Global Ecology and Biogeography (1999) **8**, 47–54

RESEARCH LETTER

Weak links: 'Rapoport's rule' and large-scale species richness patterns

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ABSTRACT

Many hypotheses have been proposed to explain regional species richness patterns. Among these, 'Rapoport's rule' has sparked considerable controversy by stating that the latitudinal gradient in species richness can be explained indirectly as a function of narrower geographic ranges for species at low latitudes. Annual climatic variability, or deviation from mean climatic conditions, has been hypothesized to moderate this phenomenon. Furthermore, taxa that avoid much of this seasonality, such as temperate zone insects that enter diapause or species that migrate, were predicted to show reduced latitudinal gradients in richness. I test the suggested link between 'Rapoport's rule' and species richness for two higher level insect taxa as well as for the class Mammalia. Although these taxa exhibit the well-known latitudinal gradient in species richness, simple annual climatic variability and deviation from mean annual climatic conditions provide very poor predictions of species richness in each of them. Potential evapotranspiration, a measurement of ambient climatic energy, explains most of the observed variance in regional species richness patterns for all three taxa, consistent with the species richness-energy hypothesis. I find no support for an indirect link between 'Rapoport's rule' and terrestrial species richness patterns in North America.

Key words Rapoport's rule, Rapoport rescue hypothesis, species richness-energy hypothesis, biodiversity, species richness, latitudinal gradients, North America.

INTRODUCTION

The basis for regional variation in species richness is the subject of a long-standing debate (for example, Dobzhansky, 1950; Pianka, 1966; Janzen, 1970; Connell, 1978; Hubbell, 1980; Fraser & Currie, 1996) the resolution of which is of fundamental ecological importance (May, 1986; Huston, 1994). Given the current extent of human-induced biodiversity loss, it seems more important than ever to achieve some understanding of why there are more species in some regions than others (Lawton *et al.*, 1996). Such knowledge has practical applications, such as in modelling species' responses to climate change (McDonald & Brown, 1992; Scheel, Vincent & Cameron, 1996; Kerr & Packer, 1998), or predicting where reserve networks should be focused (Scott *et al.*, 1990; Kerr, 1997).

'Rapoport's rule', proposed by Stevens (1989) after observations made by Eduardo Rapoport (1982), has gained much attention by claiming to explain the latitudinal gradient in species richness (for example, Pagel, May & Collie, 1991; Stevens, 1992). According to Stevens' hypothesis, the latitudinal extent of species' ranges declines toward the tropics, coincident with progressively smaller annual climatic variation. Organisms that exist at higher latitudes must be able to withstand a broad range of environmental conditions. As climatic generalists, such species are hypothesized to have relatively large ranges. Tropical species, faced with relatively little deviation from mean climatic conditions, are likely to become climate specialists, adapted for highly specific temperatures and precipitation levels. Stevens argues that the latitudinal trend toward high diversity exists because climatic stability promotes specialization, so more species may

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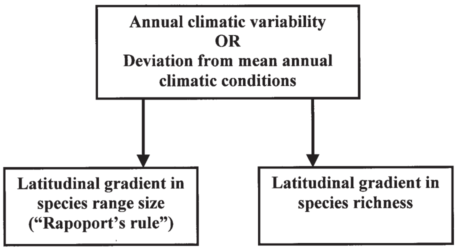

Fig. 1. The hypothetical structure (Stevens, 1989) between 'Rapoport's rule', climatic stability, and large-scale patterns of species richness. Most studies of 'Rapoport's rule' consider only the latitudinal gradient in species range size, while very few test the link between this and patterns of richness.

coexist toward the equator. The incidental result of this climatic specialization is 'Rapoport's rule' (see Fig. 1). Taxa that are dormant for much of the year or which migrate, Stevens (1989) argues, should not be influenced by climatic variability, and should exhibit reduced latitudinal species richness gradients. Stevens (1989) provides evidence showing latitudinal gradients in species range size exist (although several of his examples have been refuted, see below), but none that directly suggest that his 'rule' also explains diversity patterns. The obvious empirical prediction, if Stevens' claim is correct, is that climatic stability should provide the best overall prediction of regional species richness levels. Currie & Paquin (1987), and Currie (1991) tested seasonality as a predictor of species richness among North American trees and vertebrates, and found only non-significant or weak relationships. Neither study, however, tested deviation from mean annual conditions as a predictor of species richness, as suggested in Stevens (1989).

