Energy, water and large-scale patterns of reptile and amphibian species richness in Europe

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Abstract

We used regression analyses to examine the relationships between reptile and amphibian species richness in Europe and 11 environmental variables related to five hypotheses for geographical patterns of species richness: (1) productivity; (2) ambient energy; (3) water–energy balance, (4) habitat heterogeneity; and (5) climatic variability. For reptiles, annual potential evapotranspiration (PET), a measure of the amount of atmospheric energy, explained 71% of the variance, with variability in log elevation explaining an additional 6%. For amphibians, annual actual evapotranspiration (AET), a measure of the joint availability of energy and water in the environment, and the global vegetation index, an estimate of plant biomass generated through satellite remote sensing, both described similar proportions of the variance (61% and 60%, respectively) and had partially independent effects on richness as indicated by multiple regression. The two-factor environmental models successfully removed most of the statistically detectable spatial autocorrelation in the richness data of both groups. Our results are consistent with reptile and amphibian environmental requirements, where the former depend strongly on solar energy and the latter require both warmth and moisture for reproduction. We conclude that ambient energy explains the reptile richness pattern, whereas for amphibians a combination of water–energy balance and productivity best explain the pattern.
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1. Introduction

There is strong evidence that contemporary climate drives broad-scale species richness gradients of both plants and animals (Hawkins et al., 2003b). For plants, it is widely accepted that energy and water together drive diversity and form (e.g., Wright, 1983; Currie and Paquin, 1987; Adams and Woodward, 1989; Stephenson, 1990; Leathwick et al., 1998; O'Brien, 1993, 1998; Francis and Currie, 2003), and climatically based studies of plant richness patterns generally find that water–energy variables are strong predictors. For animals, energy alone or in combination with water has been linked to large-scale variation in diversity, depending largely on where in the world the study is focused (Hawkins et al., 2003b). In the case of animals, there is also some question as

to whether climate affects richness directly, or indirectly via the influences of climate on plant production.

In this paper, we examine the environmental correlates of richness gradients for two groups of vertebrates that are not as well studied as the better known mammals and birds. Relationships between reptile richness and climate have been examined in Australia (Pianka and Schall, 1981), the former USSR (Terent'ev, 1963) and the Iberian Peninsula (Schall and Pianka, 1977), whereas relationships for amphibians have been studied in the USSR, Iberia and North America (Terent'ev, 1963; Schall and Pianka, 1977; Allen et al., 2002). Our primary goal is to compare the ability of environmental variables associated with five well known hypotheses to explain the broad-scale diversity gradients of both groups: (1) ambient energy, that proposes that richness will be best described by energy inputs into an area (e.g., Turner et al., 1987; Currie, 1991); (2) water–energy balance, that proposes that a combination of energy and water inputs drives diver-

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sity (e.g., Hawkins and Porter, 2003; Hawkins et al., 2003a); (3) productivity, that claims that animal diversity depends primarily on the conversion of energy into plant production (e.g., Hutchinson, 1959); (4) habitat heterogeneity, that argues that greater heterogeneity of the environment facilitates diversity (e.g., Pianka, 1966; Kerr and Packer, 1997) and (5) climatic variability, that predicts that less variable climates will support more species (Currie, 1991).

2. Material and methods

2.1. The data

The Societas Europaea Herpetologica has published reptile and amphibian species distribution maps covering Europe except parts of Russia and the Caucasus (Gasc et al., 1997). Subsequently, Meliadou and Troumbis (1997) superimposed these and additional maps to obtain reptile and amphibian species richness values. The additional maps covered all of Russia, the Caucasus and Turkey. We chose to use these species richness maps because of their greater completeness. These authors divided Europe plus Turkey into quadrats following lines of latitude and longitude: 2.5° (latitude) × 5° (longitude) from 60° N to 70° N, 2.5° × 3.75° from 50° N to 60° N and 2.5° × 2.5° from 34° N to 50° N. They did not include islands smaller than Crete; whereas for larger islands, they modified quadrat location and size to avoid overlapping nearby mainland territories. This system yielded 188 quadrats. The species richness maps provided by Meliadou and Troumbis (1997) assigned the quadrats to classes of species richness of equal range (5 for reptiles and 3 for amphibians). For each taxonomic group, we used the class mark corresponding to each quadrat as its species richness value. A preliminary exploration of the data revealed that five quadrats covering the islands of Corsica, Crete, Cyprus, Ireland and Sardinia have reptile and/or amphibian richness values that are abnormally low when compared with nearby continental quadrats. We assumed that these quadrats are outliers reflecting effects of insularity and, therefore, excluded them from the analysis.

