

Lepidopteran richness patterns in North America¹

Jeremy T. KERR, Department of Biology, York University, 4700 Keele St., North York, Ontario, M3J 1P3, Canada.
 Rebecca VINCENT² & David J. CURRIE, Ottawa-Carleton Institute of Biology, University of Ottawa, Ottawa,
 Ontario, K1N 6N5, Canada.

Abstract: A long-standing objective of ecology has been to explain the basis for diversity patterns. Empirical evidence suggests that regional variation in richness of both animals and plants depends strongly on energy availability. The generality of the richness-energy hypothesis is limited by the paucity of analyses of invertebrates, which are much more diverse than the more thoroughly investigated vertebrate taxa. In this study, we consider two groups of North American Lepidoptera for which large-scale distribution data are available: the Papilionidae (swallowtail butterflies) and forest lepidopterans (moths based on the Canadian Forest Insect Survey). Energy, as measured by potential evapotranspiration (PET), statistically explains between 61 and 72% of the variability in the richness patterns of the Lepidoptera we have examined. It is the single best predictor of the richness of these groups, and the relationships have a very similar form to richness-PET relationships observed earlier in vertebrate taxa. After PET, Papilionidae richness is related to topographical heterogeneity. These patterns are true both within and among biomes. These results suggest that the richness-energy hypothesis applies generally to both vertebrates and insects in cold and temperate regions.

Keywords: diversity, species richness, energy, insects, lepidopterans, Papilionidae.

Résumé: L'un des buts principaux de l'écologie est d'expliquer la répartition spatiale de la biodiversité. Les données empiriques suggèrent que la variabilité spatiale du nombre d'espèces de plantes et d'animaux dépend fortement de la disponibilité de l'énergie. Pourtant, il y a eu très peu d'études sur la répartition spatiale de la richesse des insectes, le groupe animal terrestre comportant le plus d'espèces. Dans cette étude, nous avons abordé deux groupes de lépidoptères dont les répartitions nord-américaines sont bien connues : les Papilionidae (papillons porte-queues) et les lépidoptères forestiers du Canada. L'énergie environnementale, mesurée en terme d'évapotranspiration potentielle (ÉTP), explique statistiquement entre 61 % et 72 % de la variabilité spatiale de la richesse spécifique de ces deux groupes de lépidoptères. L'ÉTP est également la caractéristique environnementale la plus fortement corrélée avec la richesse spécifique des vertébrés. D'ailleurs, la forme des relations chez les lépidoptères est très similaires à celle des vertébrés. Une fois que l'effet de l'ÉTP est statistiquement éliminé, la richesse des Papilionidae est corrélée avec l'hétérogénéité topographique. Ces mêmes relations s'observent aussi bien à l'intérieur qu'entre les biomes individuels. Ces résultats suggèrent que l'hypothèse richesse-énergie s'applique autant aux insectes qu'aux vertébrés terrestres des régions tempérées et froides.

Mots-clés: diversité, richesse spécifique, énergie, insectes, lépidoptères, Papilionidae.

Introduction

Ecologists have long recognized the tremendous geographical variability in species richness, although the basis for this observation remains controversial (Stevens, 1989; Rohde, 1992; Ricklefs & Schluter, 1993). Numerous hypotheses have been proposed to explain latitudinal gradients in diversity, ranging from purely historical explanations (Wallace, 1878; Latham & Ricklefs, 1993), to hypotheses citing physiological tolerance of contemporary climatic conditions (Kukal, Ayres & Scriber, 1991), or local ecological interactions (Janzen, 1970; Hubbell, 1979; Shmida & Wilson, 1985).

The richness-energy hypothesis, which proposes that regions with greater energy availability are able to sustain populations of more species, has received substantial empirical support (Wright, 1983; Currie & Paquin, 1987; Turner, Gatehouse & Corey, 1987; Adams & Woodward, 1989; Currie, 1991; Wright, Currie & Maurer, 1993). Potential evapotranspiration (PET), the amount of moisture that would evaporate from a saturated surface, is consistently the best predictor of species richness patterns of

birds, mammals, amphibians, and reptiles in temperate North America (Currie, 1991). PET is essentially a measure of heat, which can strongly affect animals' energy budgets in high- to mid-latitudes (Randolph, 1973). Within these regions, the species-energy hypothesis seems to provide the best general explanation of large-scale patterns of richness.