There are several major studies of 'Rapoport's rule' *per se*, but very few studies that consider species richness patterns explicitly (but see Rohde, Heap & Heap, 1993; Rohde & Heap, 1996). Indeed, it is possible that 'Rapoport's rule' may be at least partially correct (Rohde, 1996), but that it provides no insight into the issue of the latitudinal gradient of species richness. Exceptions to 'Rapoport's rule' include Australian mammals, for example, whose ranges do not decline toward the equator (Smith, May & Harvey, 1994). Similarly, New World bird species ranges are smallest at about 17° N (Blackburn & Gaston, 1996), rather than at the equator, as predicted. The ranges of Pacific marine molluscs and marine teleosts exhibit no clear relationship with latitude (Rohde, 1992; Kaustuv, Jablonski & Valentine, 1994), although the effects of climatic variability on marine organisms should be substantially reduced relative to nearby terrestrial taxa. A complete summary is provided in Gaston, Blackburn & Spicer (1998).

Compelling evidence supports the species richness-energy hypothesis as an explanation of large-scale species richness patterns in cold-temperate regions (Begon, Harper & Townsend, 1996; Kerr & Packer, 1997). Factors that measure ambient heat energy (such as potential evapotranspiration, PET, the amount of moisture that would evaporate from a saturated surface) consistently explain 70–90% of the variance in regional species richness levels in vertebrates (Currie, 1991), vascular plants (Currie & Paquin, 1987; Adams & Woodward, 1989), Lepidoptera (Turner, Gatehouse & Corey, 1987; Kerr, Vincent & Currie, 1989, and Coleoptera (Kerr & Packer, in press; Kerr & Currie, unpublished manuscript). Based on the results of forty-one further studies, Wright, Currie & Maurer (1993) found that energy explained a median of 70% of the variance in observed species richness patterns. These studies focused on cold-temperate regions, especially North America and the United Kingdom. In warmer regions, the species richness-energy hypothesis may provide a weaker or non-significant explanation of species richness. Kerr & Packer (1997) found that habitat heterogeneity provided a better explanation of mammalian species richness patterns in areas of North America where maximal PET exceeded 1000 mm/yr. Recent studies on vertebrates (Fraser, 1998), fish (Guégan, Lek & Oberdorff, 1998), and Lepidoptera (Kerr *et al*., 1998) support these findings.

In this paper, I examine species richness patterns among three North American taxa using well-established quadrat techniques to test the hypothesized link between 'Rapoport's rule' and spatial patterns of diversity. Included in this analysis are invertebrate taxa that 'avoid' annual climatic variability through pupation and that should, according to Stevens (1989), show reduced latitudinal gradients in species richness. I test the hypothesis that climatic variability is responsible for the latitudinal gradient in species richness, and compare my results to those using the alternative species richness-energy and heterogeneity hypotheses.

METHODS

My methods follow standard quadrat-based biodiversity analysis procedures (McCoy & Connor, 1980; Currie & Paquin, 1987; Turner, Lennon & Lawrenson, 1988; Currie, 1991; Blackburn & Gaston, 1996). I divided North America, north of Mexico, into 336 quadrats, following Currie (1991). Quadrats were 2.5° × 2.5° south of 50° N, and 2.5° latitude by 5° longitude north of this area. Quadrats in this study are not of equal area, but by including quadrat area as a covariate in all analyses, I removed this potential obscuring influence on patterns in the data. By overlaying species distributions on a map of the study area, I determined total species richness scores for each quadrat. Currie (1991) compiled these data for class Mammalia, including 368 species. Species distribution data for two invertebrate groups, the blister beetles, genus *Epicauta* (Coleoptera: Meloidae; forty-nine species) and the swallowtail butterflies (Lepidoptera: Papilionidae; eighteen species), respectively, were also obtained from the literature (Pinto, 1991; Tyler, Braun & Wilson, 1993). Adult *Epicauta* (Coleoptera: Meloidae) are herbivorous on an array of angiosperms, while larvae are predators of grasshopper (Acridoidea) eggs, and have been extensively collected because they are important agricultural pests. Papilionidae (the swallowtail butterflies) are also herbivorous. Substantial amateur interest and the relative ease of specimen identification have helped establish good collection records for this taxon.

