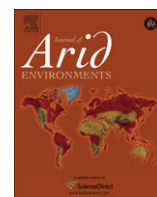




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Habitat specificity can blur the predictions of species–energy theory: A case study of tenebrionid beetles adapted to aridity

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ABSTRACT

Species–energy theory predicts a positive relationship between species richness and energy. The mechanism assumed by this theory is that high energy promotes high population abundance, which in turn promotes high species richness. Evaluations of this mechanism have rendered conflicting evidence, suggesting that more effort is needed to understand the theory's limitations. Several studies have addressed these limitations, contributing to expand the theory's scope by incorporating energy variation, whereas others have demonstrated scale dependence of the more individuals hypothesis. We propose that another limitation of this theory is related to its application to groups of species with strong habitat specificity. We suggest that the expected relationship between energy and richness is not necessarily positive at large scales for groups of species adapted to harsh environments. Using data on tenebrionid beetles from arid areas of southern South America, we contrasted four hypotheses that lead to contrasting predictions about the strength and direction of the species–energy relationship on tenebrionid richness. We found a negative relationship between richness and energy availability. We propose that this negative relationship is the result of a constraint in the mechanisms assumed by species–energy theory because organisms evolve adaptations to survive climatic harshness, which influences population abundances.

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1. Introduction

Species diversity varies greatly throughout space. One of the most striking large scale diversity patterns is the relationship between species richness and environmental energy (Wright, 1983). Wright (1983) formulated a convincing theory that predicts a positive relationship between species richness and total energy available in an area (the species–energy theory, SET). SET posits that high total energy enables species to attain larger population sizes, reducing the risk of stochastic extinction, thus promoting species richness. The generality of this mechanism (dubbed the “more individuals hypothesis” or MIH, Srivastava and Lawton, 1998) is the subject of much current debate (Currie et al., 2004; Evans et al., 2005a, 2005b; Srivastava and Lawton, 1998), indicating that more effort is needed to understand SET's limitations.

One major limitation of the original form of SET was its lack of consideration of energy variation as a limiting factor of population abundances and therefore species richness (Ruggiero and Kitzberger, 2004; Carrara and Vázquez, 2010 and references therein). As Carrara and Vázquez (2010) have shown, such consideration improves the predictive ability of SET models. Other unresolved limitations include the spatial scale dependence of MIH predictions (Evans et al., 2005c) and the effect of habitat specificity on the expected form of the relationship. For example, species restricted to arid regions must tolerate intense solar radiation, low relative humidity and scanty rainfall and food resources (Hadley, 1972; Kéfi et al., 2008), which implies that their population dynamics may be less correlated with energy than that of populations not restricted to arid environments (Holmgren et al., 2006). To our knowledge, no studies have evaluated SET focusing solely on species from harsh environments.

We suggest that there are four alternative forms of the species–energy relationship: positive, nil, negative and unimodal. The rationale for a positive relationship was given above when explaining SET's assumptions. A lack of relationship is expected when organisms are strongly tolerant to changes in energy; thus, if individual abundance is independent of energy availability, species

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richness should be as well. This prediction should hold when species are extremely adapted to aridity and have achieved strong energy independence or resistance (Koford, 1968; Meserve et al., 2003; Zachariassen, 1996). A negative relationship between species richness and energy is expected when organisms are affected negatively by high energy input, as is expected when high energy results in an extremely costly water–energy balance (Zachariassen, 1996). This prediction should hold when extreme climatic conditions of deserts influence negatively population dynamics by affecting energy flux between the environment and the organisms (Cloudsley-Thompson, 2001; Tieleman et al., 2003). Finally, a unimodal relationship can result if the above mechanisms for positive and negative relationships operate simultaneously. For example, unimodality is expected if tenebrionid richness increases with energy until high energy input becomes stressful, resulting in decreased richness.

