The species–energy theory: a role for energy variability

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Species–energy theory posits that energy availability regulates population sizes, extinction rates and ultimately species richness. This theory has focused mostly on total energy as a measure of energy availability. However, because energy variation can also influence population sizes and extinction rates, species–energy theory should arguably consider simultaneously both total energy and its variation. Using data on species richness of land birds and mammals, we compared the fit of three species–energy models including total energy, energy variation or both combined. We show that the combination of total energy and energy variation has greater predictive power than any of them considered separately. We also evaluate three crucial assumptions of this modified species–energy theory and show that they are supported by available data. These results illuminate the current debate on climate change, given that both average conditions and variability of climatic conditions are likely to change in the future.

The species–energy theory (Wright 1983) has been used widely to explain the geographic variation in species richness (Evans et al. 2005). Under this theoretical framework, energy availability regulates population sizes (Wright 1983), which in turn determine population extinction rates (Pielou 1969). Thus, areas with low energy availability result in smaller population sizes and greater extinction rates than areas with higher available energy. This model, derived from the species–area theory (MacArthur and Wilson 1967), posits that an increase in available energy (E) is equivalent to an increase in area (A) and should thus result in a proportional increase in the total number of individuals (N) with increasing E. When this relationship is coupled with a power function linking species richness (S) and N, the result is a power function linking species richness and energy (Srivastava and Lawton 1998), known as species–energy relationship (SER, Wright 1983):

$$S = kE^z, \qquad (1)$$

where k and z are constants. In this framework, energy availability is equivalent to island size in species–area theory (Wright 1983), and the use of total amount of energy (measured as the average or sum of annual energy) as an explanatory variable of SER assumes implicitly that temporal availability in resources does not influence population sizes and extinction rates. Thus, $E = E_T$, where E_T is total amount of energy available in an area irrespective of temporal variation in energy flux. However, energy availability does vary through time, and such temporal energy variation may lead to increased mortality and

reduced fecundity, thus influencing population dynamics (Sæther et al. 2002a). Population fluctuations may in turn increase extinction probability and ultimately decrease species richness (Leigh 1975, Wright 1983, Sæther 1997, Sæther et al. 2002b). Below, we propose a modification of Wright's (1983) original SER formulation by including seasonal energy variation.

Wright (1983) assumed that the total number of individuals of all species at a particular locality is proportional to the total amount of energy available, $N = \rho E_T$, where ρ is a spatially invariant parameter representing the number of individuals per unit of energy. Based on Preston's (1962) canonical theory of species abundance, Wright defined the species–energy relationship as $S = b\left(\dfrac{\rho}{m}\right)^z E_T^z$, where b is a fitted constant and m is the population size of the rarest species in the community, representing an abundance threshold of extinction (all species rarer than m will go extinct; notice that $b\left(\dfrac{\rho}{m}\right)^z$ is the constant k in eq. 1). However, if available energy varies through time, the number of individuals per unit energy will likely be lower than in a constant environment, as periods with low energy availability will represent bottlenecks that constrain population abundance and increase probability of extinction (Leigh 1975). Let

$$\rho_e = \frac{\rho_0}{E_V}, \qquad (2)$$

which is the effective number of individuals per unit energy in a variable environment, where ρ_o is the number of individuals in a constant environment and E_v is a measure of energy variability. Specifically, we define $E_v = 1 + q\,\mathrm{CV}(E)$, where $\mathrm{CV}(E)$ is the coefficient of variation of annual energy and q is a constant that determines the strength of the effect of $\mathrm{CV}(E)$ on species richness (i.e. the conversion rate from ρ_o to ρ_e). Thus, when either q or $\mathrm{CV}(E)$ are zero, $\rho_e = \rho_o$ and when q and $\mathrm{CV}(E)$ are greater than zero, $\rho_e < \rho_o$. Note that, although we have assumed for simplicity a linear form for eq. 2, this relationship could be described by more complex, non-linear functions. However, assessing the form of this relationship is beyond the scope of this paper. The species–energy relationship now becomes $S = b\left(\dfrac{\rho_e}{m}\right)^z E_T^z$, and substituting ρ_e by eq. 2 we obtain

$$S = b\left(\frac{\rho_0}{mE_V}\right)^z E_T^z. \tag{3}$$

Equation 3 is a generalization of Wright's species–energy relationship that relaxes the potentially unrealistic assumption that energy variation does not have an effect on species richness. It posits that both total energy and energy variation determine total species richness by affecting population sizes and extinction probabilities. Equation 3 can be simplified by defining $k' = b\left(\dfrac{\rho_0}{m}\right)^z$, so we propose to define the species–energy relationship as

$$\mathrm{SER_{TV}}:\ S = k'\left(\frac{E_T}{E_V}\right)^z, \tag{4}$$

where the subscripts "T" and "V" stand for total energy and its variation.