While the patterns predicted by the richness-energy hypothesis are well-supported, the generality of the hypothesis is limited by the fact that few large scale tests with invertebrate taxa have been performed. Because, to a first approximation, nearly all terrestrial animal species are insects (Wilson, 1987; May, 1988), this is a major shortcoming. Insect diversity patterns are difficult to investigate at broad spatial scales because the spatial distributions of insect species are relatively poorly known compared to vertebrate or tree taxa, and because their very high richness makes a complete investigation of the class impractical. It is necessary, therefore, to restrict analyses of insect diversity patterns to well-known subgroups for which distribution data are available. Lepidoptera are especially suitable for such an analysis since their distributions are among the best studied of the invertebrates. Turner, Gatehouse & Corey (1987) showed that butterfly richness in Great Britain covaries strongly with solar radiation; however, no continental-scale tests of this relationship have been performed.

¹Rec. 1997-06-06; acc. 1998-03-03.

²Present address: Department of Biology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada.

Other explanations of observed richness-energy patterns have also been proposed. For example, Latham & Ricklefs (1993) suggested that the correlation between richness and energy in North America and Britain (Currie & Paquin, 1987; Adams & Woodward, 1989; Currie, 1991) is an indirect consequence of differences in richness among biomes. Biomes are argued to differ in richness because different numbers of species have evolved to tolerate the conditions in any particular biome. Biomes differ in climate, and therefore, the argument continues, the relationship between energy availability and vertebrate and tree richness is an artefact of the variability in species richness among biomes. This hypothesis would be falsified if the species richness-energy relationship were observed within biomes as well as between them.

This paper has three objectives. First, we investigate the patterns of species richness among selected groups of well-sampled North American Lepidoptera. Second, we relate these patterns to environmental characteristics that are hypothesized to explain large-scale species richness patterns. Finally, we investigate the relationship between energy availability and richness within biomes to determine whether richness-PET relationships result simply from pooling biomes.

Material and methods

We performed two independent analyses of patterns of lepidopteran species richness (*i.e.*, the numbers of different species in given areas). The first analysis was for Papilionidae in North America north of Mexico, while the second was for forest Lepidoptera in Canada. Both analyses were based on a quadrat system used in previous studies of vertebrate and tree diversity patterns (Currie & Paquin, 1987; Currie, 1991). The quadrats were $2.5^\circ \times 2.5^\circ$ south of 50° N, and 2.5° (latitude) $\times 5^\circ$ (longitude) north of 50° N. There were 336 and 103 quadrats in the respective analyses of Papilionidae and Canadian forest Lepidoptera.

We generated Papilionidae richness patterns by superimposing the detailed published maps of Tyler, Brown & Wilson (1994) on our North American quadrat system. The taxonomy for Papilionidae is not stable, and numerous subspecies, frequently identifiable by fixed morphological or genetic differences, exist for some putative species (Tyler, Brown & Wilson, 1994). We therefore determined the patterns of richness for both subspecies and species. Relationships between environmental descriptors and Papilionidae richness at these two taxonomic levels were very similar (Table I); consequently, we shall generally only present results at the species level.

The diversity patterns of the forest Lepidoptera of Canada were estimated from a 22-year, intensive forest insect survey carried out by the Canadian Forestry Service (McGugan, 1958; Prentice, 1958-1965). These collections, based on hundreds of point counts, represent the most extensive investigation of the forest insect diversity available for Canada. Despite this, some areas such as the prairies and the arctic were relatively poorly surveyed because they have little commercially exploitable forest. Those areas were therefore excluded from the present analysis. From the total survey database of 998 species, we

TABLE I. Spearman rank correlations between richness and environmental characteristics. For the Papilionidae, $n = 336$ quadrats (covering Canada and the U. S.); for forest lepidopterans, $n = 103$ (covering Canada only). Correlation of $r \geq 0.02$ are significant at $p < 0.05$

	Papilionidae subspecies richness	Papilionidae species richness	Forest lepidopteran species richness
Latitude	-0.76	-0.79	-0.74
Potential evapotranspiration	0.83	0.85	0.85
Actual evapotranspiration	0.41	0.42	0.63
Mean annual temperature	0.79	0.82	0.75
Annual precipitation	0.22	0.24	0.28
Elevation	0.50	0.47	-0.02
Tree species richness	0.67	0.69	0.84

randomly selected 300 for this study to expedite analysis. The distributions of these species were superimposed over the same quadrat system used above, but only within Canada.

Climatic and topographic data for each cell in the sampling grid were drawn from atlases (sources cited in Currie & Paquin, 1987). For each variable (annual precipitation, potential and actual evapotranspiration, temperature, and elevation), we noted the highest and lowest values that occurred in each quadrat, and we calculated the median of these values.

