 95% CIs.

Model residuals may be spatially non-independent. In a second step, we repeat our analyses and account for spatial autocorrelation using maximum-likelihood spatial autoregressive models (R package spdep; Bivand 2005). Longitude and latitude were used to develop neighbourhoods with threshold distances of 500, 1000 and 2500 km. Threshold distances were selected by examining correlograms. Neighbours were weighted *a priori* using row standardization, such that the weights of all neighbours within the threshold distance sum to 1 (Haining 2003). We used 25% (n=10 078) of the database for spatial analysis due to memory limitations on the covariance matrix. We used Moran's I tests to evaluate spatial autocorrelation of the model residuals, with larger absolute values indicating higher spatial autocorrelation. The three model types account for spatial autocorrelation in the response variable (spatial lag), error term (error dependence) and both predictor and response variables (mixed; Anselin 1988). Approximate global Moran's I tests were used to assess the performance of the spatial autoregressions in reducing spatial autocorrelation (Haining 2003). Likelihood ratio tests were applied to test the significance of spatial autocorrelation coefficients. We report results of error dependence models with a 1000 km neighbourhood, which yielded the best balance of model fit and reduced spatial autocorrelation.

3. RESULTS

Amphibian species richness generally increases towards the equator, with high concentrations in tropical moist forests, particularly the Amazon Basin (figure 1). Other regions of high richness include the Congo Basin and Southeast Asia. While these patterns broadly correspond to those of birds (Orme *et al.* 2005) and mammals
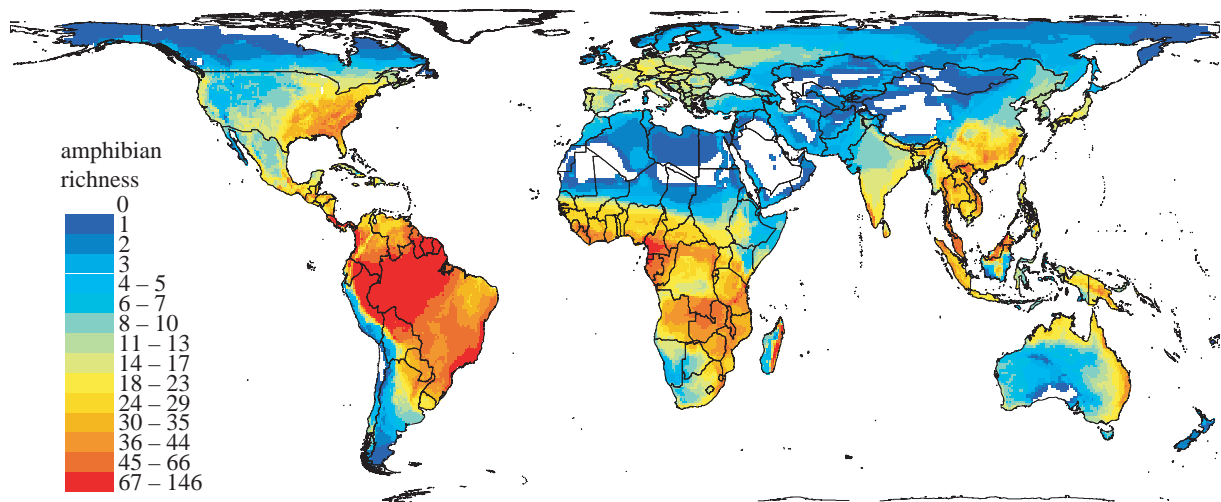
Figure 1. Global amphibian species richness. Richness was compiled within equal area quadrats equivalent to 0.5° in size by overlaying species' distribution maps (Global Amphibian Assessment).

(Ceballos *et al.* 2005), amphibians are unique in being species rich in the eastern United States. Amphibian richness is substantially higher in the eastern US than in Europe. In contrast, much of Asia and North America is depauperate of amphibian species.