In this paper we evaluate the relationship between richness of tenebrionid beetles and energy availability in southern South America. Darkling beetles (Coleoptera: Tenebrionidae) are a numerically and functionally conspicuous group among the invertebrate fauna of arid environments (Cepeda-Pizarro et al., 2005). They represent the main food source of insectivorous species (e.g., Flores, 1998), their life cycles are strongly conditioned by climatic conditions (Cepeda-Pizarro et al., 2005) and are good indicators of areas of endemism in southern South America (Domínguez et al., 2006; Morrone et al., 2002). Tenebrionids are able to survive under harsh environmental conditions as a result of physiological and behavioral adaptations (Cloudsley-Thompson, 2001). We evaluate the four above hypotheses relating tenebrionid species richness and energy availability. To this end, we assessed the fit of the four energy–richness models, three considered in Carrara and Vázquez (2010) and a fourth one representing a unimodal relationship, as well as the strength and direction of these relationships. We used data on darkling beetles from Argentina and Chile. In addition to the contribution to evaluating the generality of SET, this study represents the first attempt to identify the determinants of large scale distributional patterns of darkling beetles in this region, which may help the conservation of this endemic-rich group.

2. Materials and methods

2.1. Study area

We considered tenebrionids from a continuous area encompassing continental Chile south of the parallel 29°S, mid-western Argentina between parallels 35–40°S, and southern Argentine Patagonia south of parallel 40°S. We also included several extra-Andean mountains from Argentina as well as numerous islands in the Atlantic and the Pacific. We judged appropriate to include these areas because they have a high percentage of arid or semiarid lands in their territory (Roig-Juñent et al., 2003). Also, as much of these tenebrionids also occur in arid or semiarid areas such as southern Bolivia (Flores and Vidal, 2001) and southern Uruguay (Flores, 1997), these areas were also included in the study (Fig. 1).

It should be noted that the inclusion of islands in our analyses can introduce noise in the species–energy relationship because of island isolation. However, island tenebrionids consisted in only 80 georeferenced records, and results were unchanged when these data were excluded. Thus, we decided to work with continental and insular species together.

2.2. Data source

As our objective was to evaluate the form of the species–energy relationship on species adapted to arid areas, we chose only those

groups that live in arid ecosystems, namely the subfamily Pimeliinae and the tribe Scotobiini (Tenebrioninae). These two groups have developed important adaptations to survive in arid environments, such as the sub-elytral chamber to minimize water loss rates, large body size to increase longevity and functional control (i.e., homeostasis), and the behavioural adaptations such as nocturnal habits to avoid hours of high radiation and scavenger habits to improve water balance (Cloudsley-Thompson, 2001; Flores, 1998).

A total of 3743 records were taken, corresponding to 245 species of Pimeliinae and Scotobiini. The database was constructed by georeferencing tenebrionids from nineteen institutional collections located in seven countries. In Argentina, these institutions included: Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza (IADIZA); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN); Museo de La Plata, Buenos Aires (MLPA); Instituto Superior de Entomología "Dr. Abraham Willink", Fundación e Instituto Miguel Lillo, San Miguel de Tucumán (IMLA); Instituto Patagónico de Ciencias Naturales, San Martín de los Andes, Neuquén (IPCN) (now deposited at IADIZA, Mendoza). In Chile: Museo Nacional de Historia Natural, Santiago (MNNC); Universidad Metropolitana de Ciencias de la Educación, Santiago (UMCE); Laboratorio de Entomología Ecológica, Universidad de La Serena, La Serena (LEULS); Museo de Zoología, Universidad de Concepción, Concepción (UCCC); Instituto de la Patagonia, Punta Arenas (IPUM), and Pedro Vidal private Collection (PVGH). In the USA: National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH). In France: Muséum National d'Histoire Naturelle, Paris (MNHN).

2.3. Richness data

With the collected data we constructed a map of tenebrionid presences, where each georeferenced species record was considered as one observation. Total richness data were obtained using a geographic information system, by dividing the study area in equidistant cells of $0.5^\circ \times 0.5^\circ$, with the geographic projection and the coordinate system measured by decimal degrees of latitude/longitude. As in many cases data within one cell were repeated, we considered those records with the same collection information (i.e., date, site and collectors) as only one observation to avoid pseudoreplication.

Because survey effort varied among grid cells, we used rarefaction to estimate expected richness. To this end, we calculated rarefied species richness for cells that had at least 10 observations using the freely available software Ecosim (Gotelli and Entsminger, 2010). As the cut-off value (i.e., 10 observations by cell) may influence expected richness, we also estimated rarefied richness with cut-offs of 20 and 30 observations per cell. As there was a high correlation between these rarefied richness values (Spearman correlation coefficient > 0.95 , $p > 0.01$), we conducted the analyses considering only rarefied richness for a cut-off of 10 observations, which allowed us to include the greatest number of grid cells for the analyses (84 cells).