To delimit biomes, we used two systems. The first is Holdridge's life zones (1967; see also <http://ingrid.ldgo.columbia.edu/SOURCES/ECOSYSTEMS/Holdridge/html+viewer?>), which provide fairly coarse separation of vegetation types. Finer resolution was obtained using the "ecozones" defined for Canada based on vegetation, edaphic, and climatic factors (Figure 1, adapted from Bird & Rapport, 1986). Because ecozones are not defined consistently between the United States and Canada, it was not possible to examine within-biome richness patterns for the Papilionidae across North America at this finer level.

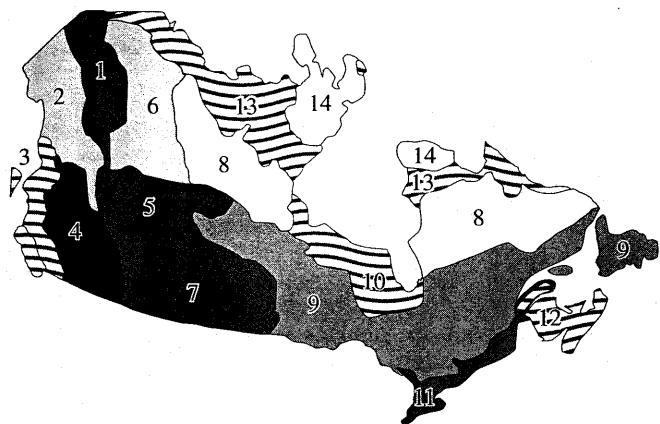


FIGURE 1. The ecozones of Canada (excluding the arctic islands), as defined by Environment Canada (Bird & Rapport, 1986). Holdridge life zones (not shown) are a similar, but somewhat coarser, categorization of biome types worldwide. Numbers refer to the following ecozones: 1: Tundra cordillera, 2: Boreal cordillera, 3: Pacific maritime, 4: Montane cordillera, 5: Boreal plain, 6: Taiga plain, 7: Prairie, 8: Taiga shield, 9: Boreal shield, 10: Hudson Bay plain, 11: Mixed-wood plain, 12: Atlantic maritime, 13: Southern arctic, 14: Northern arctic.

We inspected bivariate plots of the relationships between the environmental variables and Papilionidae and forest Lepidoptera richness to verify the shapes of relationships and their error distributions. Most were non-linear and heteroscedastic. Square-root transformation of species numbers stabilized the residual variance in regression models. Non-linear relationships were investigated using polynomial regression. Analyses of models that included ecozones or life zones (categorical variables) were performed using ANCOVA. All statistical analyses were carried out using SYSTAT version 7.

Results

As Currie (1991) observed for vertebrate groups, lepidopteran species richness shows strong latitudinal gradients (Figures 2 and 3). Papilionidae diversity is highest in the hot, dry American southwest. Within Canada, the richness of forest Lepidoptera is greatest in southern Ontario and in

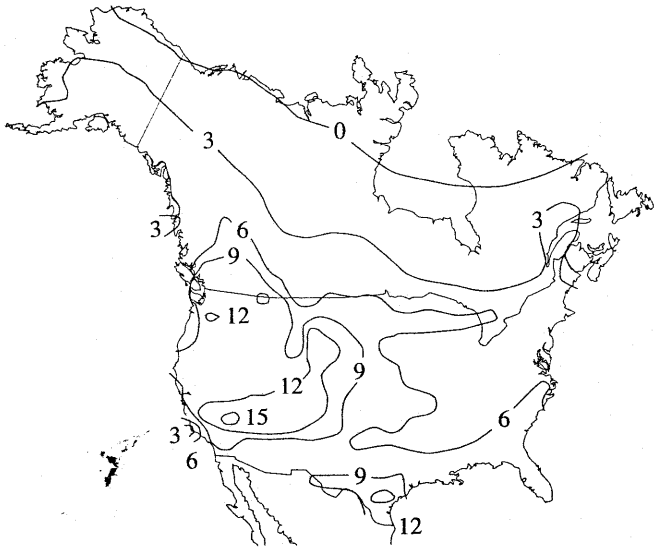


FIGURE 2. Map of Papilionidae subspecies richness patterns in North America. The map of species richness is very similar. Contours connect quadrats containing the same number of species.

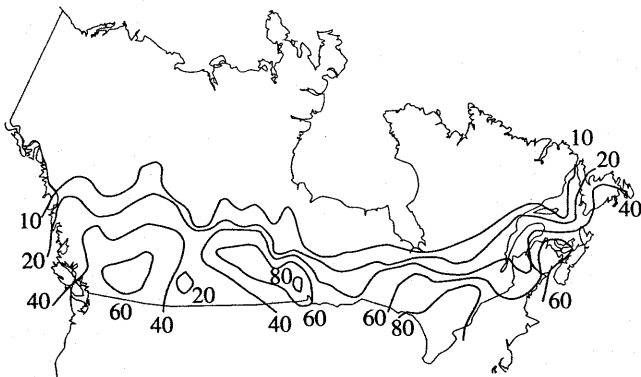


FIGURE 3. Map of the richness patterns of the Canadian forest lepidopteran species included in this study (a random subset representing 30% of the total number of taxa observed; thus total richness is 3.3 times higher). Contours connect quadrats containing the same number of species.

