



The environmental basis of North American species richness patterns among *Epicauta* (Coleoptera: Meloidae)

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Abstract. Understanding regional variability in species richness is necessary for conservation efforts to succeed in the face of large-scale environmental deterioration. Several analyses of North American vertebrates have shown that climatic energy provides the best explanation of contemporary species richness patterns. The paucity of analyses of insect diversity patterns, however, remains a serious obstacle to a general hypothesis of spatial variation in diversity. We collected species distribution data on a North American beetle genus, *Epicauta* (Coleoptera: Meloidae) and tested several major diversity hypotheses. These beetles are generally grasshopper egg predators as larvae, and angiosperm herbivores as adults. *Epicauta* richness is highest in the hot, dry American southwest, and decreases north and east, consistent with the species richness-energy hypothesis. Potential evapotranspiration, which is also the best predictor of richness patterns among North American vertebrates, explains 80.2% of the variability in *Epicauta* species richness. Net primary productivity and variables measuring climatic heat energy only (such as PET) are not generally comparable, though they are sometimes treated as if they were equivalent. We conclude that the species richness-energy hypothesis currently provides a better overall explanation for *Epicauta* species richness patterns in North America than other major diversity hypotheses. The observed relationship between climatic energy and regional species richness may provide significant insight into the response of ecological communities to climate change.

Key words: *Epicauta*, latitudinal gradients, macroecology, potential evapotranspiration, species richness-energy hypothesis

Introduction

Insects are essential to terrestrial ecosystem function, and play key roles in terms of both biomass and diversity (Soulé 1990; Wilson 1992; Kremen et al. 1993), but their species richness patterns have received relatively little attention. Socioeconomic hardship and an exponentially increasing human population (Kerr and Currie 1995) are eroding biological diversity very rapidly relative to background extinction rates (Ehrlich and Ehrlich 1992; Wilson 1992; May et al. 1995). Conservation efforts directed at reducing these extinction rates require prioritization of areas of conservation (Margules et al. 1988; Pressey et al. 1994) and generally rely on only partial knowledge of the insect component of

the local biota (Kerr 1997). Such actions can be facilitated considerably by an understanding of large scale biodiversity patterns and the factors that underline them (Ceballos and Brown 1995). Furthermore, improved understanding of interactions between regional environmental factors and species diversity is fundamentally important in planning conservation responses to ongoing global climate change (Scheel et al. 1996; Kerr and Packer 1998).

Among the many factors proposed to explain large scale variability in species richness (for reviews see Pianka 1996; Mac Arthur 1972; Begon et al. 1996), climatic energy has received the greatest empirical support (Wright et al. 1993; Fraser and Currie 1996; Fraser in press). Factors measuring heat energy consistently provide the best explanations for regional variability in species richness of vertebrates (Currie 1991), trees (Currie and Paquin 1987), and Lepidoptera (Kerr et al. in press) in North America. Potential evapotranspiration, PET (the amount of moisture that would evaporate from a saturated surface) explains between 70–90% of the variance in regional species richness levels in these taxa. In a broad review of the literature, Wright et al. (1993) also observed that energy availability explained most of the variation in large-scale species richness patterns (median $R^2 = 0.70$, based on 41 studies).

Continental scale patterns of vertebrate species richness in North America are generally found to reflect primarily thermal aspects of energy availability (Currie 1991; but see Kerr and Packer 1997), rather than net primary productivity or other variables in which water balance is important (Lieth 1975). Amphibians appear to be an exception (Currie 1991), likely due to their integument physiology. This specific taxonomic exception does not change the overall pattern toward higher vertebrate diversity in hot, dry regions in North America. Eggleton et al. (1994) found that net primary productivity, NPP, provided a rather weak prediction of termite generic richness at a global scale ($R^2 = 0.36$, $P < 0.0001$). These authors concluded that termite diversity patterns were a product of historical factors, despite observing that richness in this taxon tended to be highest in hot, dry regions. They provided no formal test of their historical hypothesis.

An alternative hypothesis that has received some support is Rapoport's rescue hypothesis (Stevens 1989, 1992) which suggests that in areas with low seasonal climatic variation, species exhibit greater specialization, and occupy narrower geographical ranges. This is hypothesized to lead to a 'mass effect' (Shmida and Wilson 1985), in which chance additions to the local species pool occur relatively frequently, with a resulting increase in species richness. Therefore, at lower latitudes, there is higher regional species richness, since species' distributions are smaller and local species pools are supplemented more frequently by immigration. Recent studies have cast doubt on both the generality of 'Rapoport's rule' and its link to species diversity patterns (Rohde 1993, 1996; Gaston et al. 1998), but it continues to receive attention.