2.4. Energy availability

There are two forms of environmental energy that can influence population size (Evans et al., 2006a). One, proposed originally by Wright (1983), are resources available for consumers usually presented using measures of plant productivity, which are interpreted as food for heterotroph species that maintain large population sizes. The other form of energy is environmental temperature,

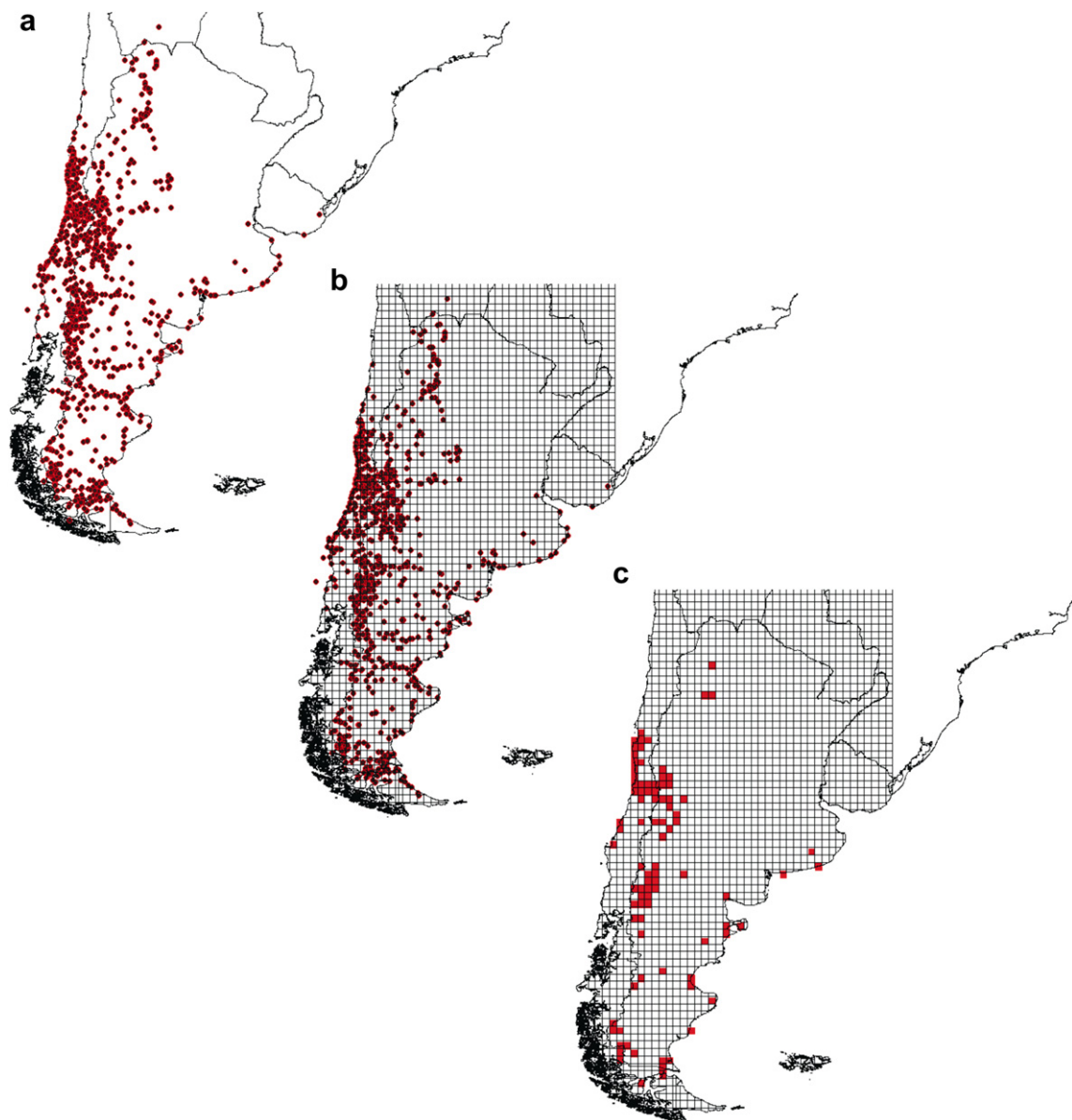


Fig. 1. Distribution of georeferenced data used to evaluate the species–energy relationship: a) Tenebrionid occurrences within the study area; b) grid at $05^{\circ} \times 05^{\circ}$ overlaid to analyze tenebrionid richness and c) grid showing the cells with 10 or more observations (red cells) used to estimate richness. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Table 1