Baseline climatic data were collected from the climatic maps and atlases (see Currie, 1991). I calculated the two different estimates of annual precipitation and temperature variability proposed by Stevens (1989). Deviation from mean climatic conditions was calculated as the difference between July and January temperature (calculations use degrees Kelvin, DFMT) and precipitation (DFMP) in an area, divided by the mean annual conditions. Conditions throughout the study area at these times of year represent the approximate climatic extremes (Rabenhorst, 1981; Atmospheric Environment Service, 1984). Simple annual climatic variability, or seasonality, is the difference between July and January temperature (seasonality in temperature, ST) and precipitation (seasonality in precipitation, SP). This approach provides a straightforward estimate of the range of regional climatic variability. I used estimates of mean annual potential evapotranspiration (PET; Korzun, 1977) to evaluate the species richness-energy hypothesis. I calculated two aspects of spatial heterogeneity: climatic and physical. Spatial variation in climatic conditions was calculated as the difference between maximum and minimum mean annual environmental conditions. Physical heterogeneity (shown to be a strong correlate of species richness in some regions; Kerr & Packer, 1997) was estimated as the difference between maximum and minimum elevation within a quadrat.

I inspected bivariate plots of the environmental variables and species richness for the three taxa included in this study. Before proceeding with regression analyses, I square-root or log transformed variables with non-normal or heteroscedastic residuals. Some PET-species richness relationships were non-linear, requiring polynomial regression modelling.

RESULTS

While Mammalia, Papilionidae, and *Epicauta* exhibit the well-known latitudinal diversity gradient, details of their species richness patterns are somewhat different in southern North America. *Epicauta* are most diverse in western Texas and Arizona. Southern Florida,

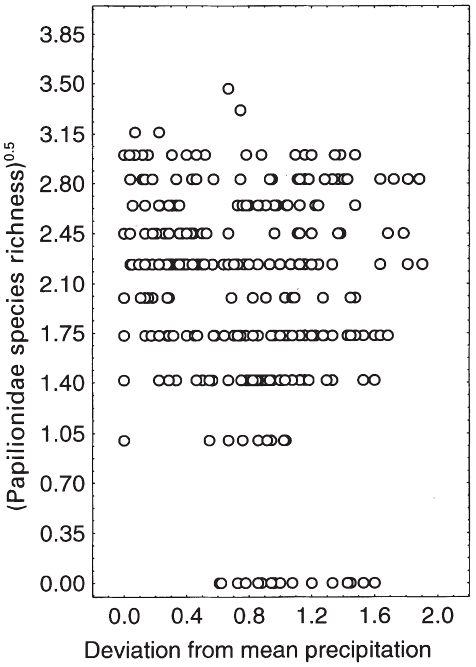

Fig. 2. Papilionidae species richness as a function of deviation from mean precipitation (DFMP) for North America. Similarly weak correlations exist between DFMP and *Epicauta* and mammal species richness, respectively. Relationships with simple annual precipitation variability are non-significant.

Table 1. The variance (adjusted R^2) in species richness for the North American study area explained by environmental factors in regression analysis. Potential evapotranspiration is always the strongest correlate of species richness and enters all regression models first. Two regression models are presented for each taxon: the first includes PET only, while the second is the 'best' regression model determined by an examination of all regression subsets. Quadrat area is forced into all final regression models. Square root and logarithmic transformations of variables helped stabilize residual variance. No seasonality measurement enters any of the final regression models.

Dependent variable	Factors in regression model	Adjusted R^2
Log (Mammal species richness)	Log (PET)	0.74
Log (Mammal species richness)	Log (PET) Log (Elevation variability) Log (PET heterogeneity) Quadrat area	0.85
(*Epicauta* species richness)$^{0.5}$	PET	0.81
(*Epicauta* species richness)$^{0.5}$	PET Quadrat area	0.82
(Papilionidae species richness)$^{0.5}$	PET	0.73
(Papilionidae species richness)$^{0.5}$	PET, PET^2 Elevation variability Quadrat area	0.80

Table 2. Spearman rank correlations between species richness, spatial climatic and physical heterogeneity, potential evapotranspiration, and the four estimates of annual climatic variability proposed by Stevens (1989) as the basis for Rapoport's rule and the latitudinal gradient in species richness.

Environmental factor	Mammalia	Papilionidae	*Epicauta*
Seasonality in temperature (ST)	−0.56*	−0.71*	−0.61*
Deviation from mean temperature (DFMT)	−0.59*	−0.73*	−0.64*
Seasonality in precipitation (SP)	NS	0.24*	NS
Deviation from mean precipitation (DFMP)	−0.13**	−0.14**	−0.15**
Spatial variability in potential evapotranspiration	0.70	0.54	0.49
Elevation variability	0.39	0.35	NS
Quadrat area	0.12**	NS	NS
Median potential evapotranspiration	0.82*	0.85*	0.90*

* $P<0.0001$, ** $P<0.05$; NS; Not significant.

however, is the area with the highest number of Papilionidae species. Highest species densities among the mammals occur in southern California, and northwestern Arizona. While species richness patterns among these taxa vary in the southern region of North America, all exhibit a broadly similar latitudinal gradient in richness, contrary to predictions in Stevens (1989).