It is important to mention here that both the original species–energy relationship proposed by Wright (1983) and the modifications proposed here ($\mathrm{SER_V}$ and $\mathrm{SER_{TV}}$) apply to resident, locally breeding species. The reason for this requirement is that the demography of non-breeding, migratory species may not be subject to local environmental conditions strongly enough to reflect those conditions, as has been also pointed out for the equilibrium theory of island biogeography (Simberloff 1976).

Our review of the literature suggests that most studies on species–energy theory have so far considered only total available energy (Hawkins et al. 2003a, Hurlbert 2004, Evans et al. 2005, 2006a, Storch et al. 2005, 2006). More recently, a few studies have considered energy variation (Hurlbert and Haskell 2003, Evans et al. 2006b, Mönkkönen et al. 2006). Note, however, that these studies have focused on bird richness in the North American breeding season which includes many migratory species, which we argue is not ideal for an evaluation of SER. To our knowledge no studies have considered both total energy and its variation simultaneously. Here we show that the combination of these two aspects of energy availability leads to better predictions of the continental variation of bird and mammal species richness than each of them considered separately.

We use data on land bird and mammal richness and energy availability (measured as actual evapotranspiration [AET] and potential evapotranspiration [PET]) in

$1° \times 1°$ cells throughout the Americas (Fig. 1) to evaluate the fit of three nested SER models to the data. The first model includes both total energy and energy variability ($\mathrm{SER_{TV}}$, eq. 4). A second model includes only total energy as a measure of energy availability:

$$\mathrm{SER_T}:\ S = k(E_T)^z. \tag{5}$$

The final model includes only energy variation:

$$\mathrm{SER_V}:\ S = k'(E_V)^z. \tag{6}$$

Materials and methods

Energy and taxon distribution maps

To estimate bird and mammal richness for the whole Americas, we used digital maps of the geographic ranges of 4247 species of birds (Ridgely et al. 2007) and 1786 species of mammals (Patterson et al. 2007). Total richness data were obtained using a geographic information system, dividing the Americas into 4220 equal-distanced cells of $1° \times 1°$, with the geographic projection and the coordinate system measured by decimal degrees of latitude/longitude (<www.ecoevol.ufg.br/index.php>). We used this scale because the use of range map data at finer scales increases the probability of false occupancies, while using coarser scales decreases that probability (Hurlbert and Jetz 2007). For each cell we estimated bird and mammal richness as the number of overlapping range maps of each of these taxa.

It should be noted that migrant species are not subject to energetic conditions of a single locality and may thus escape seasons of low energy availability (Hurlbert and Haskell 2003). Mammalian species in our dataset are mostly resident. In contrast, bird species included both residents and migrants, but with a high proportion of residents (Chesser 1994, Stotz et al. 1996). Although the inclusion of migrants can certainly generate noise, we should still be able to detect a strong energy–richness relationship if one exists.

We considered two common measures of energy availability, potential evapotranspiration (PET) and actual evapotranspiration (AET). PET and AET estimates were based on monthly averages of 60 yr of weather data (1920–1980), gridded by Ahn and Tateishi (1994) and Tateishi and Ahn (1996) at $0.5° \times 0.5°$ cells (<www.grid.unep.ch/data/download/gnv183.zip>). We used annual averages of energy availability as a measure of total energy and the coefficient of variation (CV) of the monthly average within the year of energy availability as an estimate of variability. We use this measure of variability because it is a simple and standardized measure of dispersion (Zar 1999) and it has been used before in a similar context (Leigh 1975, Saltz et al. 2006), which makes our analysis comparable to previous studies. Although there are of course other measures of energy variability besides the CV, comparing the relative fit of these measures is beyond the scope of this paper. Some cells had data available for AET but not for PET; we chose to eliminate those incomplete cells to avoid bias in regression analyses. Thus, a total of 4108 cells were analyzed.