Examining amphibian richness patterns in relation to single environmental variables reveals triangular or scattered patterns (figure 2). The most notable triangular relationship is that for temperature. The 10, 50 and 90% quantile regression slopes for the relationship between log(mean annual temperature) (K) and log(SR) are 5.22 ± 0.37, 17.55 ± 0.37 and 23.18 ± 0.29, respectively. This suggests that a given level of an environmental parameter is necessary, but not sufficient, for achieving a given level of species richness. Multiple factors appear to work in concert to constrain species richness for amphibians, more so than for mammals and birds (Currie 1991; Jetz & Rahbek 2002). Temperature alone is a relatively weak predictor of species richness ($r^2 = 0.28$). Notably, the observed triangular relationship contrasts the linear relationship predicted by metabolic theory which was used to predict gradients of amphibian richness under the untested assumption of uniform abundance (Allen *et al.* 2002). However, the slope of the 90% quantile regression for the relationship between the inverse of temperature ($1000 \, \text{K}^{-1}$) and the natural log of species richness (6.53 ± 0.06) is remotely in the vicinity of that predicted (predicted slope $= 9.0$; $F_{[1,40312]} = 51\,975$, $p < 1 \times 10^{-15}$).

As expected, given the overall importance of water for this taxon, annual precipitation has a strong positive effect on amphibian richness ($r^2 = 0.57$, slope 0.81 ± 0.01 in log–log space). Energy supply, as indicated by NPP_{min} or AET, encapsulates both temperature and precipitation and is the strongest single predictor of amphibian richness. NPP_{min} explains a considerable 76 and 86% of the variation in the non-spatial and spatial model, respectively (table 1). The strong influence of NPP_{min} is indicated by its overall accelerating relationship with amphibian richness (slope 1.13 ± 0.01 in log–log space). In combination, the balance of water and temperature has slightly more explanatory power than single energy variables with an r^2 of 0.77 in the general linear model without interactions (table 1). Model fit is consistent between

the spatial and non-spatial models. Including a second-order term substantially improved the explanatory power of most environmental variables. The analysis confirms for the broad spatial scale what has been extensively documented at smaller scales (Lips *et al.* 2003)—the crucial importance of water availability.

We next consider the potential influence of the history of speciation and extinction on the regional species pool. The number of species available to colonize an area can interact with climatic constraints on establishment to determine richness patterns (Qian & Ricklefs 2000; Ricklefs 2004). We use biogeographic realm as an indicator of the importance of history. While realm alone is a relatively weak predictor of amphibian species richness (table 1) that furthermore is collinear with environmental variables, it adds predictive power to already strong core environmental predictors (6% additional variance explained in case of the combined temperature–precipitation models; table 1). This demonstrates that the environment and the regional history constrain amphibian richness in conjunction. First, the model fit is improved in all cases when biogeographic realm is considered along with the environmental variables. Second, accounting for region strikingly disentangles the triangular relationships observed at the global scale, particularly for annual temperature. Annual temperature accounts for less than 10% of the variation in amphibian richness in all realms except the Nearctic and Neotropics. When considering these regions independently, temperature accounts for more variability ($r^2 = 0.75$ and 0.67 for the Nearctic and Neotropics, respectively) and the quantile regression slopes are much more consistent and close to the median slope throughout all parts of the data than when considering realms together. For the Nearctic, the 10, 50 and 90% quantile regression slopes for the relationship between log(Annual Temperature) and log(SR) are 21.0 ± 1.00, 27.4 ± 0.88 and 32.9 ± 1.18, respectively. For the Neotropics, the corresponding slopes are 46.5 ± 3.25, 45.3 ± 1.97 and 35.4 ± 3.29, respectively.