While hypotheses aimed at explaining diversity patterns have been investigated (see Table 1) extensively among plants and vertebrates, at least in temperate zones, the empirical record for insects remains remarkably weak (Turner et al. 1987; Kerr et al. in press). This is particularly significant since the majority of species are insects (May 1988), and no theory of species diversity may purport to be general without including them.

In this paper, we select a genus of economically important beetles (*Epicauta*; Coleoptera: Meloidae), and test hypotheses that may explain its species richness patterns in North America. Adults of *Epicauta* are herbivorous on an array of angiosperms, while larvae are grasshopper (Acridoidea) egg predators. The genus is distributed broadly, and may be found on all continents except Australia. Pinto (1991) discusses *Epicauta* systematics and ecology in considerable detail.

Methods

Our general methods follow Currie (1991) and Kerr and Packer (1997). We collected published data for *Epicauta* distributions in 336 quadrats covering

Table 1. Summary of the various factors hypothesized to determine regional patterns of species richness (Currie 1991; Latham and Ricklefs 1993). Tree species richness is used as a surrogate for plant species richness, as data for all plant species distributions in North America is lacking.

Factor	Basis	Variables used to test factor
1. Climate	Species accumulate in regions with moderate weather	Annual precipitation
2. Climatic stability	Reduced seasonality permits specialization	Difference between January and July precipitation and temperature
3. Habitat heterogeneity	Spatial heterogeneity in physical or climatic conditions provide more niches	Difference between minimum and maximum elevation, temperature, potential and actual evapotranspiration, precipitation, and solar radiation within each quadrat
4. History	Areas that were glaciated or inundated in the Wisconsinan have lower diversity	Whether a quadrat was glaciated, inundated, or clear during the Wisconsinan
5. Energy availability	A longer energy resource axis permits more species to coexist	Annual means of potential and actual evapotranspiration, and primary productivity
6. Plant species richness	Areas with a greater variety of plants permit more herbivorous species to coexist (e.g. <i>Epicauta</i>)	Tree species richness

mainland Canada and the United States (Pinot 1991). We did not include areas in Mexico or Central America because species distribution data in these regions frequently rely on small numbers of collection records, and are, consequently, comparatively unreliable. The distributions of two species-groups, Vittata and Maculata, were not mapped, and were excluded from the analysis. Offshore islands were also excluded from the analysis as island biogeographic factors would be expected to obscure hypothesized effect (MacArthur and Wilson 1967). Individual species' ranges were superimposed on the quadrat system, permitting us to count the number of species occurring in each quadrat. Quadrats were $2.5^\circ \times 2.5^\circ$ south of 50°N , and 2.5° (longitude) $\times 5^\circ$ north of 50°N . This is not an equal area grid: planimetry was used to determine the area of each quadrat, and the resulting variable was included as a covariate in all statistical analyses, definitively 'partialling' out any confounding influence of area (Zar 1984). Rosenzweig (1995) discusses the importance of accounting for area in his thorough treatment of area effects.

Tree species richness and environmental characteristics were collected from the literature (data in Currie 1991), or calculated from general climatic information (in the case of net primary productivity, Lieth 1975). Seasonality was determined by calculating the difference between January and July precipitation and temperature values. Variables describing mean conditions were determined by averaging the maximum and minimum values for the respective environmental descriptors in each quadrat. Heterogeneity was measured using topographical variability and the difference between maximum and minimum environmental conditions. The influence of glacial history was investigated by creating a dummy variable describing whether quadrats were clear, inundated, or ice-covered in the Wisconsinan period. Dummy variables were also created for quadrats that fall along coasts, including those along the shores of the Great Lakes, as well as those that are peninsular.