Akaike's Information Criterion (AIC) used for model selection. Four species–energy models are compared for each energy measure (AET and PET): SER_T , including only total energy; SER_V , including only energy variation; SER_{TV} , including both total energy and its variation; and SER_U , representing unimodal relationships between species richness and energy. AIC differences (ΔAIC) are AIC values rescaled so that the best-fitting model has $\Delta AIC = 0$, and R^2 is the percent variance explained by the model. The k' , z , q and b columns give the parameter values for the models where ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. The Rank column gives the order to the best (1) to worst (8) model fit.

Energy measure	Model	AIC	ΔAIC	Rank	R^2	k'	z	q	b
AET	SER_{TV}	299.77	15.30	5	0.11	5.69**	−0.16**	42.06ns	—
	SER_T	302.92	18.45	7	0.05	9.10***	−0.13*	—	—
	SER_V	308.31	23.84	8	0.01	6.40***	−0.59ns	0.01ns	—
	SER_U	302.89	18.42	6	0.08	4.52ns	0.19ns	—	0.01ns
PET	SER_{TV}	289.83	5.36	3	0.22	8.55ns	−0.24***	13.98ns	—
	SER_T	287.56	3.09	2	0.21	25.42***	−0.36***	—	—
	SER_V	295.48	11.01	4	0.15	20.40ns	−0.67ns	0.11ns	—
	SER_U	284.47	0.00	1	0.26	1.25ns	0.66ns	—	0.02*