It is important to justify our use of intra-annual (seasonal) variation and not inter-annual energy variation
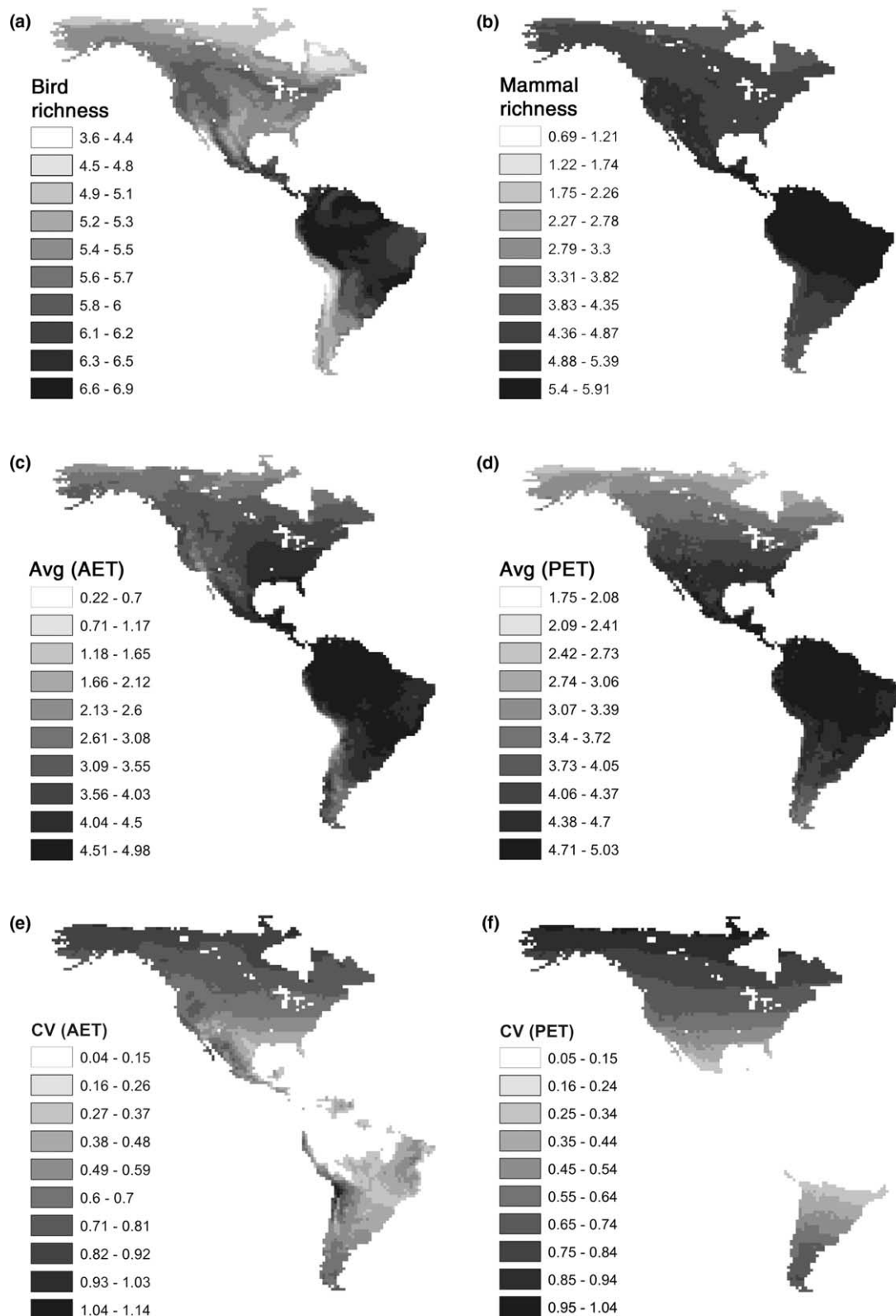
Figure 1. Energy and species richness distribution maps (all variables represented as logarithms). (a) Bird richness. (b) Mammal richness. (c) Average AET. (d) Average PET. (e) Coefficient of variation of AET. (f) Coefficient of variation of PET.

in energy availability. Seasonal climatic variation may constrain populations of permanent residents in a given area especially due to seasonality of energy resources (MacArthur 1972, Herrera 1978, Forsman et al. 2003), while migrant species avoid such constraints (Bolger et al. 2008) by moving to more benign areas. Available evidence suggests that seasonality in resource availability imposes strong reproductive, demographic and dynamic constraints

populations of birds (Herrera 1978, Pérez-Tris and Tellería 2002, Williams et al. 2003, Moreno 2004, Williams and Middleton 2008) and mammals (Ferguson 2002, Stenseth et al. 2002, Isaac and Johnson 2003, Lima et al. 2003, Isaac 2008, Trimble et al. 2009). As resident species are the focus of our study, we therefore assumed that within-year variation in energy availability is more important than among-year energy variation as a determinant of population abundance.

