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# Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances

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## ABSTRACT

**Aim** To evaluate the strength of evidence for hypotheses explaining the relationship between climate and species richness in forest plots. We focused on the effect of energy availability which has been hypothesized to influence species richness: (1) via the effect of productivity on the total number of individuals (the more individuals hypothesis, MIH); (2) through the effect of temperature on metabolic rate (metabolic theory of biodiversity, MTB); or (3) by imposing climatic limits on species distributions.

**Location** Global.

**Methods** We utilized a unique ‘Gentry-style’ 370 forest plots data set comprising tree counts and individual stem measurements, covering tropical and temperate forests across all six forested continents. We analysed variation in plot species richness and species richness controlled for the number of individuals by using rarefaction. Ordinary least squares (OLS) regression and spatial regressions were used to explore the relative performance of different sets of environmental variables.

**Results** Species richness patterns do not differ whether we use raw number of species or number of species controlled for number of individuals, indicating that number of individuals is not the proximate driver of species richness. Productivity-related variables (actual evapotranspiration, net primary productivity, normalized difference vegetation index) perform relatively poorly as correlates of tree species richness. The best predictors of species richness consistently include the minimum temperature and precipitation values together with the annual means of these variables.

**Main conclusion** Across the world’s forests there is no evidence to support the MIH, and a very limited evidence for a prominent role of productivity as a driver of species richness patterns. The role of temperature is much more important, although this effect is more complex than originally assumed by the MTB. Variation in forest plot diversity appears to be mostly affected by variation in the minimum climatic values. This is consistent with the ‘climatic tolerance hypothesis’ that climatic extremes have acted as a strong constraint on species distribution and diversity.

## Keywords

**Biodiversity patterns, forests, latitudinal diversity gradient, metabolic theory, more-individuals hypothesis, productivity–diversity relationship.**

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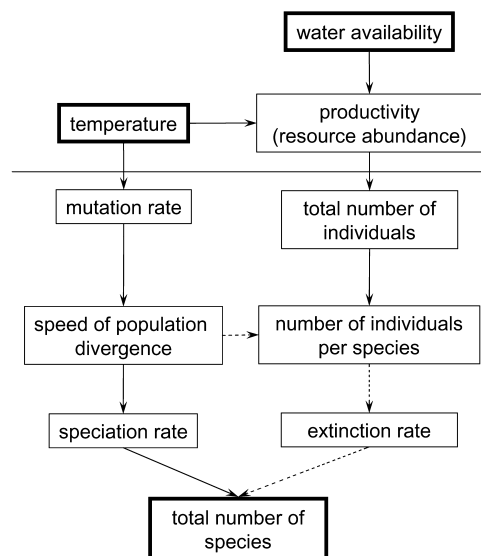
## INTRODUCTION

Diversity patterns have been studied for many decades, yet consensus regarding the major correlates of species richness has been reached only relatively recently. Extensive compilations and analyses (Francis & Currie, 2003; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Field *et al.*, 2009) have shown that the species richness of most taxa best correlates with specific climatic variables, namely temperature and precipitation, or variables characterizing ecosystem productivity, which are tightly related to temperature and water availability (O'Brien, 1993; Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Turner & Hawkins, 2004; Krefl & Jetz, 2007). Since all these variables are related to 'energy availability', it has been presumed that the main factor affecting species richness is energy (Wright, 1983; Currie, 1991).

Despite these advances, there remain several critical and non-trivial issues with linking variation in 'energy availability' to variation in species richness. First, it is unclear which form of energy is important for the generation and maintenance of richness (Clarke & Gaston, 2006). Temperature certainly represents a different form of energy from the chemical energy utilized by organisms. Moreover, even the energy directly utilized by organisms can be estimated in different ways, using measures concerning the amount or flow of resources, or some surrogates. Whereas some of these metrics concern energy or water flows through ecosystems (potential or actual evapotranspiration; PET or AET), other variables estimate standing biomass, or the rate of production of organic matter (net primary productivity, NPP). Second, and more importantly, it is not clear how 'energy availability' ultimately translates into species richness. Three possible mechanisms have been recently unravelled (Currie *et al.*, 2004).

One mechanism linking energy and species richness is the *more individuals hypothesis* (MIH). The MIH states that energy availability is simply represented by the amount (or inflow) of resources, which in turn limits the total number of individuals that can persist in an environment. Since a greater number of individuals can be divided into more species with viable populations, sites which support more individuals will then support more species (Wright, 1983; Srivastava & Lawton, 1998; Kaspari *et al.*, 2000; Evans *et al.*, 2005). Thus, the MIH states that the increase in species richness with energy availability is due to an increase in the total number of individuals, and thus predicts that the total number of individuals should be more tightly related to productivity than is the number of species. However, this is not readily observed, species richness being more strongly correlated with energy availability than is the total number of individuals (Currie *et al.*, 2004). Nevertheless, there is a problem with how the MIH has been traditionally evaluated. Specifically, it is not clear how to properly model the exact effect of number of individuals on species richness patterns.

Another theory which tries to mechanistically derive species richness from energy availability is the *metabolic theory of biodiversity* (MTB; Brown *et al.*, 2004). The MTB states that temperature affects diversity patterns via its effect on metabolic rate and consequently mutation and speciation rates (Allen *et al.*, 2006,



**Figure 1** Diagram explaining how temperature in combination with productivity affects species richness according to the metabolic theory of biodiversity (MTB; Allen *et al.*, 2007) (the dashed arrow indicates a negative relationship). First, temperature directly influences speciation rates through its effect on the metabolic rate, and consequently the mutation rate. Second, temperature together with water availability affects productivity, i.e. the amount or inflow of available resources. Higher productivity leads to a greater number of individuals, which decreases extinction rates. Note, however, that there is complex interaction between the two chains of causality, as species population sizes are affected by temperature not only positively through productivity but also negatively through population divergence.

2007). In its simplest form it predicts that species richness  $S$  scales with temperature exponentially, according to the relationship  $S \sim e^{-E/kT}$ , where  $k$  is the Boltzmann constant ( $8.62 \times 10^{-5}$  eV  $K^{-1}$ ),  $T$  is temperature in kelvin and  $E$  is the activation energy of metabolic reactions (i.e. the slope of the  $\ln(S) \sim 1/kT$  relationship) which should vary between  $-0.60$  and  $-0.70$  eV (Brown *et al.*, 2004). This prediction has been supported by some data (Allen *et al.*, 2002; see also Gillooly & Allen, 2007) but rejected by many others (Algar *et al.*, 2007; Hawkins *et al.*, 2007; Keil *et al.*, 2008; Terribile & Diniz-Filho, 2009). These differing findings may be due to a complex interaction of temperature with other forms of energy and water availability (Fig. 1) which affect population sizes and consequently extinction rates (Allen *et al.*, 2007). Thus, the MTB, as originally formulated, is difficult to test without further specification of these other confounding factors.

A third hypothesized mechanism behind the observed relationships between climatic variables and species richness patterns represents the *climatic tolerance hypothesis* (CTH). The CTH is based on the simple assumption that more species tolerate warm and humid conditions than colder and drier environments (Terborgh, 1973; Brown, 1988). Climatic extremes will act as a barrier to those species which cannot tolerate these extreme values; hence the diversity at a site reflects the diversity

of phenotypes that can tolerate the local climate. The differences in diversity can therefore be due to fundamental physiological constraints, or evolutionary history reflected in the fact that warm and humid environments represent ancestral and generally more common conditions on the earth's surface. Such historical explanations for diversity gradients also necessitate an assumption of niche conservatism (e.g. Wiens & Donoghue, 2004; Harrison & Grace, 2007), i.e. that organisms are often unable to adapt quickly to very different environments.