We use minimum net primary productivity, the strongest single predictor variable, to illustrate how accounting for history can reveal regional differences in the richness relationship (figure 3). The slopes of the relationships between energy availability and richness are
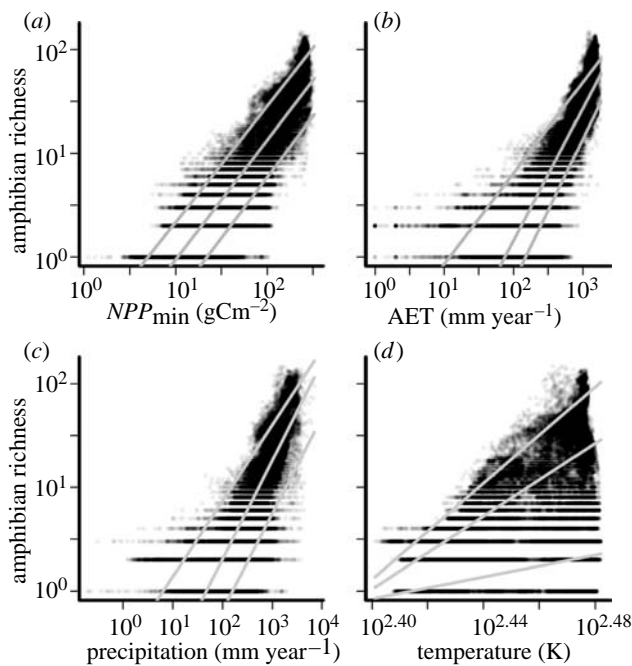
Figure 2. Amphibian species richness is constrained by multiple environmental variables. Bivariate plots of environmental effects on richness across 40 315 equal area quadrats equivalent to 0.5° size covering the world except islands showing 10, 50 and 90% quantile regressions. Quantile regressions (90% quantile mean(95% CI)) suggest the constraints imposed by each variable: (a) mean net primary productivity for the lowest three months (NPP_{min}) ($\log(SR) = -0.78(0.02) + 1.12(0.09)$ $\log(NPP_{min})$, $F_{[1,40312]} = 60\,906$, $p < 1 \times 10^{-15}$); (b) annual actual evapotranspiration (AET) ($\log(SR) = -0.94(0.05) + 0.88(0.02)\log(AET)$, $F_{[1,40312]} = 9211$, $p < 1 \times 10^{-15}$); (c) annual precipitation ($\log(SR) = -0.59(0.04) + 0.73(0.01)\log(pre)$, $F_{[1,40312]} = 12\,646$, $p < 1 \times 10^{-15}$) and (d) mean annual temperature ($\log(SR) = -55.5(0.47) + 23.18(0.29)\log(temp)$, $F_{[1,40312]} = 54\,815$, $p < 1 \times 10^{-15}$). Darker regions indicate a higher density of observations.

broadly similar (ranging from 0.73 to 1.51 in log–log space), but the intercepts differ when considering regions independently (see figure 3 for intercept values). These findings confirm and strengthen the asserted importance of contemporary environmental conditions. More broadly, they illustrate how a typical triangular or scattered macroecological relationship can be strengthened by going beyond contemporary drivers and accounting for historical contingencies.