We also evaluated three key assumptions of the SER_{TV} model. The first one is that N and $\frac{E_T}{E_V}$ are positively correlated throughout space. The second assumption is that S is a power function of N, i.e. $S = aN^x$, where a and x are constants. Exponent x should be close to 0.26 for a canonical log-normal, and between 0.16 and 0.39 for other, non-canonical log-normal distributions (Preston 1962, May 1975). The third assumption is that the direct relationships between $\frac{E_T}{E_V}$ and N and between N and S should be equal or greater than the indirect relationship between $\frac{E_T}{E_V}$ and S (i.e. $r_{\frac{E_T}{E_V},N} \geq r_{\frac{E_T}{E_V},S}$ and $r_{N,S} \geq r_{\frac{E_T}{E_V},S}$; Legendre and Legendre 1998). Notice that the parameter q (the strength of the effect $CV(E)$; see Introduction) will not be necessarily the same for the relationships between N and $\frac{E_T}{E_V}$ and between S and $\frac{E_T}{E_V}$. Thus, we used the corresponding value of q fitted to either N or S to evaluate the strength of these relationships.

Evaluating the above assumptions requires not only data on energy availability and species richness but also on species abundances. Although to our knowledge there are no available data of species abundance for the whole Americas, such data are available for season-dependent survey programs of North American birds. We used data from the Audubon Christmas Bird Count (CBC) for 1997 (Sauer et al. 1996). The CBC surveys were conducted during the winter season and thus include mostly resident species in the north and short distance wintering migrants in the south as defined by the Patuxent Wildlife Research Center, Laurel, MD. These data seem ideal for evaluating species–energy theory because, as we argued above, such evaluation requires a high proportion of resident species. In contrast, breeding season data such as the Breeding Bird Survey include a high proportion of long-distance migrants (between 55 and 90% of total species; Fig. 7D in Hurlbert and Haskell [2003]).

As in the analysis for the whole Americas, we used a $1° \times 1°$ grid cell size for species richness and abundance, and a $0.5° \times 0.5°$ grid cell size for energy availability. We considered only AET because it was the energy metric that best predicted bird richness. Because survey effort varied among grid cells, we used rarefaction to estimate richness expected for one survey per cell. To this end, we calculated average abundance among surveys of the given cell and then estimated expected richness for that abundance.

Assessment of model fit

For the whole Americas analysis, we evaluated the predictive ability of three nested models. The first model (SER_{TV}; eq. 4) assumes that species richness is determined by both total energy and energy variation: $S = k'\left(\frac{E_T}{E_V}\right)^z$. A second model ($SER_T$) assumes that energy does not vary through time (i.e. $E_V = 1$), so that species richness depends only on total energy: $S = k(E_T)^z$. A final model (SER_V) assumes that total energy does not influence species richness (i.e. $E_T = 1$), which is equivalent to assuming that total energy is geographically constant. Notice that when $E_T = 1$, our measure of energy variation simplifies to $E_V = 1 + qSD(E)$, where $SD(E)$ is the standard deviation of energy; this is because the coefficient of variation includes both the standard deviation and the average of energy $\left(\text{i.e. } CV(E) = \frac{SD(E)}{1}\right)$. Thus, species richness will depend only on energy variation: $S = k'(E_V)^z$. We performed non-linear regression analyses on these models, assessing model fit to the data with Akaike's information criterion (AIC) (Burnham and Anderson 2002). AIC was calculated using maximum likelihood optimization with the mle2 function of the bbmle package of R statistical software (Bolker 2008). It is important to mention here that the average and the coefficient of variation of available energy exhibited high multicollinearity (AET, $R^2 = 0.73$; PET, $R^2 = 0.82$); however, multicollinearity in the predictor variables is not problematic when the fitted model is used for estimating mean responses or making predictions, as we do here, provided that values of the predictor variables for which inferences are to be made follow the same multicollinearity pattern as the data on which the regression model is based (Neter et al. 1996, Graham 2003).