We identify three major problems associated with most analyses that attempt to assess the basis of the three abovementioned hypotheses. First, the large-scale data used to assess MIH, MTB and CTH often lack information about the abundance structure of the studied communities, necessary for testing or filtering out the effect of number of individuals. Second, almost no study has tested predictions of several of the possible mechanisms using the same data set (but see Sanders *et al.*, 2007). Third, the studies that have assessed the role of available energy (or productivity) used different expressions of energy, not necessarily corresponding to the mechanisms mentioned above. Here we attempt to overcome these limitations by: (1) using data which comprise the abundance structure of communities; (2) utilizing *individual-based rarefaction* (Gotelli & Colwell, 2001; Hurlbert, 2004) to control for number of individuals; and (3) testing and comparing multiple effects of candidate environmental variables. Specifically, we test following predictions:

1. If species richness is driven by the more-individuals effect, the patterns of species richness should disappear when controlling for the effect of number of individuals, either by rarefaction (Gotelli & Colwell, 2001; Hurlbert, 2004) or by using it as a covariate when testing the correlation between environmental variables and species richness. Moreover, the number of individuals should be more closely related to environmental variables than is the number of species (Currie *et al.*, 2004). Additionally, if species richness is affected primarily by the amount or inflow of resources, it should be tightly related mainly to proxies for productivity.

2. If the MTB holds, we should either observe the exponential relationship between  $1/kT$  and species richness predicted by the theory (Brown *et al.*, 2004), or a specific deviation from it, which can be attributed to factors affecting total number of individuals, namely water availability (Fig. 1).

3. If species richness patterns are driven by climatic limits of species distributions, as stated by the *climatic tolerance hypothesis*, we should expect that extreme values of respective climatic variables play at least as important a role as their mean values.

We test these predictions utilizing a unique, individual-based, global forest dataset included in the SALVIAS Project (<http://www.salvias.net>), which is an updated and expanded version of the Alwyn Gentry (1988) forest data set. Subsets of these data have been used for testing particular aspects of theories concerning richness patterns (e.g. Clinebell *et al.*, 1995; Currie *et al.*, 2004; Currie, 2007; Weiser *et al.*, 2007), but so far no study has simultaneously explored a multitude of potential explanatory variables and mechanisms while controlling for the effect of the total number of individuals in each community. To accurately assess the individual and combined contributions of all proposed environmental drivers, we used a model competition framework to find which proxy of available energy and combinations of variables best describe variation in forest plot diversity.

## METHODS

### Data

We analysed 370 forest plots distributed across six continents (Fig. 2), consisting of tropical, subtropical, temperate and boreal forests. The dataset we used is included in the SALVIAS project (2002 and onward; retrieved 12 January 2008 from <http://www.salvias.net/pages/index.html>) and contains the original 'Alwyn H. Gentry forest transect data set' (196 plots; Gentry, 1988; Phillips & Miller, 2002; <http://www.mobot.org/MOBOT/research/gentry/transect.shtml>) plus numerous additional 'Gentry-style' plots (174 plots). The portion of the SALVIAS

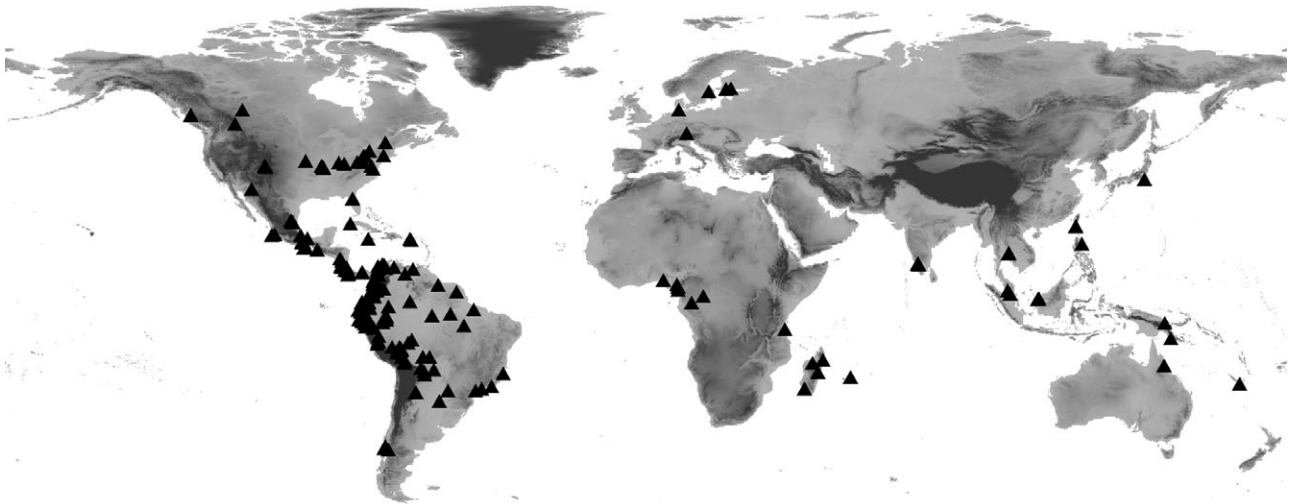


Figure 2 Locations of the forest plots. A darker grey background indicates higher altitudes.

dataset we use for our analyses here is almost twice as large as Gentry's original dataset. These additional plots include part of the Amazonian RAINFOR network (<http://www.geog.leeds.ac.uk/projects/rainfor>), the Boyle forest transects from Central and South America, and Enquist Lab forest plot inventories from Costa Rica, Mexico, Canada, Colorado and Arizona. All plots we used follow a 'Gentry-style' sampling methodology (see also Phillips & Miller, 2002), are all 0.1 ha in area, and contain counts and stem measurements of individual trees  $\geq 2.5$  cm d.b.h. (diameter at breast height). The geographical extent of the data ranges between 40.7° S and 60.7° N latitude and from 1 to 3113 m altitude. The number of species varies between 1 and 275, and the samples include some of the most species-rich forests in the world (Phillips & Miller, 2002). The total number of sampled individuals varies greatly – between 52 and 1005. In the process of analysing these data we found a significant number of erroneous location and elevation data, mostly in the original Gentry dataset as well as in Phillips & Miller (2002). These errors were corrected using the original site description, a digital elevation model (<http://www.worldclim.org>) and digital maps (<http://www.maps.google.com>). For all plots, species names were standardized according to the International Plant Names Index (IPNI, <http://www.ipni.org>) using the application TaxonScrubber (Version 2.0, <http://www.salvias.net/pages/taxonscrubber.html>), to eliminate spurious taxa resulting from data entry error and alternative spellings. These data are unique in representing the largest global compilation yet of standardized 0.1-ha 'Gentry' plots.