When accounting for biogeographic realm, the balance of temperature and precipitation is the best overall predictor, accounting for 88% of the variation in global amphibian richness (table 1). Minimum *NPP* and mean annual *NPP* are the next best predictors when incorporating realm. Controlling for realm consistently improves the model fit, indicating that, for a given value of an environmental variable, richness is consistently greater in some regions. Including the interaction between the environmental variables and realm improved the model fit, suggesting that, to a small degree at least, the shapes of the relationships between the environment and history vary between regions (table 1). However, the relative importance of environmental constraints is consistent across realms despite inter-realm differences in species pools. The water–temperature balance is the primary determinant of richness patterns for all realms except the
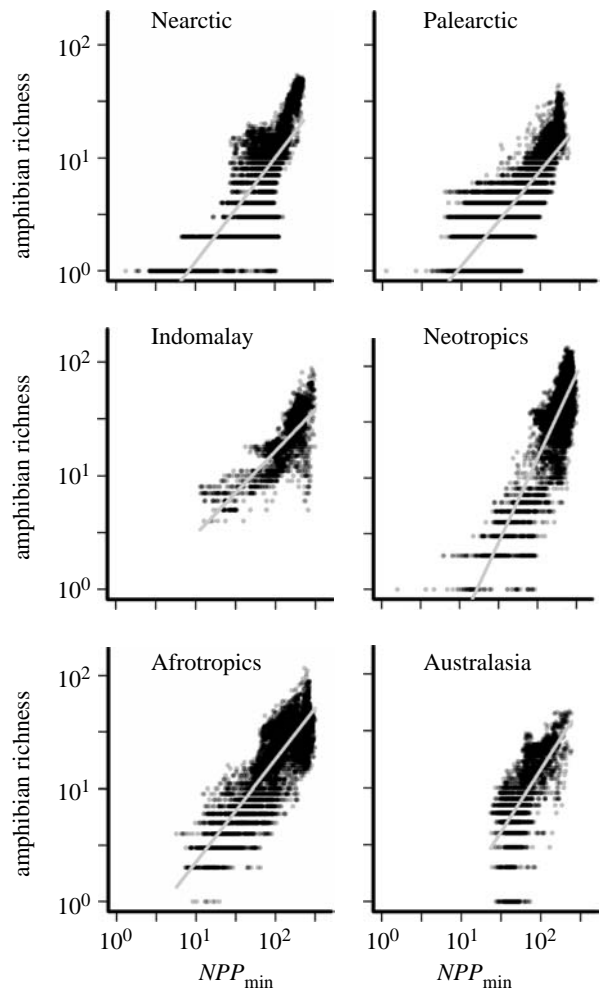

Figure 3. Regional species pools influence environmental constraints on amphibian richness. The relationships between three-month mean minimum net primary productivity (NPP_{min}) and richness is relatively consistent between the six biogeographic realms (mean(95% CI)): Nearctic ($\log(SR) = -0.84(0.01) + 0.92(0.01)\log(NPP_{min})$, $F_{[1,6309]} = 12\,700$, $p < 1 \times 10^{-15}$, $r^2 = 0.67$); Palearctic ($\log(SR) = -0.80(0.01) + 0.84(0.00)\log(NPP_{min})$, $F_{[1,16523]} = 35\,470$, $p < 1 \times 10^{-15}$, $r^2 = 0.68$); Indomalay ($\log(SR) = -0.25(0.03) + 0.73(0.01)\log(NPP_{min})$, $F_{[1,2200]} = 3404$, $p < 1 \times 10^{-15}$, $r^2 = 0.61$); Neotropics ($\log(SR) = -1.84(0.02) + 1.51(0.01)\log(NPP_{min})$, $F_{[1,6115]} = 18\,620$, $p < 1 \times 10^{-15}$, $r^2 = 0.75$); Afrotropics ($\log(SR) = -0.55(0.01) + 0.91(0.01)\log(NPP_{min})$, $F_{[1,6715]} = 16\,640$, $p < 1 \times 10^{-15}$, $r^2 = 0.71$); and Australasia ($\log(SR) = -1.03(0.04) + 1.10(0.02)\log(NPP_{min})$, $F_{[1,2240]} = 2107$, $p < 1 \times 10^{-15}$, $r^2 = 0.46$). Darker regions indicate a higher density of observations.

Palearctic, where energy (NPP_{min}) is a better predictor (by AIC value). Energy and the temperature–water balance are the top two predictors in all realms excepting the Nearctic, where temperature is an important factor.