The 'best' regression model for each taxon is presented in Table 1, and excludes any aspect of seasonality. While annual temperature variability (as measured by ST and by DFMT) is strongly correlated with species richness in all three taxa (Fig 2; Table 2), this is due to covariation with PET and climatic and physical spatial heterogeneity. Annual precipitation variability (as measured by SP and by DFMP) shows little latitudinal or longitudinal trend in North America, and its relationship with the species richness patterns of the taxa in this study is weak or non-significant (Fig. 3; Table 2). SP and DFMP are not very strongly correlated ($R^2=0.240$, $P<0.0001$), while ST and DFMT are nearly identical ($R^2=0.99$, $P<0.0001$).

Potential evapotranspiration is strongly related to the observed species richness patterns of mammals, papilionids, and *Epicauta* (Fig. 4), explaining between 73% and 81% of the variability in these groups when using transformed richness data (Table 1). Mammalian and papilionid species richness is a saturating

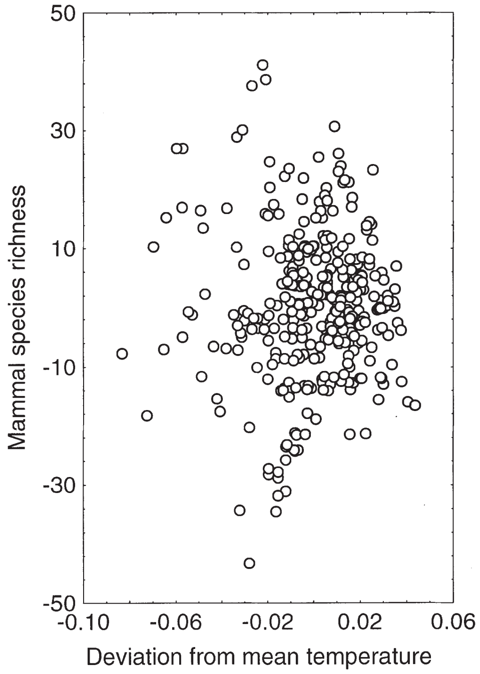

Fig. 3. North America mammal species richness and deviation from mean temperature (DFMT) after controlling for PET, which is a stronger correlate of richness than DFMT. This relationship is similar to those observed for *Epicauta* and Papilionidae species richness, respectively.

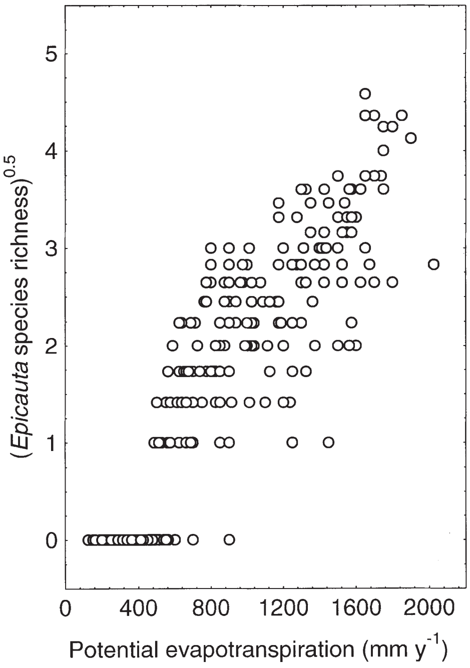

Fig. 4. The highly significant relationship between potential evapotranspiration (PET), a measurement of crude atmospheric energy, and *Epicauta* species richness in North America. Similar relationships exist between PET and both Mammalia and Papilionidae species richness, respectively.

function of PET, increasing linearly until about 800–1000 mm y^{-1}, and then remaining constant. Kerr & Packer (1997) and Kerr *et al.* (1998) found that habitat heterogeneity explained mammal and Papilionidae richness patterns in the high energy regions of North America, while concluding that the richness-energy hypothesis provides the best continental-scale explanation of the observed variability. Recent studies provide support for this two-factor view of diversity patterns (Fraser, 1998; Guégan *et al.*, 1998), although studies on terrestrial plant species richness suggest that the overall water balance is of primary importance in some regions (Currie & Paquin, 1987; O'Brien, 1993, 1998; O'Brien, Whittaker & Field, 1998). Species richness among *Epicauta*, however, continues to increase as a function of PET. This deviation from the patterns exhibited by Mammalia and Papilionidae is not unexpected: at lower taxonomic levels, predicting diversity patterns will often be more difficult, as taxon-specific ecological characteristics will play an increasingly important role.