### Environmental variables

We used various surrogates of available energy: variables based on data from meteorological stations (temperature, precipitation and derived variables including AET and PET), variables obtained by remote sensing (normalized difference vegetation index (NDVI) based on the remote-sensing spectral properties of landscape, i.e. 'greenness' of vegetation), proxy variables for ecosystem primary production (NPP) and also data calculated from the allometric equations concerning individual trees in the plots, using stem diameter of each tree (water flux and total biomass), both (1) without considering and (2) considering temperature as a factor entering the respective equation. (For a detailed description see Table 1.) Temperature and precipitation data were taken from the WorldClim database (Hijmans *et al.*, 2005; <http://www.worldclim.org>; resolution 30"). AET and PET were estimated by the modified Thornthwaite method (Willmott *et al.*, 1985) using an AET calculator program (<http://geography.uoregon.edu/gavin/AETcalculator.pdf>). An annual composite of NDVI from the years 1997–2002 was taken from the SeaWiFS Project (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>; resolution app. 5'). NPP was estimated from the Potsdam model (Cramer *et al.*, 1999; resolution 1°). However, although this has been commonly used as an estimate of productivity, it is quite a coarse-scale measure of NPP, so that information about actual biomass production per plot might be biased. We thus included variables based on allometric equations that link stem diameters

to ecosystem attributes (i.e. water flux and standing biomass). To estimate actual stand water flux, which is proportional to total energy flux, we used an equation from Enquist *et al.* (1998):

$$Q_{\text{Tot}} \propto \sum_{i=1}^N D_i^{1.8} \quad (1)$$

where  $Q_{\text{Tot}}$  is the sum of whole-plant xylem flux through the main stem of the tree (litres per day),  $D$  is stem d.b.h. and 1.8 is the empirically determined scaling exponent linking the stem diameter to water flux. This relationship may be affected by the temperature dependence of metabolism (which, however, may not hold across broad temperature gradients; see Enquist *et al.*, 2003, 2007), so we also used a temperature-dependent version of equation 1 where

$$Q_{\text{Tot}} \propto \sum_{i=1}^N D_i^{1.8} \times e^{-E/kT} \quad (2)$$

$E$  is the average activation energy for plant metabolism, which is approximately 0.65 eV,  $k$  is the Boltzmann constant ( $8.62 \times 10^{-5}$  eV K $^{-1}$ ) and  $T$  is temperature in kelvin (see West *et al.*, 1999; Gillooly *et al.*, 2002).

Total standing tree biomass was estimated based on the equation from Brown (1997):

$$M_{\text{Tot}} \propto \sum_{i=1}^N D_i^{2.53} \quad (3)$$

where  $M_{\text{Tot}}$  is the sum of aboveground tree biomass (kg of dry matter) and 2.53 is an empirically determined scaling exponent. Although more precise equations have been developed for particular forest types (Chave *et al.*, 2005), only this equation for biomass calculation seems to be general enough to be valid across biomes. We used both temperature-independent and temperature-dependent (including the term  $e^{-E/kt}$ ) equations, similarly to the abovementioned case of water flux.

### Testing the MIH

So far the MIH has not been properly formalized. The only exact formalism linking number of species ( $S$ ) to the number of individuals ( $N$ ) is the neutral sampling theory (e.g. Hubbell, 2001) in which the local community that gathers more individuals from the surrounding metacommunity will also gather more species. In theory, if we have information about species identity for all individuals within local communities (which is the case in using the 'Gentry plot' protocol for sampling) we should be able to randomly resample any community and obtain the species richness ( $S_{\text{exp}}$ ) expected for a given number of individuals. This is equivalent to the technique called individual-based rarefaction (Gotelli & Colwell, 2001) which is otherwise routinely used to standardize sampling effort in biodiversity surveys. Using the individual-based rarefaction, we calculated  $S_{\text{exp}}$  at each plot for 100 and 300 individuals. If the

**Table 1** Overview of environmental variables used in the regression analyses.

Abbreviation	Description	Details	Units
$t$	Mean annual temperature		°C
$t_{\text{gws}}$	Mean annual temperature for growing season	Mean temperature for the months of sufficient temperature and water availability for plant growth (calculated according to Kerkhoff <i>et al.</i> , 2005)	°C
$\text{min}T$	Minimum temperature of coldest month		°C
$P$	Annual precipitation		mm
$\text{min}P$	Precipitation of driest month		mm
$R$	Annual rainfall		mm
$t + P$	Mean annual temperature with annual precipitation		
$1/kT$	Boltzmann temperature factor		$\text{eV}^{-1}$
$1/kT + P$	Boltzmann temperature factor with precipitation		
$1/kT + (1/kT)^2 + P + P^2 + (1/kT) \times P$	Polynomial effect of Boltzmann temperature factor, precipitation, and their interaction	Currie (2007)	–
$\text{min}T + \text{min}T^2 + \text{min}P + \text{min}P^2$	Polynomial effect of minimum temperature of the coldest month and precipitation of the driest month		–
AET	Actual evapotranspiration	The amount of water that is actually removed from a surface due to the processes of evaporation and transpiration	$\text{mm year}^{-1}$
Biomass	Biomass calculated from the temperature-independent tree metabolic rate	Standing above-ground dry biomass	kg
Biomass_ $T$	Biomass calculated from the temperature-dependent tree metabolic rate	Standing above-ground dry biomass	kg
NDVI	Normalized difference vegetation index	Measure of the vegetation cover on the land surface	–
NPP	Net primary production	The rate at which all the plants in an ecosystem produce net carbon	$\text{gC m}^{-2} \text{year}^{-1}$
PET	Potential evapotranspiration	The amount of water that would be removed from the surface if a sufficient water source was available	$\text{mm year}^{-1}$
$\text{min}PET$	Minimum potential evapotranspiration	Minimum mean-monthly PET	$\text{mm year}^{-1}$
$PET + PET^2 + WD + PET \times WD$	Polynomial effect of PET together with water deficit ( $WD = PET - AET$ ) and their interaction	Currie (2007)	–
$\text{min}PET + \text{min}PET^2 + R$	Water dynamics model	O'Brien (1993, 1998)	–
WF	Water flux calculated from the temperature-independent tree metabolic rate	Whole-plant xylem fluid flux summed across all individuals	$\text{litre day}^{-1}$
WF_ $T$	Water flux calculated from the temperature-dependent metabolic rate	Whole-plant xylem fluid flux summed across all individuals	$\text{litre day}^{-1}$

increase in species richness is caused by an increase in the number of individuals, all plots should lie along the same rarefaction curve, i.e. their  $S_{\text{exp}}$  should be similar for the given number of individuals, and there should be no relationship between  $S$  and  $S_{\text{exp}}$ .

Using rarefaction, we assume that the MIH is formally identical to the sampling effect. However, this may not necessarily be true. For this reason we adopted an additional approach of Currie *et al.* (2004), based on the prediction that if the MIH holds, the total number of individuals  $N$  should be more closely related to the environmental parameters than is the number of species  $S$ . Similarly,  $S$  should be more tightly related to  $N$  than to the environmental variables, because  $N$  is the

proximate driver of richness patterns. We therefore tested: (1) the explanatory power of number of individuals (in comparison to the abovementioned environmental variables) for species richness patterns, and (2) the effect of the environmental variables on the number of individuals. Additionally, we performed variation partitioning analysis for our best model and the model that included the polynomial term of  $N$ . Since our second best environmental model was almost as good as the first one (see below), we performed the same variation partitioning analysis using the second best model as well. In doing so we were able to reveal which part of variability in species richness was attributable to the effect of  $N$  versus the pure effect of the environmental variables.