The best fitting model for amphibian species richness is consistent, but the scatter increases, at coarser grid sizes. Accounting for biogeographic realm, the balance of temperature and precipitation is a better predictor than AET or minimum *NPP* at grain sizes of 2 and 4° (table 1, see tables 3 and 4 of electronic supplementary material). The balance of temperature and precipitation is also the best model when accounting for spatial autocorrelation. The models' increasing predictive power with finer spatial resolution is unexpected for multi-scale assessments of

Table 1. Environmental and historical models for global amphibian richness patterns. (The potential of the following variables to account for global amphibian richness using general linear models (GLM, $n = 40\ 315$) and spatially autoregressive linear models (SLM, $n = 10\ 078$): T, annual temperature (K), PET, mean annual potential evapotranspiration (mm); pre, annual precipitation (mm); NPP, annual net primary productivity (gCm^{-2}); NPP_{min}, mean NPP for lowest three months (gCm^{-2}); AET, mean annual actual evapotranspiration (mm); topography (count of 300 m elevational bands); vegetation (count of vegetation classes); and realm. AIC values are compared to the best fitting model. We indicate the direction of the effect of single predictor variables with $+$ or $-$. For the SLMs, we report pseudo r^2s (r^2 for fitted versus observed) for the linear model components and including the spatial component ($r^2_{spatial}$). Moran's I values range from 0 to 1, with 1 indicating perfect spatial determination. A ^{2} symbol indicates that both the linear and quadratic terms were included. The analyses were done across the equal area equivalent of 0.5° grid cell size (3091 km^2 area). See table 2 in electronic supplementary meterial for effect sizes and additional variables.)

hypothesis	model	$+/-$	GLM			SLM			
			ΔAIC	i	r^2	ΔAIC	i	r^2	$r^2_{spatial}$
temperature	T	$+$	70 970	0.66	0.27	11 797	0.56	0.27	0.80
	PET	$+$	68 594	0.61	0.31	11 595	0.56	0.30	0.80
water	pre	$+$	49 422	0.51	0.57	8263	0.46	0.57	0.81
	pre^2		36 546	0.35	0.69	6922	0.35	0.69	0.82
temperature and water	$T+pre$		23 663	0.28	0.77	4517	0.29	0.77	0.86
	$T \times pre$		23 472	0.27	0.78	4515	0.29	0.77	0.86
	$T \times pre^2$		17 604	0.23	0.81	3774	0.24	0.68	0.86
	$T^2 \times pre^2$		14 047	0.23	0.82	2947	0.23	0.69	0.87
energy	NPP	$+$	36 468	0.41	0.69	6070	0.38	0.69	0.84
	NPP^2		27 973	0.30	0.75	5399	0.31	0.71	0.85
	NPP_{min}	$+$	25 870	0.35	0.76	4178	0.34	0.76	0.86
	NPP^2_{min}		18 959	0.28	0.80	3577	0.26	0.78	0.87
	AET	$+$	41 090	0.45	0.65	6967	0.40	0.65	0.83
	AET^2		18 500	0.27	0.80	3667	0.24	0.72	0.87
heterogeneity	topography	$-$	71 429	0.62	0.26	12 002	0.57	0.26	0.81
	vegetation	$+$	78 257	0.81	0.12	11 966	0.65	0.12	0.84
history	realm		58 188	0.47	0.47	10 739	0.48	0.45	0.78
environment and history	$NPP^2_{min}+realm$		10 346	0.23	0.84	2001	0.22	0.83	0.89
	$NPP^2_{min} \times realm$		6278	0.20	0.85	1361	0.21	0.85	0.89
	$AET^2+realm$		16 202	0.25	0.81	3330	0.23	0.81	0.87
	$AET^2 \times realm$		13 110	0.24	0.83	2656	0.23	0.82	0.88
	$T^2 \times pre^2 + realm$		11 799	0.21	0.83	2522	0.22	0.82	0.88
	$(T^2 \times pre^2) \times realm$		0	0.18	0.88	0	0.18	0.87	0.91

biodiversity patterns (Rahbek & Graves 2001), but supports amphibian's close tracking of environmental conditions. The consistency of determinants towards coarser grid sizes corroborates their importance irrespective of potential range map interpolations that may compromise high resolution analyses.