Because the presence of spatial autocorrelation on richness and environmental energy data can result in an overestimation of the number of degrees of freedom (Legendre and Legendre 1998), we conducted partial regression analysis to remove the spatial influence in both dependent and independent variables. Following Legendre and Legendre (1998), we applied trend-surface analysis to express response variables as a nonlinear function of the geographic coordinates (i.e. longitude and latitude) of the sampled grids where the variables were observed. We fitted a third order polynomial with richness or energy measures as response variables:

$$f(x,y) = b_0 + b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 xy^2 + b_6 x^3 \\ + b_7 x^2 y + b_8 xy^2 + b_9 y^3$$

where x and y represent longitude and latitude respectively. Nonsignificant terms were removed and the residuals of each regression analysis were saved and considered partialled out of any spatial structure. We then assessed the fit of the SER models using richness residuals as the response variable and energy residuals as the predictor variables as explained above.

Results and discussion

For both birds and mammals, the SER_{TV} model fitted the data substantially better than the other two SER models (Table 1). Thus, total energy availability and its temporal variation considered simultaneously lead to better predictions of species richness than any of them considered separately. However, the energy measure providing the

Table 1. Akaike's information criterion (AIC) used for model selection. Three species–energy models are compared for each energy measure (AET and PET): SER_T, including only total energy (eq. 5); SER_V, including only energy variation (eq. 6); and SER_{TV} including both total energy and its variation (eq. 7). AIC differences (ΔAIC) are AIC values rescaled so that the best-fitting model has ΔAIC $= 0$, and R^2 is the percent variance explained by the model. The k', z and q columns give the parameter values for the models (all parameters were significative with $p < 0.01$). The Rank column gives the order to the best (1) to worst (6) model fit.

Taxon	Energy measure	Model	AIC	ΔAIC	Rank	R^2	k'	z	q
Birds	AET	SER_{TV}	48639.48	0.00	1	0.77	97.42	0.43	2.61
		SER_T	49259.49	620.01	3	0.73	22.76	0.69	–
		SER_V	54663.00	6023.52	6	0.01	228.89	0.05	68.72
	PET	SER_{TV}	49141.56	502.08	2	0.74	243.19	0.29	46.88
		SER_T	50663.97	2024.49	4	0.62	12.39	0.78	–
		SER_V	52769.78	4130.3	5	0.37	2327.04	-0.55	1.18
Mammals	AET	SER_{TV}	41301.15	1738.15	2	0.81	52.98	0.41	4.33
		SER_T	42448.93	2885.63	3	0.75	9.38	0.71	–
		SER_V	48102.24	8539.24	6	0.02	166.42	-0.01	21.62
	PET	SER_{TV}	39563.00	0.00	1	0.87	114.94	0.32	65.43
		SER_T	42725.49	3162.49	4	0.73	3.48	0.89	–
		SER_V	45535.77	5972.77	5	0.47	510.04	-0.84	0.12

best fit was different for birds and mammals: while AET was a better predictor of species richness than PET for birds, PET was better than AET for mammals, in agreement with previous studies (Currie 1991, Hawkins et al. 2003b) (Fig. 2). The variance explained by the best fitting model was always high (birds: $R^2 = 0.77$; mammals: $R^2 = 0.87$).

Although the above results support the predictions of the SER_{TV} model, a strong test of the theory requires evaluating not only the theory's predictions but also its assumptions. The three assumptions considered here (see Methods) were supported by the data. First, there was a positive, statistically significant correlation between $\frac{E_T}{E_V}$ and N (Spearman $r_s = 0.40$, $p < 0.001$, $n = 682$). Second, the power relationship between S and N was statistically significant, with the slope x within the expected range ($x = 0.35 \pm 0.01$, $R^2 = 0.68$, $p < 0.001$, $n = 682$). Third, the direct relationships between $\frac{E_T}{E_V}$ and N and between N and S were indeed equal or greater than the indirect relationship between $\frac{E_T}{E_V}$ and S (Spearman $r_{\frac{E_T}{E_V},N} = 0.40$, $r_{N,S} = 0.83$, $r_{\frac{E_T}{E_V},S} = 0.42$). Notice that although $r_{\frac{E_T}{E_V},N}$ is slightly lower than $r_{\frac{E_T}{E_V},S}$, which would contradict the assumptions of the SER_{TV} model, the confidence intervals of these coefficients are broadly overlapping $r_{\frac{E_T}{E_V},N} = [0.33, 0.47]$ and $r_{\frac{E_T}{E_V},S} = [0.35, 0.49]$. Furthermore, as before, the best fitting model was SER_{TV} (AIC values: $SER_{TV} = 6926.50$; $SER_T = 7011.85$; $SER_V = 7045.86$), again supporting the modified species–energy theory proposed here. As CBC survey effort varies among individual surveys, we also conducted rarefaction considering the abundance of individuals per survey hour. Results did not differ from those presented above; in fact the relationship between N and S was even stronger than before ($x = 0.36 \pm 0.01$, $R^2 = 0.86$, $p < 0.001$, $n = 680$).