## Testing the effects of environmental variables

We first tested univariate models containing individual environmental variables (Table 1) and their quadratic terms. Then we included all combinations of variables which have been used previously by other authors and/or which can be used for distinguishing the three major mechanisms depicted above.

1. A simple model that included a combination of temperature with precipitation.

2. a model based on water balance, combining PET and water deficit (WD;  $WD = PET - AET$ ) (Francis & Currie, 2003; Currie, 2007)

$$S \approx PET - PET^2 + WD + PET \times WD. \quad (4)$$

3. A water–energy model that combines minimum PET and rainfall ( $R$ ) (O'Brien, 1993, 1998)

$$S \approx \min PET - \min PET^2 + R. \quad (5)$$

4. A combination model that includes the effect of temperature predicted by the MTB with precipitation (Currie, 2007). The MTB predicts the natural logarithm of species richness to be a linear function of  $1/kT$ . As there is evidence of nonlinearity in empirical data (Algar *et al.*, 2007; Hawkins *et al.*, 2007), we included  $1/kT$  both as a linear and quadratic term. According to the suggestion of Currie (2007) and evidence of Wang *et al.* (2009) for a combined effect of  $1/kT$  and precipitation, we used a pure combination of both  $1/kT$  and precipitation, as well as the multiple-term model

$$\ln S \approx 1/kT + 1/(kT)^2 + P - P^2 - (1/kT) \times P \quad (6)$$

where  $P$  is annual precipitation and  $(1/kT) \times P$  represents the interaction between the Boltzmann temperature factor and precipitation. We tested this multiple-term model also using annual rainfall ( $R$ ) instead of annual precipitation. However, the results were similar based on the Akaike information criterion ( $\Delta AIC < 1$ ), so we proceeded by keeping just the model with annual precipitation for the rest of our analyses.

5. To explore the climatic limits of species distributions we included a combination of minimum temperature of the coldest month and the sum of precipitation of the driest month and their polynomial terms

$$\ln S \approx \min T - \min T^2 + \min P - \min P^2. \quad (7)$$

6. In order to explore the role of minimum values versus mean values of temperature and precipitation, we also included a combination of equations 6 and 7. Specifically, we put all the terms comprising these environmental variables into the right-hand side of the equation, and tested their significance using backward stepwise elimination of models terms (according to the AIC; Burnham & Anderson, 2002). The same approach was applied to the other models as well, with the aim of simplifying them.

We compared the strength of evidence for these models using the AIC (Burnham & Anderson, 2002). Since some plots are

close to each other, so that they share many environmental characteristics as well as species richness, we did our analyses both using non-spatial models (ordinary least squares, OLS) in R (R Development Core Team, 2008) and using spatial generalized least squares (GLS) regression in SAM (Spatial Analysis in Macroecology; Rangel *et al.*, 2006) to control for this autocorrelation effect. The residual spatial component in GLS was modelled using the exponential model of covariance structure (whose fit was the best). To test the predictions of the MTB, we examined if the relationship between  $\ln S$  and  $1/kT$  was linear, and whether the slope fell between  $-0.6$  and  $-0.7$ . The probability that the model with the lowest AIC was the best of all the models compared was assessed by comparing Akaike weights ( $W$ ) (Burnham & Anderson, 2002).

Individual environmental variables were measured at various resolutions. This may affect the results, as microclimate – and its potential effect on local species richness – is not well assessed by variables estimated at coarse resolution (e.g. NPP). For this reason, we repeated all analyses using the same (i.e. the coarsest) scale for all parameters, thus losing information concerning small-scale variability in a given parameter by averaging it over larger regions. Also, since most of the plots are located in the New World (which could cast doubts on the generality of the results; see Fig. 2), we repeated the analyses using a subset containing Old World samples only. As species richness may be at least partially affected by different evolutionary histories of different regions (Latham & Ricklefs, 1993; Qian & Ricklefs, 1999; but see Francis & Currie, 2003), we also repeated all the analyses controlling for the effect of region (tropical Asia, Africa, Europe, North, South and Central America) and the major climatic zone (tropical and temperate).

The effect of individual variables on species richness may be quite complex, including nonlinear relationships and interactions between variables. For this reason, we also performed regression tree analysis (package *tree*; R Development Core Team, 2008) using all single-term variables from Table 1.

## RESULTS

Individual environmental variables strongly differed in their effect on local tree species richness (Table 2). In both spatial and non-spatial regressions, the model with the lowest AIC (at the top of the table) had an Akaike weight  $W$  close to 1, whereas all the other models had  $W \approx 0$ , indicating that the differences in AIC distinguishing the best model from the others were substantial. Variables which included temperature appeared as generally better predictors of species richness than the other variables. The best model comprised the combination of  $1/kT$ , minimum temperature and minimum precipitation, whereas the commonly used measures of productivity like AET, NDVI or NPP performed relatively poorly (Table 2, Fig. 3). Tree species richness increased with temperature and precipitation (both mean and minimum values), the relationship being downward accelerating, as indicated by significant negative quadratic terms of these variables (see Appendix S1 in Supporting Information). Although the AIC difference between our first and second

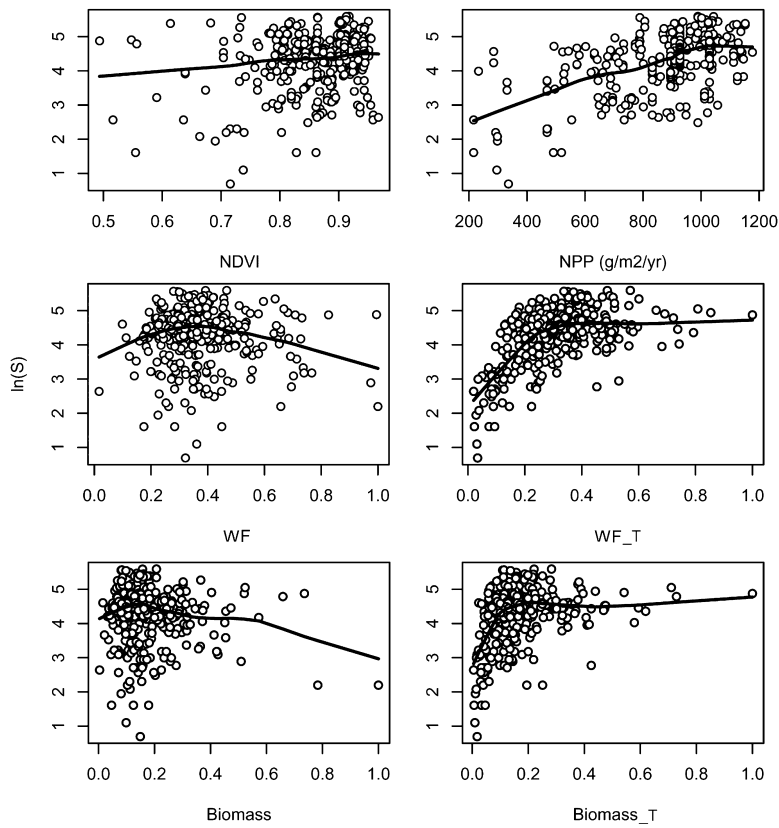
**Table 2** Results from the non-spatial and spatial linear regressions concerning effects of particular environmental variables (listed in Table 1) and their polynomial terms on the logarithm of species richness. Models are sorted according to their Akaike information criterion (AIC) for ordinary least squares (OLS) regressions. The  $R^2$  and AIC from the generalized least squares (GLS) regression are estimated: (1) for the full model which contains both the environmental variables and the spatial component, and (2) for the environment only, after accounting for space. See Table 1 for explanations and definitions of individual variables.