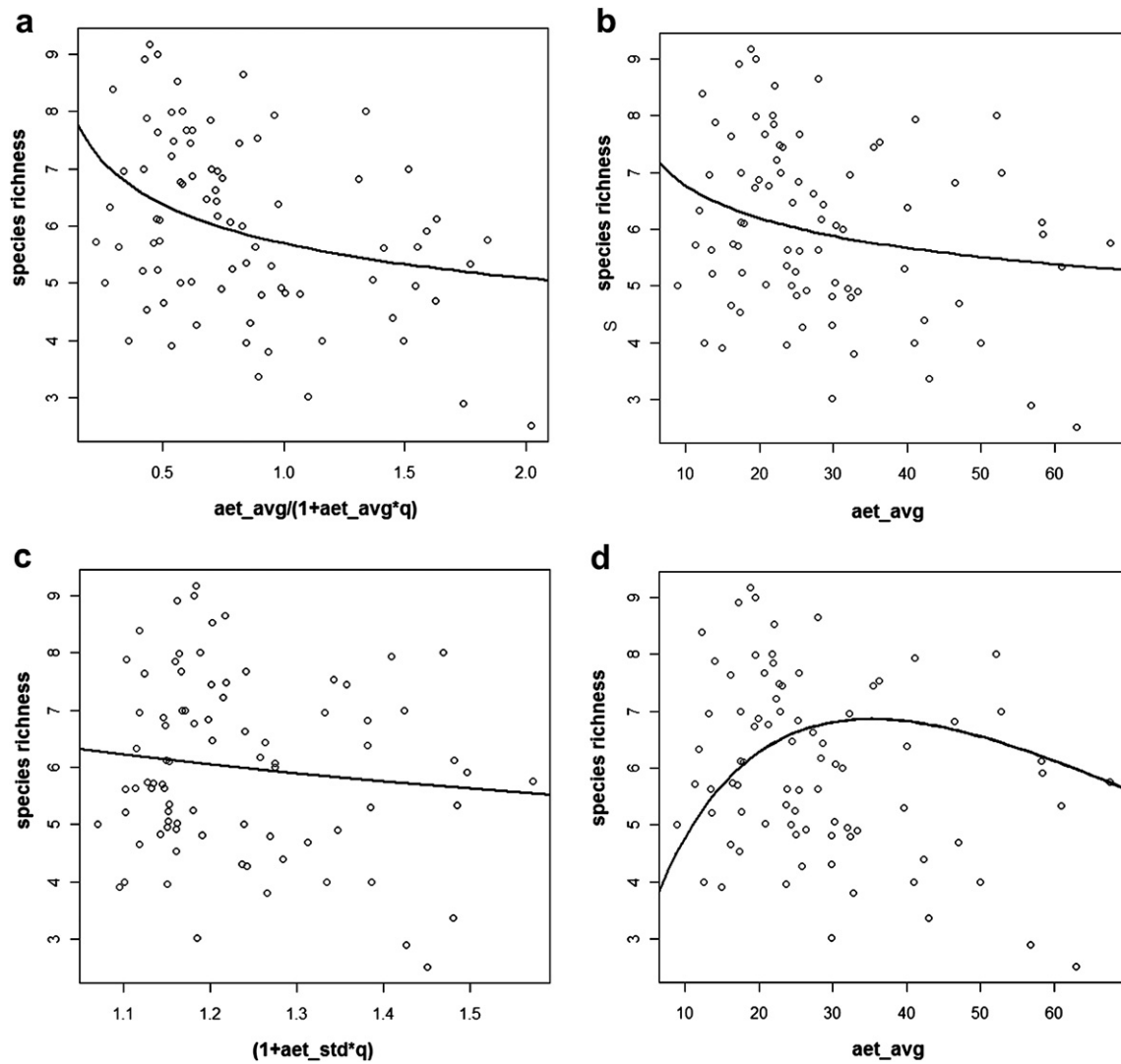


Fig. 2. Non-linear regressions showing the slopes of four nested models SER_{TV} , SER_T , SER_V and SER_U regards AET (a, b, c and d) and PET (e, f, g and h). See parameter estimations in Table 1; aet_avg, mean annual AET; aet_cv, annual AET coefficient of variation; aet_std, annual AET standard deviation; pet_avg, mean annual PET; aet_cv, annual PET coefficient of variation; aet_std, annual PET standard deviation.

which enhances metabolic rates, especially in ectotherms, which in turn influences population abundances (Allen et al., 2006). Thus, as tenebrionid beetles are heterotrophic ectotherms, we considered that both sources of energy could influence tenebrionid population sizes.

We considered two common measures of energy availability representing environmental temperature and water availability (plant resources): potential evapotranspiration (PET) and actual evapotranspiration (AET), respectively. PET and AET estimates were based on monthly averages of 60 years of weather data (1920–1980), gridded by Ahn and Tateishi (1994) and Tateishi and Ahn (1996) at $0.5^\circ \times 0.5^\circ$ cells (<http://www.grid.unep.ch/data/download/gnv183.zip>).

2.5. Assessment of model fit

We evaluated the predictive ability of four nested models. The first model (SER_{TV}) assumes that species richness is determined by both total energy and energy variation: $S = k'(E_t/E_v)^2$. Following Carrara and Vázquez (2010) we define $E_v = 1 + qCV(E)$, where $CV(E)$ is the coefficient of variation of annual energy and q is a constant

that determines the strength of the effect of $CV(E)$ on species richness. A second model (SER_T) assumes that energy variation is unrelated to richness (i.e., $E_v = 1$), so that species richness depends only on total energy: $S = k'E_T^2$. A third model (SER_V) assumes that total energy does not influence species richness (i.e., $E_T = 1$), so that it depends only on energy variation: $S = k'E_v^2$. 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 (i.e., $CV(E) = SD(E)/1$). The final model evaluated was one representing an unimodal species–energy relationship (SER_U). For this model we start considering the SER_T model, which represents the positive exponential function between species richness and energy, adding a term representing the rate of loss or decay of species richness at high energy inputs: e^{-bE_T} , where b is a fitted constant. Thus, our SER_U model is finally represented by: $S = k'E_T e^{-bE_T}$. Notice that the SER_U model is a modified version of Ricker's model of population dynamics (cf. Bolker, 2008).