We inspected plots of the respective environmental variables and *Epicauta* species richness. Based on these, we calculated Spearman rank correlations (summarized in Table 2) between species richness and all other variables. We then entered the independent variables into regression models using both forward and backward stepwise approaches. Regressions were calculated separately for each hypothesis presented. The 'best' regression model contained the fewest variables but maximized the adjusted R^2 statistic (Zar 1984). We examined residual plots of linear models to investigate possible violations of statistical tests. We found deviations from homoscedasticity and normality to be generally minor, but logarithmic or square root transformations were performed to stabilize variance when these assumptions were clearly not met. ANCOVA was used instead of multiple regression analysis to test the significance of dummy variables (glacial history, coastal and peninsular location). ANCOVA models were constructed using backward and forward

Table 2. Spearman rank correlations ($n = 336$) between environmental characteristics and *Epicauta* species richness. Dummy variables are not included in this table, and were tested separately in ANCOVA models.

Environmental variable (per quadrat; after Currie 1991)	Spearman rank correlation ($n = 336$)
Mean potential evapotranspiration	0.90*
Mean solar radiation	0.88*
Mean annual temperature	0.86*
Mean actual evapotranspiration	0.57*
Primary productivity (Lieth's model)	0.57*
Mean annual precipitation	NS
Elevation variability	NS
Spatial precipitation variability	NS
Potential evapotranspiration variability	0.49*
Annual temperature variability	-0.61*
Annual precipitation variability	NS
Longitude	-0.17**
Latitude	-0.87*
Quadrat area	NS

Note: * - $P < 0.0001$, ** - $P < 0.005$, NS - Not significant.

stepwise elimination procedures, similar to those for the simple multiple regressions.

Results

Epicauta species richness patterns show a strong latitudinal trend, with the centre of highest diversity in northern Arizona (Figure 1). In general, richness is higher in the west, with relatively few species inhabiting the prairie regions of central North America. There are very few species in the arctic, with no records of *Epicauta* farther north than the southern region of the Northwest Territory in Canada. Latitude (included in this analysis for reference rather than for any hypothesized biological significance) is not the strongest predictor of richness, suggesting that any significant influence of this variable is due to covariation with other factors.

Potential evapotranspiration is the best predictor of *Epicauta* richness patterns (adjusted $R^2 = 0.802$, $F = 1358$, $P \ll 0.00001$; Figure 2). Other variables that measure climatic energy gradients, such as mean annual temperature, are almost as closely related to *Epicauta* richness (Table 2). Net primary productivity (NPP), which is strongly dependent on water availability, is a comparatively weak predictor (adjusted $R^2 = 0.321$, $P \ll 0.0001$; Figure 3). NPP and integrated climatic energy availability, as measured by PET (Begon et al. 1996), are not the same, though many do not distinguish