	OLS regression		GLS regression Environment + space		GLS regression Environment only	
	AIC	$R^2$	AIC	$R^2$	AIC	$R^2$
$\min T + \min T^2 + \min P + \min P^2 + 1/kT + (1/kT)^2$	429	0.72	385	0.76	469	0.69
$\min T + \min T^2 + \min P + \min P^2$	463	0.69	427	0.72	478	0.68
$1/kT + (1/kT)^2 + P + P^2 + (1/kT) \times P$	505	0.66	399	0.75	528	0.64
$\min T$	529	0.63	473	0.68	548	0.61
$\min T + \min T^2$	531	0.63	438	0.71	542	0.62
$\min PET + \min PET^2 + R$	531	0.63	404	0.74	549	0.61
$1/kT + P$	542	0.62	486	0.67	594	0.56
$t + P$	548	0.61	481	0.67	585	0.57
$\min PET + \min PET^2$	567	0.59	435	0.71	586	0.57
$t + t^2$	578	0.58	411	0.73	590	0.56
$1/kT + (1/kT)^2$	579	0.58	407	0.74	599	0.56
$PET + PET^2 + WD + PET \times WD$	604	0.55	446	0.70	622	0.53
$1/kT$	614	0.53	512	0.65	659	0.48
$t_{\text{gws}} + t_{\text{gws}}^2$	615	0.53	461	0.69	649	0.48
$t$	620	0.52	511	0.64	658	0.47
$\min PET$	624	0.52	571	0.58	704	0.40
$AET + AET^2$	634	0.51	476	0.68	657	0.47
$t_{\text{gws}}$	667	0.46	531	0.62	709	0.39
$PET + PET^2$	670	0.46	503	0.65	698	0.41
$WF\_T + WF\_T^2$	682	0.44	565	0.59	767	0.30
$AET$	688	0.43	523	0.63	716	0.37
$R + R^2$	738	0.35	571	0.58	791	0.24
$PET$	739	0.34	568	0.58	790	0.24
$NPP + NPP^2$	755	0.31	571	0.59	806	0.21
$NPP$	756	0.31	574	0.58	810	0.20
$P + P^2$	760	0.31	576	0.58	806	0.21
$R$	764	0.30	568	0.58	777	0.26
$WF\_T$	771	0.28	604	0.55	832	0.16
$P$	779	0.27	573	0.58	789	0.24
$Biomass\_T + Biomass\_T^2$	828	0.16	621	0.53	868	0.07
$\min P + \min P^2$	834	0.16	595	0.56	843	0.14
$\min P$	835	0.15	601	0.55	847	0.13
$Biomass\_T$	855	0.09	614	0.53	881	0.04
$NDVI$	872	0.06	584	0.56	868	0.06
$NDVI + NDVI^2$	874	0.06	587	0.56	870	0.06
$WF + WF^2$	880	0.03	651	0.48	884	0.03
$Biomass + Biomass^2$	880	0.02	661	0.47	886	0.02
$Biomass$	884	0.01	655	0.47	888	0.01
$WF$	889	< 0.01	635	0.50	892	< 0.01

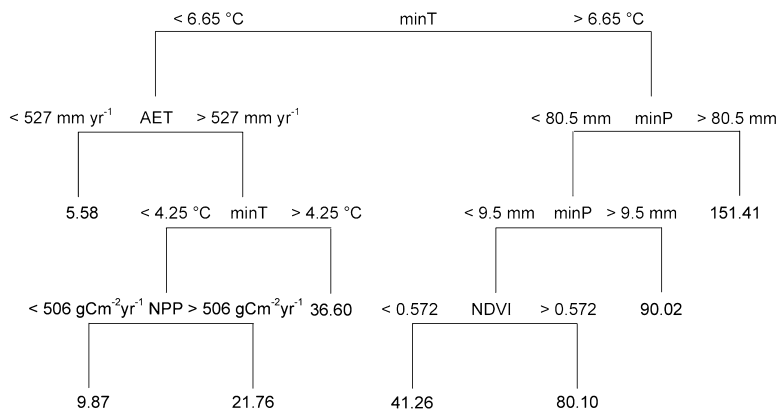
model (which contained only polynomial effects of  $\min T$  and  $\min P$ ) appeared to be substantial,  $1/kT$  and  $\min T$  in the best model were strongly correlated ( $r = -0.943$ , see Appendix S2), which somehow undermines its superiority over the simpler model (but see Appendix S3). For this reason, we consider the first and second best models as the models that capture the determinants of tree species richness equally well, which stresses

the overall importance of minimum values of temperature and precipitation for species richness patterns.

Surprisingly, the variables based on stem diameters and individual tree metabolism correlated weakly with other environmental variables, especially when temperature was not accounted for in calculating the energy flux through the community (Fig. 3) (the correlation was even negative in this case;



**Figure 3** Relationships between various measures of productivity and species richness (in logarithmic scale). The left-hand column shows models in which temperature did not enter the calculation of the respective variables, and the right-hand column refers to those for which temperature has been used. See Table 1 for explanations and definitions concerning individual variables. The solid lines represent locally weighted regression lines (lowess smoother). Note that units of biomass and water flux are standardized to a 0–1 scale as these variables have been estimated from the equations using stem diameter, and thus the units are only relative.



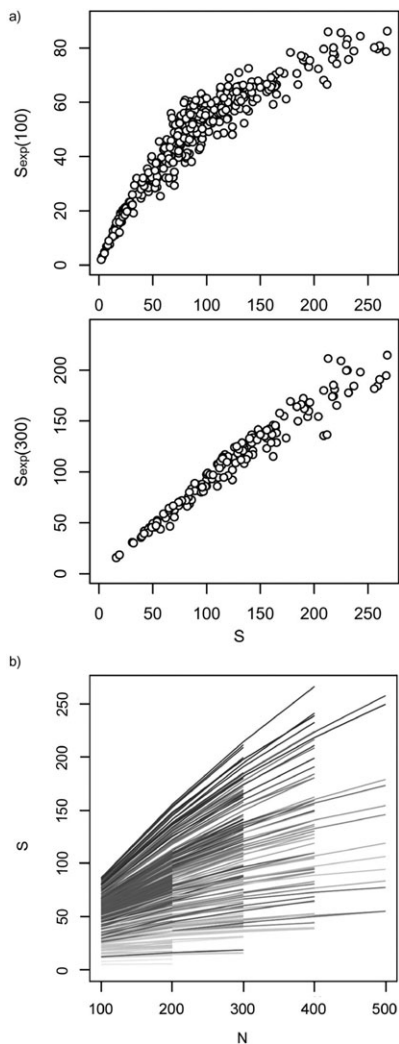
**Figure 4** Regression tree for species richness of forest plots based on binary recursive variance partitioning. As explanatory variables we used all single-term variables from Table 1. Names of the splitter variables and their split value are indicated at each node. Geometric means for species richness in each terminal group are given at each terminal branch.

see Appendix S2). The high AIC of the models containing these variables and their low correlation with species richness remained unchanged even after removing outliers. When accounting for spatial autocorrelation, the ordering of the models according to their AIC did not change substantially (Table 2). We obtained similar results when using both log-transformed and non-transformed species richness.