We performed non-linear regression analyses on these models, assessing model fit to the data with Akaike's information criterion

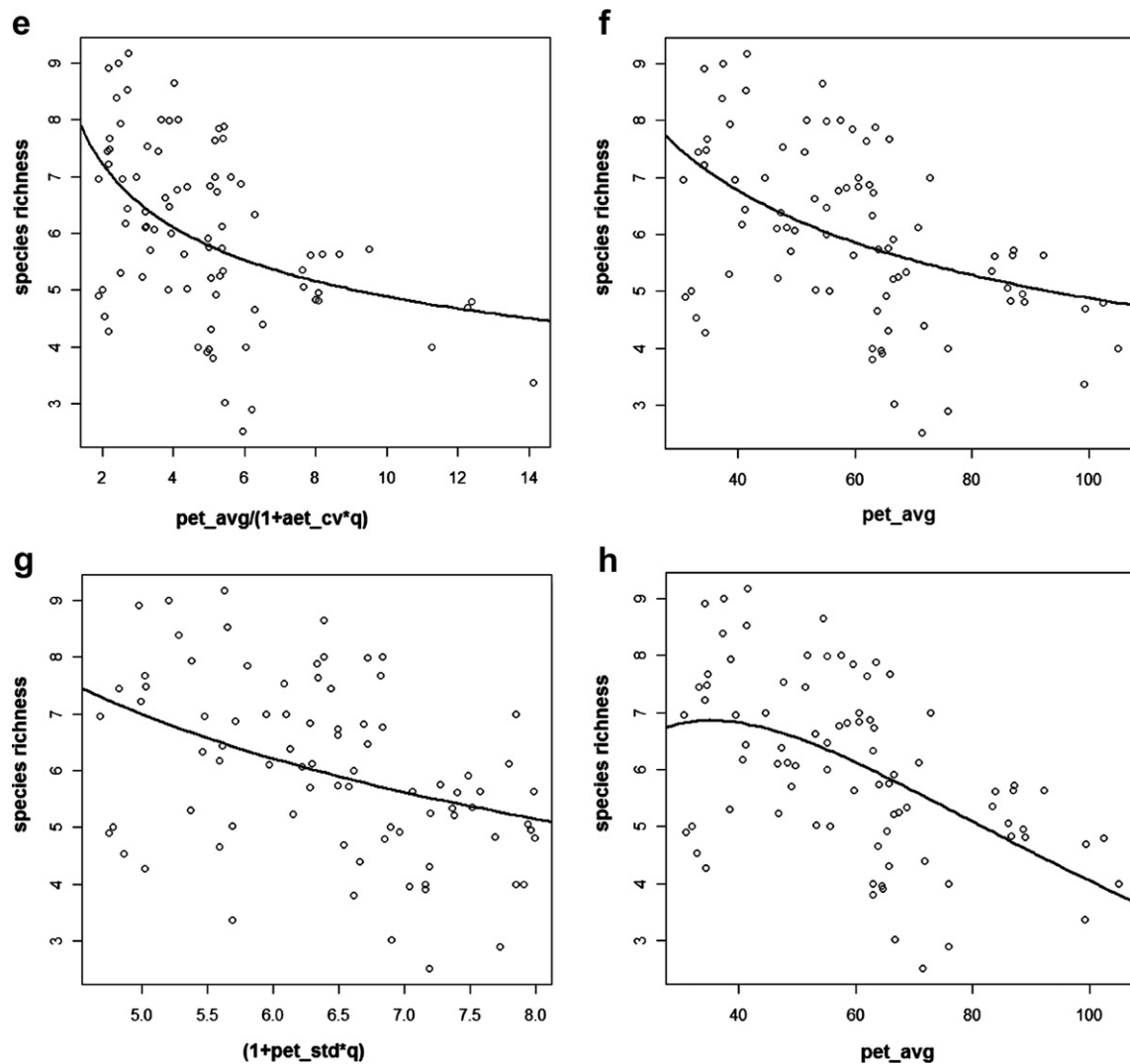


Fig. 2. (continued).

(AIC) (Burnham and Anderson, 2002). AIC was calculated using maximum likelihood optimization with the `mle2` function of the `bbmle` package (Bolker, 2008) of R statistical software (R Development Core Team, 2008). Finally, we excluded two outlying data points with values of standardized residuals greater than 3 in the regression between species richness and both energy measures. Thus, analyses of richness and energy had only 82 cells.

Because the presence of spatial autocorrelation on richness and energy data can result in an overestimation of the number of degrees of freedom (Legendre and Legendre, 1998), we conducted partial regression analysis to decompose 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 non-linear 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:

$$f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4y^2 + b_5xy + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \quad (1)$$

where x and y represent longitude and latitude respectively. Thereafter, the trend-surface was introduced into modeling to

interpret the real influence of spatial heterogeneity on energy variables and species richness. With partial regression analyses it was possible to split the variation of tenebrionid richness into four components: (a) the non-environmental spatial fraction (the component of the spatial variation in species richness that is not shared with the environmental variables); (b) the spatially structured environmental fraction (the spatial structuring in the species richness data that is shared with the environmental variable data); (c) the non-spatial environmental fraction (the component of the spatial variation in species richness that can be explained by the environmental variables independent of any spatial structure); and (d) the unexplained (residual) variation (Legendre and Legendre, 1998).