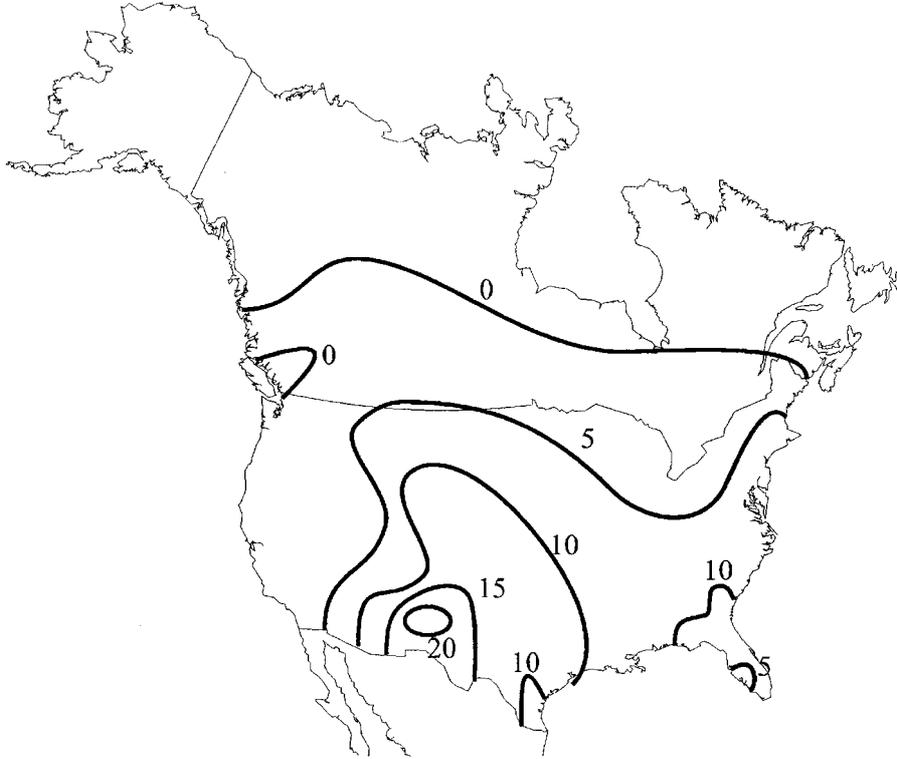


Figure 1. The geographical pattern of species richness in *Epicauta* of North America north of Mexico. Richness is highest in the hot dry regions of the American southwest. At comparably warm, but much wetter regions, such as the Florida peninsula, richness is considerably lower.

between these aspects of energy availability in evaluations of the species richness-energy hypothesis (e.g. Eggleton et al. 1994). NPP is highest in the warm, wet areas of North America, such as Florida, while PET is highest in the hot, dry regions, such as New Mexico. In cold regions, NPP and PET are very similar (Pearson $r = 0.882$, $P \ll 0.0001$; correlation for regions in North America where $PET < 800$ mm/yr, including most of Canada), but they diverge sharply in warmer areas (Pearson $r = 0.0384$, $P = 0.625$; correlation for regions in North America where $PET \geq 800$ mm/yr, corresponding to southern Canada and the USA).

If the Rapoport-rescue hypothesis (Stevens 1992) is an important explanation of species richness patterns, we would expect measurements of seasonality (annual variability in temperature and precipitation) to relate strongly to the observed patterns of *Epicauta* richness. The mass effect hypothesized by Stevens relies on the expectation that species ranges will be smaller in regions with relatively low seasonality (such as Florida, for example), and therefore, a

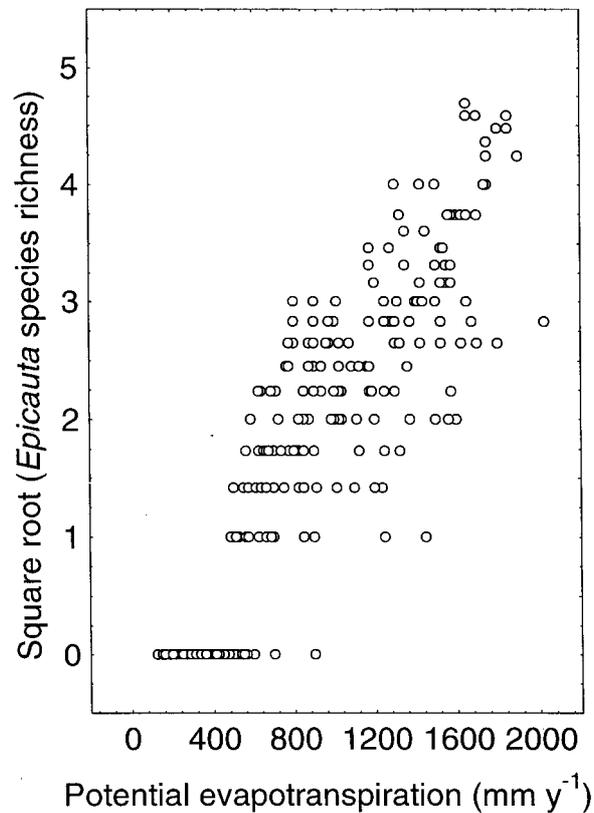


Figure 2. *Epicauta* species richness (square root transformed) vs. potential evapotranspiration (PET) for North America north of Mexico. This relationship is similar to those observed for vertebrates and trees in the same geographical area, though no peak is reached within the study region for *Epicauta*.

correspondingly larger number of species will coexist. Annual variability in temperature and precipitation, respectively, are non-significant or only weakly related to *Epicauta* richness (see Table 2), and do not contribute to our final model. Consequently, we reject this hypothesis as an explanation of richness patterns among North American *Epicauta*. These results are consistent with earlier results for vertebrates (Currie 1991; Kerr and Packer 1997), trees (Currie and Paquin 1987), and Lepidoptera (Kerr et al. in press), which showed uniformly weak or non-significant correlations with seasonality.

We find little support for alternative hypotheses relying on glacial history, spatial variability in climatic and physical conditions, or seasonality. In regression with PET, spatial and annual variation in temperature and precipitation were non-significant or added less than 1% to the adjusted multiple R^2 value. Glacial history was non-significant when included with PET in the ANCOVA.