When the spatial autocorrelation was taken into account the results also showed that the SER_{TV} model had the better
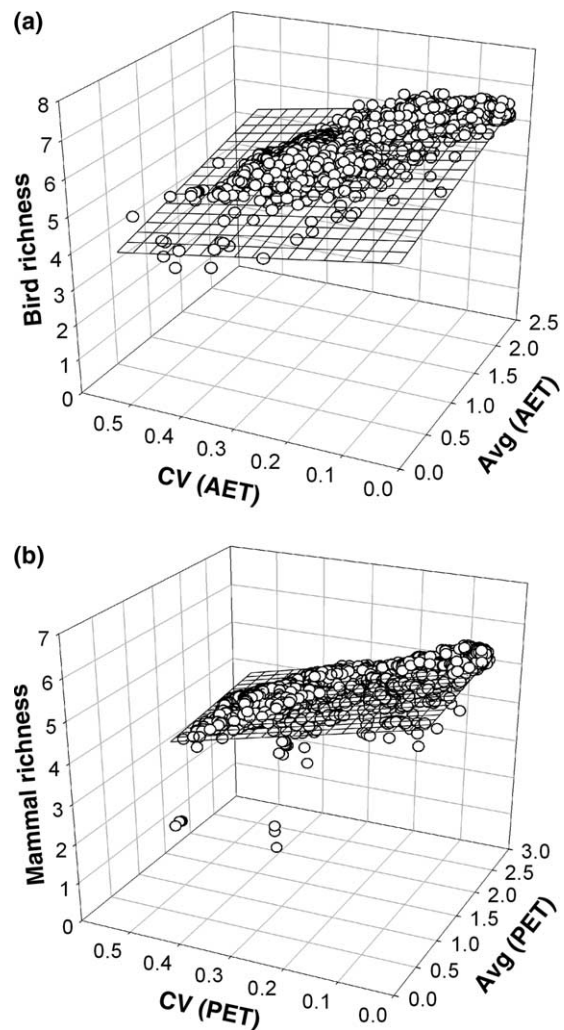

Figure 2. Bird and mammal species richness versus the average (AVG) and the coefficient of variation (CV) of available energy (all variables represented in logarithms). (a) Birds. (b) Mammals.

fit to the data than SER_T and SER_V models. Differences among models were large for bird richness for both energy measures (AET AIC values: $SER_{TV} = -1130.28$; $SER_T = 378.16$; $SER_V = 1261.08$, and PET AIC values: $SER_{TV} = 641.66$; $SER_T = 877.54$; $SER_V = 1486.71$), the same qualitative results were found for mammals although the differences in model fits were not so large as for birds (AET AIC values: $SER_{TV} = -10419.65$; $SER_T = 10353.65$; $SER_V = -7321.43$, and PET AIC values: $SER_{TV} = -10463.01$; $SER_T = -10185.87$; $SER_V = -8072.89$); finally, the CBC data also identified SER_{TV} as the best fitting model, although again with a smaller difference than for the whole Americas (AIC values: $SER_{TV} = -2078$; $SER_T = -2071.92$; $SER_V = -2043.87$).

Although the generality of the above results remains to be evaluated in other organisms and at different scales, we believe our study and that by Willis et al. (2007) strongly suggest that, as a predictive tool, SER must include an evaluation of the influence of total energy and its variation as a determinant of species richness. Species–energy theory has long been controversial (Currie et al. 2004) and ecologists are still far from a predictive theory of species richness (Gaston 2000). However, our proposal brings us closer to that goal.

Our results have important implications for predicting the consequences of global climate change on biodiversity. Most scenarios predict not only a change in average climatic conditions but also increased climatic variability (Meehl et al. 2007). Our study suggests that the effect of climate change on species richness will depend both on the relative magnitude of future changes in average climatic conditions and their temporal variability. Thus, there is a need for studies providing predictions of the future geographic distribution of average PET and AET and their temporal variation to evaluate this question.

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