4. DISCUSSION

Amphibians provide an example of how a historical approach can complement environmental approaches to understanding geographical gradients in species richness. Geographical differences in amphibian radiations suggest the potential for a strong role of history in determining their richness patterns (Smith *et al.* 2005). The New World experienced large radiations of taxa absent or rare in the Old World (Duellman 1999). Four families that are sparsely represented in the Old World (Plethodontids, Centrolenids, Dendrobatids and Leptodactylids) account for 80% of New World amphibian fauna and 97% of that in the Neotropics (Duellman 1999). Additionally, only three of the families that are well represented in both the Old and New Worlds exhibit greater diversity in the Old World (Duellman 1999). These historical radiations interact with modern climate to determine richness. For example, Australian amphibian richness may be limited

because toads (*Bufo*), a widespread and diverse clade with unique adaptations to life in dry environments, are not native to the largely arid and semiarid Australia (Duellman 1999). Strong influences of history on amphibian richness patterns have been documented in particular regions. Phylogenetic histories of speciation and migration account for the modern habitat use and distribution of Amazonian frogs better than do current environmental conditions (Zimmermann & Simberloff 1996). Our results confirm the role of regional history in shaping distributions and diversity at broad scales (Jetz *et al.* 2004) and highlight the importance of considering historical biogeography when crafting conservation efforts aimed at maintaining global amphibian diversity. There is a substantial overlap in the variation in species richness explained by history (i.e. realm membership) and environment as environmental conditions covary with realms. Beyond this shared variance, environment is by far the stronger predictor of species richness. History accounts for a limited amount of additional unexplained variation and helps resolve triangular or scattered relationships between environmental predictors and species richness. The relationships within regions have distinct slopes (as for temperature) or intercepts (as for NPP).

We find that environmental conditions do not translate into absolute species richness but do indicate relative

position along richness gradients set by the regional species pool. Notably, the amount of energy available in the environment (as indicated by *NPP*) does not directly determine the number of species that the environment sustains. A detailed molecular phylogenetic analysis of hylid frogs revealed similar latitudinal gradients but different absolute richness between biogeographic regions (Smith *et al.* 2005). Regional species pools of variable richness were attributed to differential *in situ* diversification (Smith *et al.* 2005). In the absence of detailed phylogenetic information, we use statistical techniques to set these findings in a broader, clade-wide and global context. The consistency with which water and temperature constrain amphibian richness across realms is striking and expected from amphibian ecophysiology. This consistency is in contrast to mammals and birds that show a poleward tendency towards increasing energetic constraints (Hawkins *et al.* 2003a; Whittaker *et al.* 2007). Whittaker *et al.* (2007) documented the consistent importance of water availability for European amphibians.

The tight coupling of water and temperature, which is encapsulated by energy availability, suggests that environmental change will probably have dramatic consequences for amphibians as geographical patterns of precipitation and temperature shift largely independently. Despite the influence of temperature on rates of energy use, energy assimilation and performance among ectoderms, water availability appears to more strongly constrain amphibian richness when considered singly. Indeed, changes in precipitation are predicted to pose a greater threat to European amphibians than increasing temperature under future climate change scenarios (Araujo *et al.* 2006). As we show, regional histories of speciation and extinction will probably influence the implications of environmental change for amphibian diversity.

Ongoing population declines and documented extinctions provide further evidence that amphibians are strongly constrained by water and temperature and that shifts in the water–temperature balance threaten amphibians. The degree to which amphibian species are associated with water was identified as the strongest predictor of which species were undergoing population declines in Central America (Lips *et al.* 2003). In one Costa Rican highland forest, population crashes affecting nearly half of frog and toad species were attributed to cloud banks receding upward following atmospheric warming (Pounds *et al.* 1999). This dependence on mist suggests that the complexity of the water–temperature balance constraining amphibians may exceed that demonstrated by our analysis. Our analysis extends the significance of water dependence to the global scale. We furthermore demonstrate how, in addition to water availability, regional histories of speciation and extinction limit the degree to which areas become hot spots of amphibian richness. Considering both the environment and the regional history is crucial to understanding gradients of amphibian richness.

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