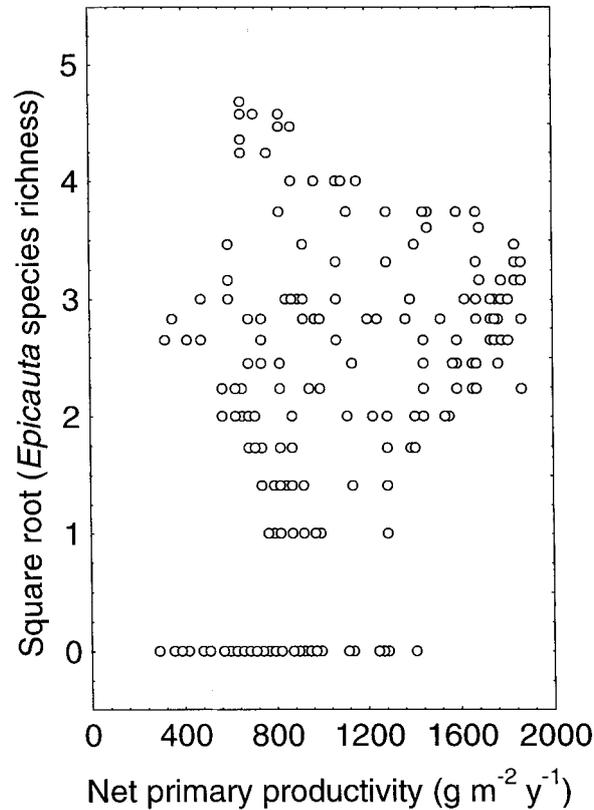


Figure 3. *Epicauta* species richness (square root transformed) vs. net primary productivity (NPP; Lieth's 1975 model) for North America north of Mexico. The predictive power of the species richness-energy relationship is reduced substantially if NPP is used.

Surprisingly, *Epicauta* species richness patterns do not reflect plant diversity, as approximated by tree species richness (Figure 4). Indeed, tree and *Epicauta* species richnesses are unrelated after controlling for potential evapotranspiration. The spatial variation in diversity in *Epicauta*, which are strictly herbivorous as adults, might have been expected to show a stronger relationship to plant richness than the mixed carnivorous/herbivorous bird and mammal faunas of North America, however, it does not (Currie 1991; Kerr and Packer 1997).

Discussion

Our results lend further support to the species richness-energy hypothesis, and extend its generality further into the extraordinarily diverse insect fauna. North American richness patterns exhibited by *Epicauta* are strikingly similar to those

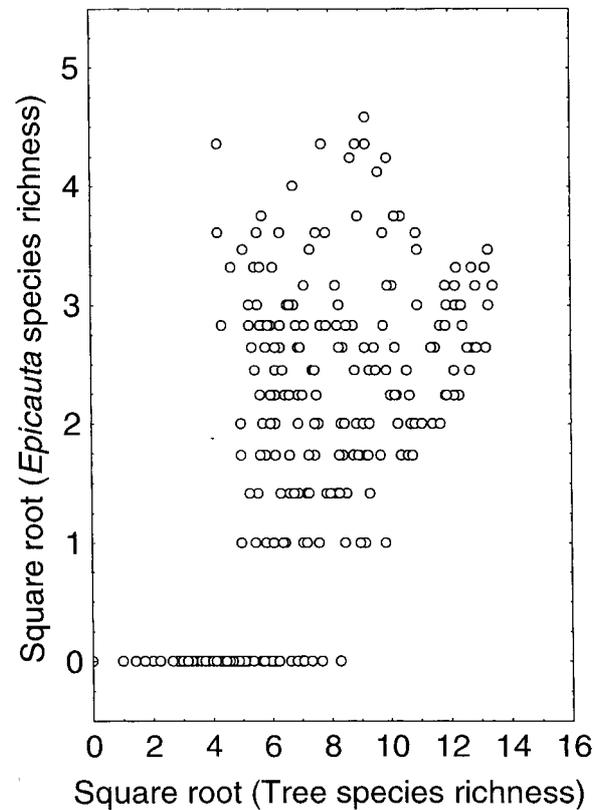


Figure 4. *Epicauta* species richness vs. tree species richness (both variables area square root transformed) for North America north of Mexico. There is only a weak correlation between these factors despite the herbivorous nature of *Epicauta*.