DISCUSSION

'Rapoport's rule' indirectly attempts to explain regional variability in species richness by linking species' range size with latitude, and latitude with climatic variability. Climatic variability, or deviation from mean climatic conditions, is hypothesized to promote specialization, so in relatively stable environments more species may coexist (Stevens, 1989). I have not investigated 'Rapoport's rule' *per se* but the proposed link between its mechanism and species richness patterns. Seasonality and deviation from mean climatic conditions, respectively, provide consistently weak or non-significant explanations of species richness among mammals, *Epicauta*, and Papilionidae in North America. 'Rapoport's rule' may be correct in its prediction of declining species ranges in the tropics, at least for some taxa, but I have observed no evidence to suggest that it provides insight into patterns of species richness.

North American species richness patterns among

Epicauta, Papilionidae, and mammals are best explained by the species richness-energy hypothesis, rather than annual climatic variability. Higher levels of atmospheric energy may lead to greater species density by improving food acquisition and use, and, in the case of endotherms, reducing the metabolic demands of maintaining body temperature (Root, 1988; Turner *et al*., 1988; Currie, 1991; Begon *et al*., 1996; Turner, Lennon & Greenwood, 1996), thereby permitting species to devote a larger proportion of their metabolic budget to the use of food resources. These mechanisms may explain the observation that population densities tend to be lower in high energy regions (Currie & Fritz, 1993)—high population density may be required for a species to persist when metabolic demands are severe, while, in warmer climates, species may persist even with low population density.

The link between 'Rapoport's rule' and large-scale species richness patterns suffers from severe empirical and logical shortcomings. Stevens (1989) argues that taxa that do not experience the full range of annual climatic conditions would not follow 'Rapoport's rule', nor show a latitudinal gradient in species richness. Contrary to this assertion, both *Epicauta* and Papilionidae, respectively, exhibit a strong latitudinal gradient in species richness, despite seasonal life cycles. Moreover, Turner *et al*. (1987) show that British insect species richness declines in areas with milder winters, possibly because the metabolic rates of diapausing insects increase with mild winter temperatures, depleting their energy reserves. Kerr *et al*. (1998) provide further evidence that strong latitudinal gradients, consistent with the species richness-energy hypothesis, exist among North American Lepidoptera. Potential explanations of diversity patterns must include insects, the majority of species, a major difficulty with Stevens' (1989) hypothesis. 'Avoiding the weather' is analogous to being able to survive the regional climate, a situation that applies to all taxa: if they were not so adapted, they could not persist in an area. Stevens' (1989) arguments against the inclusion of such taxa in his hypothesis are logically questionable and inconsistent with empirical evidence presented here and elsewhere, some of which was published before his paper (e.g. Turner *et al*., 1987).

Is it possible for a latitudinal trend in species range size to exist independently of regional patterns of species richness? Perhaps, but there are at least two major mechanisms that can lead to a Rapoport artefact, rather than a 'rule' describing trends in species range size. Blackburn & Gaston (1996) suggest that New World bird distributions (including 3906 species) are smallest just south of Mexico because many species' ranges are limited by major floristic changes that occur in that area. Colwell & Hurtt (1994) point out the possibility that the Rapoport effect may be spurious since per-species sampling effort is inversely related to overall species richness, and observed species range is related to sampling effort. In the tropics, therefore, species ranges may seem smaller because sampling effort there is low relative to temperate regions (Voss & Emmons, 1996). As climatic variability does not explain observed species richness patterns in North America, alternative explanations for a Rapoport phenomenon among individual taxa that do exhibit the range size-latitude correlation merit greater attention.

The proposed mechanism for the Rapoport phenomenon—climatic variability or deviation from mean climatic conditions—shows weak or non-significant independent relationships with the species richness patterns of Mammalia, Papilionidae, and *Epicauta*. A correlation between range size and latitude among some taxa may be a function of climatic variability, deviation from climatic means, or a biogeographical artefact, but there is no apparent basis to suggest that 'Rapoport's rule' incidentally explains regional species richness patterns among the taxa considered in this study.

ACKNOWLEDGMENTS

David Currie provided much of the source data for this study, and is a continuing source of excellent advice. I thank Laura Kerr for her insightful discussion and editorial assistance. Klaus Rohde, John Turner, Michael Huston and Laurence Packer made many helpful comments that improved this manuscript considerably. Conversations with Robert Whittaker provided further perspective. This research was supported through a doctoral scholarship from the Natural Science and Engineering Research Council of Canada, and NSERC and CAUT research funds to Laurence Packer.

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