Because a substantial proportion of several coastal grid cells fell in water, it was necessary to evaluate the influence of land area on tenebrionid richness. It is widely accepted that area availability (A) is related positively with richness (see Rosenzweig, 1995) and can introduce noise in the results of the species–energy relationship. Thus, we evaluated the contribution of area on tenebrionid diversity. To this end, we measured the surface area within each cell as in Rahbek et al. (2007) and performed standard least squares regression between these values and rarefied tenebrionid richness.

Table 2Partial regression analyses showing the partition of variance explained (R^2) by space and energy on tenebrionid richness by nested models.

Energy measure	Model	Total (a + b + c)	Space only (a)	Spatial structured environmental variation (b)	Environment only (c)	Unexplained variation (d)
AET	SER _{TV}	0.27	0.16	0.06	0.05	0.73
	SER _T	0.25	0.20	0.02	0.03	0.75
	SER _V	0.24	0.22	0.01	0.01	0.76
	SER _U	0.27	0.19	0.03	0.05	0.73
PET	SER _{TV}	0.32	0.10	0.12	0.10	0.68
	SER _T	0.31	0.10	0.12	0.09	0.69
	SER _V	0.29	0.13	0.09	0.06	0.71
	SER _U	0.31	0.05	0.17	0.09	0.69

3. Results

The model assuming a unimodal relationship between richness and energy measured as PET achieved the best fit to data (lowest AIC value; Table 1). It should be noted that the slope of this relationship was negative in almost all the range of variation of PET (Fig. 2) and that the only significant parameter in this SER is b , which represents the decay of species richness at high energy inputs (Table 1). The slopes of the other SER models were also significantly negative in almost all models. The exception was the SER_V model for AET and PET, which showed a non significant but still negative relationship and the SER_U model for AET, which showed a non significant unimodal relationship (Table 1). Thus, contrary to SET's expectations, temperature and water availability were mostly inversely related to tenebrionid richness (Fig. 2). The parameter q estimated for each model was never significantly different from zero, which suggests that the effect of energy variation on tenebrionid richness was weak. Finally, only three models had relatively high values of explained variance, SER_U, SER_T and SER_{TV} for PET, while the other models explained little variation (Table 1). Surface area had no effect on species richness ($S = 6.11-0.17A$, $P = 0.62$, $R^2 = 0.03$, $N = 82$), and thus it did not influence the species–energy relationship.

Partial regression analyses left unexplained a high percent of variance on tenebrionid richness, suggesting that other factors besides energy are responsible for tenebrionid diversity. In addition, of the variation, the greatest proportion corresponded to the pure contribution of space, followed by the spatially structured environmental variables and, finally, by the pure contribution of energy (Table 2). The higher proportion of variance explained by pure space suggests a strong spatial autocorrelation of tenebrionid richness. Specifically, the influence of SER_U, SER_T and SER_{TV} for PET on tenebrionid richness is mostly represented by the spatial structure of energy, rather than by the pure contribution of energy.

4. Discussion

We have reported what to our knowledge is the first negative relationship between invertebrate richness and energy at large scales. This result suggests that high abundances are more likely at low than at high energy levels, contradicting SET's expectations (see Wright, 1983). These findings are particularly interesting given the frequent assumption that temperature and water availability influence positively the development, reproduction and survival of insects (Gullan and Cranston, 2005; Kerr and Packer, 1999). In fact, past studies evaluating SET with invertebrate data have always found either no relationship (Currie et al., 2004; Romanuk and Kolasa, 2002; Srivastava and Lawton, 1998), or a positive relationship between richness and energy (Kaspari et al., 2000; Ríos-Casanova and Bestelmeyer, 2008; Yee and Juliano, 2007).