for vertebrates, and Lepidoptera (Turner et al. 1987; Kerr et al. in press). The most notable difference between these taxa and *Epicauta* with respect to their richness patterns is that the PET-richness relationship for *Epicauta* does not show any sign of reaching a plateau within North America north of Mexico. This is uncharacteristic of energy-richness relationship in this region (Currie and Paquin 1987; Currie 1991; Kerr and Packer 1997). It is possible that a peak in the PET-richness relationship might be reached further south, as richness in this taxon seemingly increased considerably toward the equator (Pinto 1991), whereas PET does not. If the PET-richness relationship reaches a plateau, other factors may become important in determining species richness levels, as has been noted for mammals (Kerr and Packer 1997).

Why are more *Epicauta* and other insect species (Cicindelidae: Pearson et al. 1997; Lepidoptera: Kerr et al. in press) able to maintain populations in hot, dry (high PET) regions? This pattern is unlikely to be attributable to lower rates of

post-glacial recolonization in regions with lower energy availability after the Wisconsinan. A basic prediction of such a mechanism is that areas that are close to sources of post-glacial colonists from the south, such as southeastern Texas, should have higher richness than distant areas, such as southern Saskatchewan. This is not the case; in fact, some areas in the southern Canadian prairies are more diverse for *Epicauta* than parts of the American south. Similarly, there should be more species in regions that were refugia, such as parts of Alaska, which certainly is not the case with this taxon. Glacial history seems to provide little insight into contemporary species richness patterns.

Root (1988) and Kukul et al. (1991) provide evidence of a physiological basis for the species richness-PET relationship. These authors found that cold tolerance limited the northern distributions of the bird and butterfly species they examined. The PET-species richness relationship may be a function of physiological intolerance of low-PET environments or reduced availability of metabolic energy to meet ecological requirements. This explanation of large-scale richness patterns depends on thermal conditions, rather than food availability or variety, consistent with the observations that NPP and tree richness provide relatively poor explanations of *Epicauta* species richness patterns in North America.

One of the only other large scale examinations of factors which control insect biodiversity is that of Eggleton et al. (1994), who concluded that historical effects, not net primary productivity, were the main determinants of termite generic diversity at a global scale. When we use net primary productivity instead of a direct measure of climatic energy, our ability to predict *Epicauta* richness patterns is severely diminished (adjusted $R^2 = 0.321$, $F = 160$, $P < 0.0001$). This is similar to the predictive power of NPP in explaining termite diversity found by Eggleton et al. (1994; $R^2 = 0.36$, $P < 0.01$). The difference between NPP and PET is that the former relies on local water availability in addition to climatic energy, whereas PET is based primarily on climatic energy. The species richness-energy hypothesis should not be rejected for termites based on this analysis. Our data suggest that historical effects have not been important in determining *Epicauta* richness patterns and Eggleton et al. themselves state that their historical hypothesis was currently untestable. It is worthwhile to investigate the basis for the dichotomy between potential evapotranspiration and primary productivity in terms of their ability to predict species richness patterns.

Human-induced climate change is likely to cause many species ranges to shift (see Peters and Lovejoy 1992), a result that seems particularly likely given the very close relationship observed between climatic energy balance and species richness patterns. The most substantial climatic changes are expected in the same, high latitude regions in which the relationship between PET and species richness is particularly strong (Kerr and Packer 1997). There is general

agreement between theoretical, experimental, and field evidence (Peters and Darling 1985; Parmesan 1996; Davis et al. 1998; Kerr and Packer 1998) that understanding the link between environmental factors and biological diversity will be an important part of coping with, or at least predicting, the effects of ongoing, anthropogenic climate change.