2.2. Environmental variables

We included 11 variables, selected because they can be related to the five hypotheses under test. We also included quadrat area to test for area effects. The hypotheses and their associated variables are:

(1) Ambient energy—We tested this hypothesis with potential evapotranspiration (PET) and mean annual temperature, which are widely used as indicators of ambient energy inputs (e.g., Schall and Pianka, 1978; Turner et al., 1987; Currie, 1991; Kerr and Packer, 1997). PET is available at http://www.grid.unep.ch/data/grid/gnv183.html, and temperature at http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a04/lw.htm#top.

(2) Water–energy balance—This hypothesis was originally derived to explain plant richness gradients (O'Brien, 1993), but it also applies to animals (Hawkins et al., 2003a,b). Whereas the ambient energy hypothesis focuses on limits to diversity from thermoregulatory stress due to cold temperatures, this hypothesis is based on the need for animals to have access to water as well as to tolerable temperatures and is expected to be most important in hot climates where desiccation may be a serious problem. This may also be of special importance to amphibians, which require moisture for reproduction. We use actual evapotranspiration (AET) (available at http://www.grid.unep.ch/data/grid/gnv183.html) as our measure of water–energy balance, and annual precipitation (available at http://www.grid.unep.ch/data/grid/gnv183.html) to examine the importance of water per se.

(3) Productivity—We used three variables as indicators of plant biomass and net primary productivity (NPP). The first is the gobal vegetation index (GVI) (an indicator of standing plant biomass), obtained from radiometer data from the NOAA polar orbiting environmental satellites (NCDC Satellite Data Services Division, 1985–1988). GVI is associated with the density and greenness of the plant canopy, total standing biomass, green leaf-area index (LAI) and per cent vegetation cover. We used the yearly average of the index which we obtained by averaging the monthly average values. These data are available at http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a01/mgv.htm#top.

The other two estimates of plant production, plant biomass and NPP, were taken from a database by Bazilevich (1994). This database was based on ~5000 worldwide peak-growing season field measurements that were undertaken for most terrestrial vegetation types between 1960 and 1990. The data were then assigned to areas of similar vegetation type included in the World Vegetation Cover Map (Fedorova and Volkova, 1990). These variables provide independent estimates of plant production, even though they are less detailed than that of GVI. They also suffer from subjectivity, as values were assigned to broad areas which are assumed to have similar natural primary vegetation cover. These data are available at: http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_b/datasets/b02/baz.htm#top.

(4) Habitat heterogeneity—We used the within-quadrat variability (standard deviations) of elevation and land-cover diversity as indicators of habitat heterogeneity (Currie, 1991; Kerr and Packer, 1997). Standard deviations were calculated from the elevation values of points evenly distributed within the quadrats. The number of these points ranged from 7 to 9 depending on the land area covered by each quadrat. Elevation data were obtained from http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a13/fnoc.htm#top. Following Kerr (2001) and Kerr et al. (2001), land-cover data were taken by summing land-cover types in each quadrat classified from 8-km resolution global AVHRR data (http://gaia.umiacs.umd.edu:8811/landcover/).

(5) Climatic variability—We used standard deviations of mean monthly temperature and precipitation between Janu-

ary and July (Currie, 1991; Kerr and Packer, 1997) to test the hypothesis that decreasing climatic variability results in increased species richness (Currie, 1991).

2.3. Data analysis

We used simple correlation/regression and stepwise multiple regression analyses to identify minimally adequate explanatory models. We examined the distribution of all variables before analysis, and log-transformed elevation variability because it had a highly skewed distribution. We also checked for non-linearities in the relationships between response and explanatory variables by adding quadratic terms to the models when necessary.