Results of the analysis of nested models indicate that richness is more conditioned by quantities of total energy than by quantities of energy variation. This result may be explained by the developmental adaptations of tenebrionids to avoid unfavorable seasons. As holometabolous organisms, entering diapause or torpor may help these beetles to avoid extinctions (Hodkinson, 2005). Thus, under these assumptions it is possible that tenebrionids escape low energy periods by adapting their development to the favorable seasons. The nested models also indicated that tenebrionid richness responds strongly to PET than to AET. This difference in the fit of energy measures resulted from the strong spatial structure exhibited by PET (see Table 2). It is possible that the broad latitudinal span of the study region generates this high spatial structure of PET, because temperature varies markedly with latitude (Brown and Lomolino, 1998). In contrast, AET exhibited a reasonably low spatial autocorrelation, presumably due to the homogeneity of water availability throughout the study area.

Despite the relatively low fraction of variance explained by species–energy models, the relationships were mostly significant and negative. These results reject SET as a possible explanation of the unequal distribution of tenebrionid richness in arid regions. However, we suggest that this negative species–energy relationship was caused by a constraint in the mechanisms assumed by MIH, because tenebrionids have evolved adaptations to survive climatic harshness, which can influence population dynamics. Tenebrionid beetles are ectotherms, and thus environmental energy regulates metabolic rates directly (Allen et al., 2002). However, metabolic rates are also directly related to water loss (Chown and Gaston, 1999). Thus, high environmental energy represents a conflicting environmental force for tenebrionids in arid environments: high metabolic rates resulting from high energy inputs also mean high water loss, which increases mortality. To solve this problem, tenebrionid beetles seem to have evolved reduced metabolic rates to regulate water loss (Zachariassen, 1996). In turn, low metabolic rates may lead to low population abundances, as suggested by studies that show that reduced metabolic activity reduces reproductive output and causes declines in population sizes (Allen et al., 2002; Brown et al., 2004; Dahlhoff et al., 2008). Because high population sizes prevent extinctions (Evans et al., 2006b), tenebrionids from relatively cool areas should have greater population abundance than tenebrionids from warmer areas. Furthermore, mechanisms generating positive and negative SERs may act simultaneously, with the net direction of the relationship depending on the relative strengths of the negative and positive components. This situation may apply to the tenebrionids considered here.

Our results also show that tenebrionid richness is significantly, negatively related to water availability. This result contrasts with that of Hawkins et al. (2003), who found a strong positive correlation between water availability and richness in water-limited environments for a wide range of plant and animal groups. They argue that water availability can influence positively species

richness both directly by influencing insect development, and indirectly, via plant resources availability (i.e., food; O'Brien et al., 2000). What explains the negative relationship found between tenebrionid richness and water? We suggest this relationship may change in strength and direction if energy availability influences population abundances negatively and if there is a positive relationship between energy and water availability. One plausible explanation of this negative relationship between water availability and tenebrionid richness involves an effect of environmental harshness on metabolic rates: as increased resource consumption results in increased metabolic rates (Brown et al., 2004), water loss can also increase, which means that organisms inhabiting areas with high energy and water availability may decrease their resource consumption rates to avoid water loss. Thus, the net effect on richness would depend on the relative strength of the opposite effects of water and energy, as has been reported by some studies (Mueller and Diamond, 2001; Williams and Tieleman, 2002).

Our results suggest that the form of the species–energy relationship depends on how energy availability influences species extinction risk and how organisms evolve adaptations to avoid extinctions. This finding relates to that of Evans et al. (2005a), who found that common and rare species contribute differently to the species–energy relationship; species with high population abundance and range size respond more strongly to variations of energy availability than species with lower population abundance and range sizes, thus contradicting MIH's assumptions. We suggest that these differential contributions of rare and common species may be associated with inter-specific differences in habitat specialization, because of the negative relationship between habitat specialization and population abundance (Evans et al., 2005a).

To conclude, we have argued that the mechanisms assumed by species–energy theory can lead to a variety of relationships between species richness and energy availability, from positive to negative, and have provided evidence that for southern South-American tenebrionids the relationship is negative. In addition, energy variation does not contribute to explain tenebrionid richness. This finding suggests that population dynamics of tenebrionids are not affected by energy variation possibly because tenebrionids have evolved strategies to avoid strong energy fluctuations. It also suggests that for a deep understanding of SET it is necessary to develop alternative mechanistic hypotheses such as those proposed here. Furthermore, our results offer the opportunity to generate testable predictions about the relationship among metabolic rates, population abundance and species richness on species adapted to arid environments.

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