When we used variables at the coarser resolution, most results remained unchanged. Only the water–energy model of O’Brien

(1993) and minimum temperature performed slightly better than the combination of  $1/kT$  with precipitation (see Table 3). When considering the small subset of the Old World, the effect of evapotranspiration (AET, and the combination of PET and WD) exceeded the effect of  $1/kT$  and precipitation; however, the best model again included minimum temperature and minimum precipitation (see Table 3). To control for unbalanced regional sampling (most of the Old World samples are located on the islands of tropical Asia, with only a few in central Africa





**Figure 5** (a) Relationship between pure species richness ( $S$ ) and species richness estimated from rarefaction ( $S_{\text{exp}}$ ) for two different levels of the number of individuals [ $S_{\text{exp}}(100)$  for 100 individuals,  $S_{\text{exp}}(300)$  for 300 individuals]. Pearson's correlation coefficients are 0.91 and 0.98 for species numbers rarefied to 100 and 300 individuals, respectively. (b) The rarefaction curves for individual forest plots constructed using 100, 200, 300, 400 and 500 individuals. Productivity [here measured using actual evapotranspiration (AET); darker shading represents plots with higher AET] apparently does not affect species richness via increasing number of individuals, as the curves concerning more productive sites lie above those concerning less productive sites, and are steeper.

and in boreal and temperate Europe) we repeated the overall analysis including both region and major climatic zone (tropics versus the temperate zone) as model effects. The fit of all models was improved and the best model again included the combination of minimum temperature with minimum precipitation.

The regression tree (Fig. 4) revealed that high-richness plots and low-richness plots are best distinguished by the minimum temperature of each site. Moreover, the distinction within high-richness plots is based on the value of minimum precipitation.

In the case of plots characterized by lower minimum temperature, measures characterizing productivity (AET, NPP) play some role in distinguishing plots with high and low richness.

Rarefied species richness  $S_{\text{exp}}$  correlated tightly with pure species richness  $S$  (Fig. 5a) and the relative ranking of individual environmental variables in terms of their effects on  $S_{\text{exp}}$  was very similar to ranks obtained using  $S$  (Table 4). This indicates that individual sites do not lie on one common rarefaction curve (Fig. 5b), and differences in species richness between sites are not attributable to the differences in numbers of individuals. Moreover, the environmental parameters which affect species richness patterns apparently do not affect them through the number of individuals. This is supported by the fact that  $N$  is a worse predictor of species richness than are the environmental variables, and also by the fact that the environmental variables do not predict  $N$  very well in comparison to their ability to predict  $S$  (Table 4). Variation partitioning for the model which combined our best model with the number of individuals (in polynomial terms, which fitted better than pure  $N$  or  $\ln N$ ) indicated that from the 83% variance explained in total, the explained variance shared between individuals and environmental variables was only 30%, pure environmental effects being 43%, whereas the pure effect of  $N$  explained only 10% of the total variance (Fig. 6). Similar results were obtained for our second best model (Appendix S4). These results indicate that the major effect of available energy is independent of the total number of individuals.

As predicted by the MTB, species richness decreased with  $1/kT$ , the slope of linear regression being  $-0.70$ . The effect was similar, although weaker, when using mean growing season temperature instead of annual mean temperature. When using both linear and quadratic terms of  $1/kT$ , the fit was better (Table 2, Fig. 7), indicating that the functional relationship between  $1/kT$  and  $\ln S$  was curvilinear. When considering the effect of  $1/kT$  together with precipitation, AIC decreased even more. Since this full model included the polynomial effect of  $1/kT$  together with the effect of precipitation, the curvilinearity of the relationship between  $1/kT$  and species richness cannot be attributed to the effect of precipitation. Moreover, the effect of precipitation cannot be mediated by the number of individuals (as is implied by Fig. 1), because the results remained unchanged when controlling for this effect by rarefaction (Table 4).

## DISCUSSION

We did not find evidence for a direct effect of productivity per se on local tree species richness. All estimates of productivity, including NDVI, NPP and AET, and also those derived more directly from stem diameters and the xylem flux of trees in respective sites, performed poorly in comparison to a simple combination of temperature and water availability. These two variables certainly affect ecosystem productivity, but since their effect was comparatively stronger than productivity estimates themselves, it seems that it is not productivity through which these two factors affect species richness. Moreover, all species richness patterns were maintained after controlling for number

**Table 3** Comparison of results from the ordinary least squares (OLS) linear regressions using environmental data of original resolution and the resolution of 1° latitude × longitude, results considering plots only from the Old World (only 38 samples in total) and results in which either region or the distinction between tropical and temperate zone (or both) were used as covariates. See Table 1 for explanations and definitions of individual variables.