Because of spatial autocorrelation in the data, non-significant variables can appear significant in correlation and regression analyses. To correct for this we used a modified *t*-test (Duetilleul, 1993) to obtain unbiased estimates of the significance of correlations. However, this test is for simple correlations only, and we cannot generate the corrected significance levels for either non-linear or multiple regression models. We therefore focus in the explanatory power of the variables rather than on probability levels. At each step, we evaluated each variable based on the coefficient of determination and stopped when the addition of a variable (including a quadratic term if the relationship was non-linear) did not improve the model R^2 by at least 5%. Finally, we used the technique described by Diniz-Filho et al. (2003) to assess the sources of spatial autocorrelation in the data. First, we quantified the pattern of autocorrelation at 10 distance classes by using the Spatial Autocorrelation Analysis Program (SAAP) 4.3 (Wartenberg, 1989) to generate a correlogram of the raw diversity data (see Fig. 2 for distance classes). We then fitted the multiple regression model, and recalculated the Moran's *I* on the residuals. If no detectable spatial autocorrelation remains in a distance class, then the spatial pattern of species richness is well explained by the spatial pattern of the environmental predictors at that distance. In contrast, significant remaining spatial autocorrelation at any distance class among the residuals indicates that the environmental model does not adequately describe the pattern in richness at that scale, and spatially patterned variables not included in the model are contributing to the diversity pattern.

3. Results

3.1. Reptiles

Reptile species richness is correlated with all but one of the environmental variables (Table 1). However, after correcting for spatial autocorrelation (in those cases in which it was possible), the variables describing less than 10% of the variance became non-significant (Table 1). The multiple regression analysis identified PET as the primary explanatory variable, accounting for 70.9% of the variance, with variability in log elevation explaining an additional 6% (Table 1). We also tested for area effects by adding quadrat area to the minimal model and found no significant relationship with richness. The relationship between PET and reptile richness appeared curvilinear and accelerating (Fig. 1a), but an exponential model explained only 1% more variance than the linear model. Among the plant productivity variables, NPP described the most variance (11.0%), but it ranked seventh as a single predictor of reptile richness. Furthermore, fitting NPP to the two-factor environmental model increased the explanatory power of the model by only 0.4%, suggesting that the correlation between NPP and reptile richness reflects collinearity of NPP with PET rather than any independent effect of productivity.

Table 1
Simple and multiple regressions of predictor variables against reptile species richness

Variable		Probabilities	
	R^2	Uncorrected	Corrected
(a) Simple regressions			
Potential evapotranspiration	0.709	<0.0001	0.0001
Mean annual temperature	0.589	<0.0001	0.0015
Log(elevation variability)—Log(elevar)^2	0.447	<0.0001	
Habitat richness—habrich^2	0.344	<0.0001	
Actual evapotranspiration	0.276	<0.0001	0.0329
Precipitation temporal variability	0.132	<0.0001	0.0290
NPP–NPP^2	0.110	<0.0001	
Temperature temporal variability[a]	0.086	0.0001	0.3530
Global vegetation index	0.031	0.0181	0.4988
Plant biomass—planbio^2	0.029	0.0690	
Annual precipitation	0.007	0.2530	0.7197
(b) Multiple regression			
Potential evapotranspiration	0.709	<0.0001	
Log elevation variability—Log (elevar)^2	0.060	<0.0001	

The coefficients of determination and significance levels are also provided. Corrected probabilities are based on the modified *t*-test developed by Duetilleul (1993), which cannot be used for the polynomial or multiple regression models. (a) Simple regression variables are ranked by their coefficient of determination and non-linear models are indicated by inclusion of squared terms. (b) Coefficients of determination of the multiple regression analysis indicate the increment of variance described by the model after adding each variable.
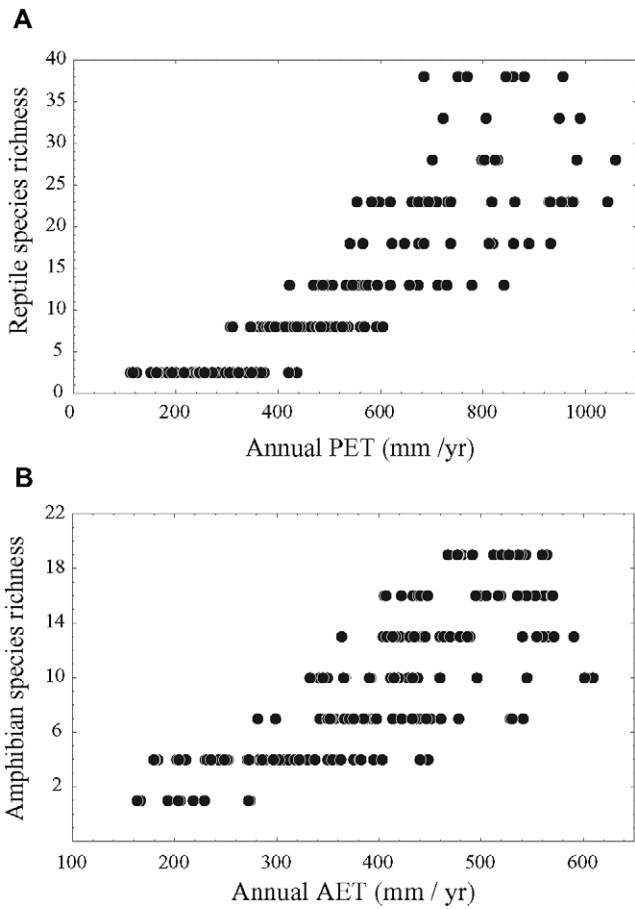
[a] Negative correlation.