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References

- Begon M, Harper JL and Townsend CR (1996) *Ecology: Individuals, Populations, and Communities*. Blackwell Science, Boston
- Ceballos G and Brown JH (1995) Global patterns of mammalian diversity, endemism, and endangerment. *Conservation Biology* 9: 559–568
- Currie DJ and Paquin V (1987) Large-scale biogeographic patterns of species richness of trees. *Nature* 329: 326–327
- Currie DJ (1991) Energy and large-scale patterns of animal and plant species richness. *American Naturalist* 137: 27–49
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B and Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391: 783–785
- Eggleton P, Williams PH and Gaston KJ (1994) Explaining global termite diversity: productivity or history? *Biodiversity and Conservation* 3: 318–330
- Ehrlich PR and Ehrlich AH (1992) The value of biodiversity. *Ambio* 21: 219–226
- Fraser RH and Currie DJ (1996) The species-richness-energy hypothesis in a system where historical factors are thought to prevail: coral reefs. *American Naturalist* 148: 138–159
- Fraser RH (in press) Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. *Global Ecology and Biogeography Letters*
- Gaston KJ, Blackburn TM and Spicer JI (1998) Rapoport's rule: time for an epitaph? *TREE* 13: 70–74
- Kerr JT (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology* 11: 1094–1100
- Kerr JT and Currie DJ (1995) Effects of human activity on global extinction risk. *Conservation Biology* 9: 1528–1538
- Kerr JT and Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385: 252–254
- Kerr JT and Packer L (1998) The impact of climate change on mammal diversity in Canada. *Environmental Monitoring & Assessment* 49: 263–270

- Kerr JT, Vincent RL and Currie DJ (in press) Determinants of Lepidoptera richness in North America. *EcoScience*
- Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF and Sanjayan MA (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7: 796–808
- Kukal O, Ayres MP and Scriber JM (1991) Cold tolerance of the pupae in relation to the distribution of swallowtail butterflies. *Canadian Journal of Zoology* 69: 3028–3037
- Lieth H (1975) Modelling the primary productivity of the world. In: Lieth H and Whittaker RH (eds) *Primary Productivity of the Biosphere*, pp 237–263. Springer-Verlag, New York
- MacArthur RH (1972) *Geographical Ecology*. Harper and Row, New York
- Margules CR, Nicholls AO and Pressey RL (1988) Selecting networks of reserves to maximise biological diversity. *Biological Conservation* 43: 63–76
- May RM (1988) How many species are there on Earth? *Science* 241: 1441–1449
- May RM, Lawton JH and Stork N (1995) Assessing extinction rates. In: May RM and Lawton JH (eds) *Extinction Rates*, pp 1–24. Oxford University Press, New York
- Parmesan C (1996) Climate and species' range. *Nature* 382: 765–766
- Pearson DL, Barraclough TG and Vogler AP (1997) Distributional range maps for North American species of tiger beetles (Coleoptera: Cicindelidae). *Cicindela* 29: 33–84
- Peters RL and Darling JD (1985) The greenhouse effect and nature reserves. *BioScience* 35: 707
- Peters RL and Lovejoy TE (1992) *Global Warming and Biological Diversity*. Yale University Press, New Haven
- Pianka ER (1996) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100: 33–46
- Pinto JD (1991) The taxonomy of North American *Epicauta* (Coleoptera: Meloidae), with a revision of the nominate subgenus and a survey of courtship behavior. University of California Press, Berkeley, CA
- Pressey RL, Johnson IR and Wilson PD (1994) Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. *Biodiversity and Conservation* 3: 242–262
- Rohde K (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist* 142: 1–16
- Rohde K (1996) Rapoport's rule is a local phenomenon and cannot explain latitudinal gradients in species diversity. *Biodiversity Letters* 3: 10–13
- Root T (1988) Energy constraints on avian distributions and abundances. *Ecology* 69: 330–339
- Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge
- Scheel D, Vincent TLS and Cameron GN (1996) Global warming and the species richness of bats in Texas. *Conservation Biology* 10: 452–464
- Shmida A and Wilson MV (1985) Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20
- Soulé ME (1990) The real work of systematics. *Annals of the Missouri Botanical Gardens* 77: 4–12
- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133: 240–256
- Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist* 140: 893–911
- Turner JRG, Gatehouse CM, Corey CA (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos* 48: 195–205
- Wilson EO (1987) The little things that run the world. *Conservation Biology* 1: 344–346
- Wilson EO (1992) *The Diversity of Life*. Harvard University Press, Cambridge
- Wright DH, Currie DJ, Maurer BA (1993) Energy supply and patterns of species richness on local and regional scales. In: Ricklefs RE and Schluter D (eds) *Species Diversity in Ecological Communities*, pp 66–74. University of Chicago Press, Chicago
- Zar JH (1984) *Biostatistical Analysis*. Prentice-Hall, Toronto