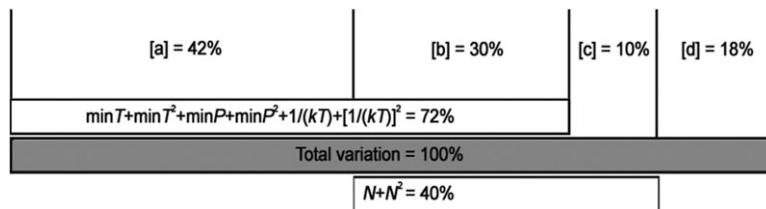
Environmental predictors in the model	Original resolution		1 degree resolution		Old World (original resolution)		Regions as a covariate		Tropics-temperate as a covariate		Tropics-temperate + regions as covariates	
	AIC	R <sup>2</sup>	AIC	R <sup>2</sup>	AIC	R <sup>2</sup>	AIC	R <sup>2</sup>	AIC	R <sup>2</sup>	AIC	R <sup>2</sup>
$\min T + \min T^2 + \min P + \min P^2 + 1/kT + (1/kT)^2$	429	0.72	532	0.63	67	0.79	363	0.77	399	0.75	352	0.78
$\min T + \min T^2 + \min P + \min P^2$	463	0.69	542	0.62	62	0.77	427	0.73	440	0.71	410	0.74
$1/kT + (1/kT)^2 + P + P^2 + (1/kT) \times P$	505	0.66	612	0.54	73	0.72	425	0.73	462	0.70	414	0.74
$\min T$	529	0.63	598	0.55	79	0.66	505	0.66	521	0.64	497	0.67
$\min T + \min T^2$	531	0.63	599	0.55	78	0.62	503	0.66	519	0.64	496	0.67
$\min PET + \min PET^2 + R$	531	0.63	595	0.56	74	0.67	483	0.68	520	0.64	468	0.70
$1/kT + P$	542	0.62	624	0.52	72	0.67	463	0.70	494	0.67	447	0.71
$t + P$	548	0.61	628	0.52	72	0.65	466	0.70	496	0.66	451	0.71
$\min PET + \min PET^2$	567	0.59	612	0.54	84	0.56	538	0.63	557	0.60	531	0.64
$t + t^2$	578	0.58	657	0.48	83	0.56	516	0.65	535	0.63	507	0.66
$1/kT + (1/kT)^2$	579	0.58	657	0.48	83	0.57	516	0.65	535	0.63	507	0.66
$PET + PET^2 + WD + PET \times WD$	604	0.55	634	0.51	65	0.76	500	0.67	504	0.66	484	0.69
$1/kT$	614	0.53	667	0.46	84	0.52	537	0.63	550	0.61	528	0.64
$t_{\text{gws}} + t_{\text{gws}}^2$	615	0.53	681	0.44	87	0.51	511	0.66	544	0.62	509	0.66
$t$	620	0.52	679	0.45	86	0.50	540	0.63	553	0.60	531	0.64
$\min PET$	624	0.52	647	0.49	85	0.51	542	0.62	561	0.60	530	0.64
$AET + AET^2$	634	0.51	649	0.49	68	0.71	517	0.65	521	0.64	504	0.67
$t_{\text{gws}}$	667	0.46	700	0.41	89	0.46	549	0.62	567	0.59	540	0.63
$PET + PET^2$	670	0.46	725	0.37	90	0.45	553	0.61	566	0.59	542	0.63
$WF\_T + WF\_T^2$	682	0.44	848	0.12	78	0.62	571	0.59	575	0.58	545	0.62
$AET$	688	0.43	700	0.41	79	0.58	532	0.63	535	0.62	517	0.65
$R + R^2$	738	0.35	725	0.37	77	0.63	531	0.64	571	0.59	492	0.68
$PET$	739	0.34	765	0.30	97	0.34	578	0.59	590	0.56	560	0.61
$NPP + NPP^2$	755	0.31	755	0.31	87	0.48	550	0.62	577	0.58	517	0.65
$NPP$	756	0.31	756	0.31	87	0.45	548	0.62	576	0.58	517	0.65
$P + P^2$	760	0.31	753	0.32	80	0.59	535	0.63	575	0.58	497	0.67
$WF\_T$	764	0.30	761	0.30	86	0.51	531	0.64	573	0.58	493	0.67
$P$	771	0.28	881	0.03	96	0.36	584	0.59	597	0.55	559	0.61
$Biomass\_T + Biomass\_T^2$	779	0.27	779	0.27	88	0.48	534	0.63	576	0.58	497	0.67
$\min P + \min P^2$	828	0.16	880	0.03	107	0.14	608	0.55	623	0.52	577	0.59
$\min P$	834	0.16	836	0.15	106	0.20	515	0.65	528	0.63	478	0.69
$Biomass\_T$	835	0.15	835	0.15	104	0.20	521	0.65	538	0.62	486	0.68
$NDVI$	855	0.09	890	0.003	103	0.23	608	0.55	526	0.52	577	0.59
$NDVI + NDVI^2$	872	0.06	848	0.06	112	<0.01	616	0.54	634	0.51	586	0.58
$WF + WF^2$	874	0.06	850	0.06	113	0.04	618	0.54	635	0.51	588	0.58
$Biomass + Biomass^2$	880	0.03	888	0.03	112	0.05	603	0.55	635	0.50	588	0.57
$Biomass$	880	0.02	880	0.03	113	0.03	601	0.56	633	0.50	584	0.58
$WF$	884	0.01	884	<0.01	111	0.03	600	0.56	631	0.50	582	0.58
None (only covariates)	889	<0.01	889	<0.01	110	0.05	604	0.55	635	0.50	586	0.57
None (only covariates)	—	—	—	—	—	—	610	0.55	—	—	—	—
None (only covariates)	—	—	—	—	—	—	—	—	634	0.51	—	—
None (only covariates)	—	—	—	—	—	—	—	—	—	—	585	0.58

**Table 4** Comparison of the models (ordinary least squares, OLS) concerning pure species richness ( $\ln S$ ), species richness estimated from rarefaction for 100 and 300 individuals [ $S_{\text{exp}}(100)$  and  $S_{\text{exp}}(300)$ , respectively] and number of individuals ( $\ln N$ ). The three last rows refer to the explanatory power of the number of individuals. See Table 1 for explanations and definitions of individual variables.

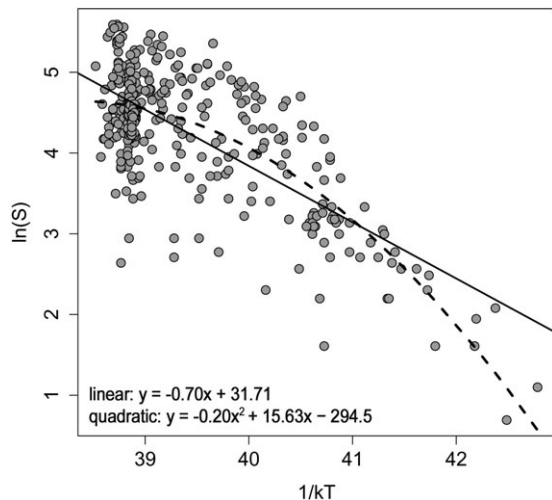
	$\ln S$		$S_{\text{exp}}(100)$		$S_{\text{exp}}(300)$		$\ln N$	
	AIC	$R^2$	AIC	$R^2$	AIC	$R^2$	AIC	$R^2$
$\min T + \min T^2 + \min P + \min P^2 + 1/kT + (1/kT)^2$	429	0.72	2783	0.65	1677	0.49	371	0.21
$\min T + \min T^2 + \min P + \min P^2$	463	0.69	2787	0.64	1676	0.48	386	0.17
$1/kT + (1/kT)^2 + P + P^2 + (1/kT) \times P$	505	0.66	2823	0.61	1690	0.44	405	0.13
$\min T$	529	0.63	2870	0.54	1714	0.32	389	0.13
$\min T + \min T^2$	531	0.63	2861	0.55	1716	0.32	394	0.14
$\min \text{PET} + \min \text{PET}^2 + R$	531	0.63	2826	0.6	1690	0.43	399	0.13
$1/kT + P$	542	0.62	2837	0.58	1706	0.36	417	0.09
$t + P$	548	0.61	2837	0.58	1707	0.36	417	0.08
$\min \text{PET} + \min \text{PET}^2$	567	0.59	2873	0.54	1716	0.32	400	0.12
$t + t^2$	578	0.58	2949	0.43	1745	0.18	407	0.11
$1/kT + (1/kT)^2$	579	0.58	2924	0.47	1743	0.2	408	0.11
$\text{PET} + \text{PET}^2 + \text{WD} + \text{PET} \times \text{WD}$	604	0.55	2884	0.53	1696	0.41	429	0.07
$1/kT$	614	0.53	2924	0.47	1743	0.19	422	0.07
$t_{\text{gws}} + t_{\text{gws}}^2$	615	0.53	2933	0.40	1745	0.18	431	0.04
$t$	620	0.52	2925	0.47	1743	0.2	423	0.06
$\min \text{PET}$	624	0.52	2897	0.51	1721	0.29	415	0.08
$\text{AET} + \text{AET}^2$	634	0.51	2947	0.43	1702	0.37	435	0.04
$t_{\text{gws}}$	667	0.46	2947	0.43	1744	0.19	415	0.09
$\text{PET} + \text{PET}^2$	670	0.46	3025	0.3	1755	0.14	434	0.04
$\text{WF}_T + \text{WF}_T^2$	682	0.44	2981	0.36	1745	0.1	388	0.15
$\text{AET}$	688	0.43	2920	0.47	1698	0.38	440	0.02
$R + R^2$	738	0.35	2989	0.37	1735	0.24	428	0.06
$\text{PET}$	739	0.34	3002	0.34	1752	0.15	440	0.02
$\text{NPP} + \text{NPP}^2$	755	0.31	3028	0.26	1729	0.17	416	0.05
$\text{NPP}$	756	0.31	3026	0.26	1727	0.18	415	0.05
$P + P^2$	760	0.31	3077	0.19	1751	0.16	432	0.05
$R$	764	0.3	3012	0.32	1736	0.23	426	0.06
$\text{WF}_T$	771	0.28	3039	0.24	1748	0.07	413	0.09
$P$	779	0.27	3021	0.31	1736	0.23	430	0.05
$\text{Biomass}_T + \text{Biomass}_T^2$	828	0.16	3074	0.17	1753	0.06	433	0.01
$\min P + \min P^2$	834	0.16	3070	0.21	1722	0.3	433	0.04
$\min P$	835	0.15	3074	0.2	1725	0.28	432	0.04
$\text{Biomass}_T$	855	0.09	3100	0.1	1756	0.03	445	< 0.01
$\text{NDVI}$	872	0.06	3133	0.06	1779	< 0.01	448	< 0.01
$\text{NDVI} + \text{NDVI}^2$	874	0.06	3133	0.06	1779	0.01	447	< 0.01
$\text{WF} + \text{WF}^2$	880	0.03	3142	< 0.01	1766	0.01	420	0.08
$\text{Biomass} + \text{Biomass}^2$	880	0.02	3135	< 0.01	1758	< 0.01	427	0.06
$\text{Biomass}$	884	0.01	3133	< 0.01	1756	< 0.01	442	0.01
$\text{WF}$	889	< 0.01	3140	< 0.01	1765	< 0.01	441	0.02
$N + N^2$	706	0.40	–	–	–	–	–	–
$\ln N$	714	0.39	–	–	–	–	–	–
$N$	761	0.30	–	–	–	–	–	–