Fig. 1. Relationships between (a) annual potential evapotranspiration (PET) and reptile richness; and (b) annual actual evapotranspiration (AET) and amphibian richness.

Species richness data for reptiles were spatially autocorrelated at nine of the 10 distance classes (Fig. 2a), and the pattern is indicative of a clinal trend of reptile richness with a slight reversal at the longest distance. However, the two-factor environmental model reduced the amount of spatial autocorrelation in all the distance classes and successfully removed it from the eight classes corresponding to moderate- and long-distances. A small but significant amount of spatial autocorrelation remains in the two shortest distance classes (Fig. 2a), indicating that additional factors not included in our analysis are needed to fully account for spatial variation in reptile richness at smaller spatial extents.

3.2. Amphibians

Similar to reptiles, all but one of the predictor variables (in this case temporal variability in precipitation) was associated with amphibian richness in simple regressions (Table 2). However, after correcting for spatial autocorrelation, the variables describing $\leq 31\%$ of amphibian richness variance became non-significant. Simple regression analyses identified AET and GVI as the best single predictors of amphibian richness (Fig. 1b, and Table 2). However, AET and GVI were also significantly correlated with each other ($r = 0.725$,
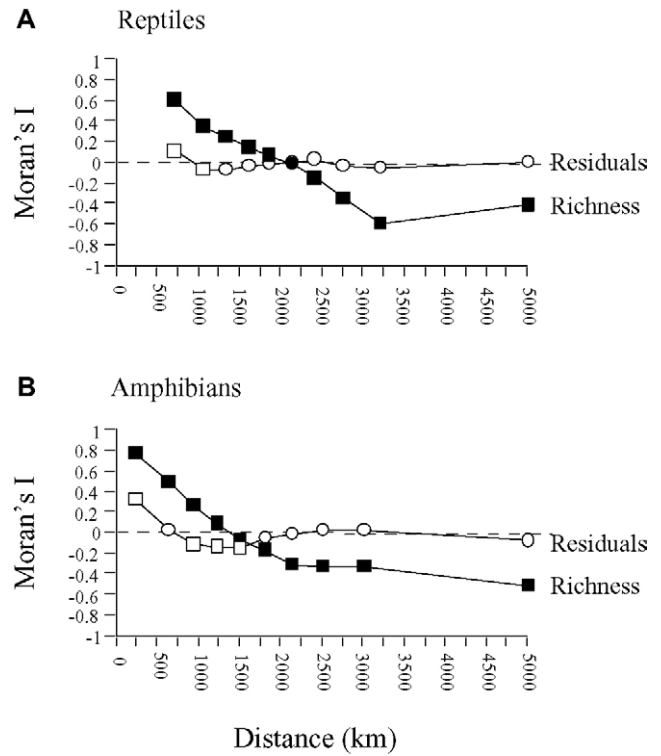

Fig. 2. Correlograms for raw (a) reptile and (b) amphibian species richness data and for residuals after fitting the significant variables in the climate models shown in Table 1 and 2. Significant Moran's Is (after Bonferroni adjustment of the critical alpha to correct for multiple tests) are shown in squares. Circles are non-significant values.

$P < 0.0001$), as would be expected since water–energy balance strongly influences plant production. Despite this collinearity, two analyses suggest both AET and GVI have partially independent effects on amphibian richness. First, these variables are the only ones remaining in the multiple regression model after deleting all non-significant terms (Table 2). Second, amphibian richness is associated with both AET and GVI when these variables are included together in a partial correlation analysis ($r_{partial} = 0.509$, $P < 0.0001$, and $r_{partial} = 0.487$, $P < 0.0001$, respectively). Thus, amphibian richness variation is associated simultaneously with the joint levels of energy/water and vegetation. We added quadrat area to the minimal model and found no significant relationship with amphibian richness.

Amphibian species richness data were spatially autocorrelated at all distance classes (Fig. 2b). The two factor environmental model reduced the amount of spatial autocorrelation in all the classes, and removed it from six of them, primarily at longer distances. Again, this indicates that additional factors not included in our analysis are needed to fully account for spatial variation in amphibian richness at small to moderate scales.

4. Discussion

The data suggest that energy, either alone or in combination with water availability, is a major predictor of reptile and

Table 2

Simple and multiple regressions of predictor variables against amphibian species richness. Presentation as in Table 1

Variable		Probabilities	
(a) Simple regressions	R^2	Uncorrected	Corrected
Actual evapotranspiration	0.611	<0.0001	0.0019
Global vegetation index	0.602	<0.0001	0.0047
NPP–NPP^2	0.398	<0.0001	
Potential evapotranspiration—PET^2	0.361	<0.0001	
Mean annual temperature—$anntemp^2$	0.370	<0.0001	
Plant biomass	0.310	<0.0001	0.0819
Annual precipitation—$annprec^2$	0.281	<0.0001	
Temperature temporal variability[a]	0.228	<0.0001	0.2578
Log elevation variability	0.118	<0.0001	0.2216
Habitat richness	0.071	0.0003	0.1250
Precipitation temporal variability	0.011	0.1556	0.5599
(b) Multiple regression			
Actual evapotranspiration	0.611	<0.0001	
Global vegetation index	0.092	<0.0001	

[a] Negative correlation.

amphibian richness variation in Europe. This agrees with previous studies of other animals in the same region (e.g., Schall and Pianka, 1977; Diniz-Filho et al., 2003; Hawkins and Porter, 2003), and in other parts of the world (Hawkins et al., 2003b), and lends further support to the hypothesis that contemporary climate drives diversity at large scales.

The data also show a secondary role of elevation variability in driving reptile richness variation, which corresponds with previous findings in other animal groups (e.g., Kerr and Packer, 1997). Elevation variability has frequently been used as a proxy variable for habitat heterogeneity in broad-scale studies of biodiversity (e.g., Currie, 1991; Kerr and Packer, 1997). However, this rests on the assumption that the greater the elevation variability of an area, the greater the mesoscale spatial variability of its climate and, therefore, the more likely that the area will have a larger number of habitats. Thus, the observed relationship between reptile richness and elevation variability may also be associated with climate at finer scales.

The data also indicate that the way climate and large-scale patterns of diversity are linked may differ in different animal groups. For reptiles, the primary predictor of richness was ambient energy (as measured by PET), with virtually no detectable effect of water availability. In contrast, available energy plus water (as measured by AET) is the best predictor for amphibians. These results are expected based on the physiological requirements of the two groups. Reptiles are extreme solar ectotherms, and measures of energy usually describe their richness gradients best (Terent'ev, 1963; Schall and Pianka, 1977; Pianka and Schall, 1981), whereas amphibians, although ectothermic and sensitive to temperature as well, also usually require water for reproduction. These facts suggest that diversity gradients are being driven primarily by direct climate effects operating on physiological requirements rather than indirectly via food availability or habitat structure for these two groups.

Plant biomass (GVI) is almost as good as AET at predicting amphibian richness, suggesting that plant productivity plays a role in determining diversity for this group. However,

it should be remembered that amphibians are almost exclusively predators. Therefore, if plant biomass effects on amphibian richness are related to food availability, they will be indirect and mediated by consumer biomass. In other words, if this hypothesis is correct, the indirect effects of climate on amphibian richness would occur through a process with at least three steps: climate determines production at the first trophic level, which in turn determines production at the second trophic level, which in turn influences amphibian richness. An alternative explanation for the observed relationships between amphibian richness and plant biomass is that amphibians are associated with plant cover or other habitat characteristics rather than through their prey items. This requires fewer links in the chain of causation, but we are unable to test this possibility with our data. Future analyses focusing on the habitat requirements of amphibians would clarify this issue.

To conclude, we find that in this cool part of the world energy inputs, either by themselves or in conjunction with water inputs, place strong constraints on diversity. Our analysis thus corroborates other studies that identify elements of contemporary climate as a strong explanation for broad-scale gradients in species richness for a wide range of taxa, further supporting the role of climate in the distribution of species across the face of the planet.

Acknowledgements

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