of individuals via rarefaction, and number of individuals did not appear as an important determinant of species richness. This indicates that species richness does not simply follow the total number of individuals, as predicted by the MIH, which is the most straightforward explanation of the richness–productivity relationship. However, our rejection of the MIH does not mean that productivity, and consequently number of

individuals, does not play any role in species richness patterns. Obviously, in very unproductive environments (e.g. deserts or tundra), population sizes are strongly limited and species richness cannot exceed the total number of individuals. The regression tree indeed suggested that species richness was affected by productivity measures in areas characterized by low minimum temperature. Nonetheless, our data concern forest



**Figure 6** Variation partitioning for our best model [ $\ln S \sim \min T + \min T^2 + \min P + \min P^2 + 1/kT + (1/kT)^2$ ] and number of individuals ( $\ln S \sim N + N^2$ ). (a) represents variability explained by our best model only, (b) is the explained variability shared by both models, (c) represents variability explained by number of individuals only and (d) is unexplained variability.



**Figure 7** The relationship between mean annual temperature, expressed according to the metabolic theory of biodiversity (MTB) as  $1/kT$ , and the natural logarithm of species richness ( $\ln S$ ). The solid line represents linear regression, and the dashed line is the quadratic fit.

plots where the total number of individuals is generally not strongly limited, so that this effect is negligible.

The MIH has always been controversial. On one hand, some evidence has been found that species richness follows number of individuals quite closely (Kaspari *et al.*, 2000; Hurlbert, 2004; Evans *et al.*, 2006), although species richness could never be attributed to pure sampling effect (Evans *et al.*, 2008). However, the close correlation between number of individuals and number of species does not imply a causal link from individuals to species. The causality may be in fact reversed. If there is (for any reason) a higher number of species, it probably positively affects the total number of individuals as well. This possibility is in accord with our findings that species richness is more closely correlated with energy availability measures than is the total number of individuals (see also Currie *et al.*, 2004). Overall, our finding that species richness patterns are largely independent of total numbers of individuals provides strong evidence against the MIH.

Our results concerning the effect of temperature (Fig. 7) correspond to the original predictions of the MTB (Allen *et al.*, 2002), although, unlike the MTB prediction, the relationship is

significantly curvilinear. Moreover, the observed curvilinearity cannot be attributed to the effect of other environmental factors, indicating that the effect of temperature itself is more complex than assumed by the MTB. These findings are also in accord with the conclusions of Currie (2007) who stated that only a complex model containing quadratic terms of both temperature and water availability explained species richness in forest plots (although his study did not explore the effect of other environmental variables). In fact, it is not clear how exactly MTB predictions depend on other conditions including water availability and resource abundance (Gillooly & Allen, 2007). Another problem concerns the scale dependency of richness patterns. The constant (scale-independent) slope of the temperature–richness relationship should be expected only if the species–area relationship had constant slope across environmental gradients, which is usually not the case (Storch *et al.*, 2005), and has been shown to be violated for regional tree species richness patterns as well (Wang *et al.*, 2009).

Water is considered to be the most important confounding factor interacting with temperature (Allen *et al.*, 2007). Water and energy determine biological dynamics including photosynthesis (O'Brien, 1993); the problem is, however, how these biological processes ultimately translate into species richness. The MTB has assumed that water controls the total number of individuals (Allen *et al.*, 2007; see Fig. 1). However, this proposed mechanistic linkage is in conflict not only with our finding that the effect of water availability concerns rarefied species richness as well, but also with results of Clinebell *et al.* (1995), who showed that precipitation had a strong effect on species richness of tropical lowland trees and lianas but not on the total number of individuals. The causal links between temperature, water and variation in biodiversity thus remain unclear. This is exacerbated by the fact that species richness patterns cannot be determined solely by a metabolic dependence of speciation rates, because other factors including extinction rates, trophic interactions (Stegen *et al.*, 2009) or species spatial dynamics (Storch *et al.*, 2006) must also necessarily play a role in generating diversity patterns.

These results beg an important question: to what extent are limits of species distribution given by their environmental tolerances important for determining species richness patterns? Variation in forest plot diversity is consistent with the 'climatic tolerance hypothesis', as the minimum values of both temperature and precipitation represent, together with mean values, the

most important predictors of species richness. This is in accord with the assumption that more species have adapted to humid and warm low-latitude environments which have had historically both greater area and greater temporal stability than high-latitude environments (Latham & Ricklefs, 1993; Clarke, 2007), and these adaptations still constrain species from spreading out of the warm and humid areas due to conservatism of their niches (Wiens & Donoghue, 2004). However, some problems with this explanation remain (see Algar *et al.*, 2009). Moreover, higher reported diversification rates in warmer temperatures (Allen *et al.*, 2006; Svenning *et al.*, 2008) indicate that the differential speed of evolutionary processes cannot be neglected. Temperature can thus have several independent effects on species richness patterns, in accord with our finding that the best models include several terms concerning temperature.

In summary, our findings provide little support for the determination of species richness via regulation of the total number of individuals, and only a limited support for a purely metabolic explanation of species richness patterns. Our analyses show that factors that limit the spatial distribution of species are among the primary drivers influencing local species richness. These findings support the thesis that such climatic extremes play an important role in shaping global variation in species richness.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** List of full regression models from ordinary least squares (OLS) regression including coefficients and intercepts.

**Appendix S2** Pearson correlation matrix of variables used in the regression analysis.

**Appendix S3** The problem of independence of  $\min T$  and  $1/kT$ .

**Appendix S4** Variation partitioning for the second best model and the number of individuals.

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## BIOSKETCH

**Irena Šimová** is a PhD student interested in macroecology, biodiversity and vegetation science. Her research concerns mechanisms generating species richness patterns in plants at various spatial scales.

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