British Columbia, the warmest parts of the country. Although the richness of both groups covaries with latitude, correlations with other environmental variables are stronger, suggesting that factors other than latitude probably determine species richness (Table I).

Of the factors we considered, potential evapotranspiration (PET) is the best single predictor of species richness patterns of both Papilionidae and forest Lepidoptera (Table II, models 1, 4, and 10; also Figures 4 and 5). For the Papilionidae, richness is a decelerating function of PET, increasing until PET reaches 800-1000 mm/yr, and then remaining essentially constant. Other factors presumably then become important in these warmer regions. A polynomial function of PET statistically explains 72% of the variability in North American Papilionidae diversity patterns. The relationship between Canadian forest Lepidoptera richness and PET is less obviously curved because the range of PET within Canada is smaller; nonetheless, a second-degree polynomial function of PET statistically accounts for a very similar proportion (69%) of the variation in Canadian forest lepidopteran richness (Table II: model 10). These results are very similar to those obtained with terrestrial vertebrates (Currie, 1991) and are consistent with the hypothesis that energy determines continental patterns of richness in terrestrial invertebrates as well as vertebrates.

After controlling for PET, Papilionidae richness is also significantly related to the within-quadrat elevation: in other words, there are more species in mountainous areas (Table II: model 3). Results at the sub-species level are essentially indistinguishable (Table II: model 6). Similar results have been found for trees (Currie & Paquin, 1987) and mammals (Kerr & Packer, 1997). Variables other than topography do not improve the fit of the regression. Forest lepidopteran richness (which was tallied at the species level) was unrelated to elevational range ($F_{1,99} = 0.20, p = 0.84$).

Richness also differs significantly among different biomes, whether defined by Holdridge's life zones or Environment Canada's ecozones (Table II: models 2, 5, 8, and 11). However, after PET and elevation are included in predictive models, only a small amount of residual variance remains attributable to differences among biomes (Table II: models 3, 6, 9 and 12). Interestingly, post-hoc tests of the residual differences in Papilionidae richness among biomes show that, even after controlling for climate and elevation, richness in lifezones designated by Holdridge as tropical is higher than richness elsewhere (Figure 6). Considering the forest lepidopterans, after accounting for PET, richness did not differ among the four Holdridge life zones represented in Canada (Table II: model 9). However, richness did differ among the nine more finely defined ecozones (Figure 7). Post-hoc tests show that greater numbers of species than one would predict from climate alone were observed in the mixed-wood plains ecozone of southern Ontario and Québec than in some other zones, while fewer species were observed in ecozones in the far North.

Discussion

The relationships between richness and PET that we observed in this study are very similar to those observed for vertebrates. The forms of the relationships are similar, as

TABLE II. Models relating the richness of North American Papilionidae, and of Canadian forest lepidopterans, to annual potential evapotranspiration (PET, in mm yr⁻¹), elevation (m) and biome (life zones as defined by Holdridge (1967) and, in Canada, ecozones as defined by Bird & Rapport (1986)). In the Canadian data, the arctic and the prairie biomes were excluded because of undersampling. The number of quadrats that this excluded differed between Holdridge's and Bird & Rapport's systems (models 7-9 versus models 10-12); thus the number of degrees of freedom differs between these two data sets. In all cases where PET was included in a model, a second-degree polynomial function (*i.e.*, PET and PET²) was fitted

Model	Dependent variable	Independent variable(s)	df	Variable		Model		
				partial r ²	partial p	R ²	p	n
1	(Papilionidae species richness) ^{1/2}	PET & PET ²	2	—	—	0.72	< 0.001	336
2		Holdridge zone	13	—	—	0.48	< 0.001	336
3		PET & PET ²	2	0.34	< 0.001	0.84	< 0.001	336
		Holdridge zone	13	0.12	< 0.001			
		log(elevation)	1	0.22	< 0.001			
4	(Papilionidae sub-species richness) ^{1/2}	PET & PET ²	2	—	—	0.61	< 0.001	336
5		Holdridge zone	13	—	—	0.46	< 0.001	336
6		PET & PET ²	2	0.39	< 0.001	0.84	< 0.001	336
		Holdridge zone	13	0.16	< 0.001			
		log(elevation)	1	0.21	< 0.001			
7	(Forest lepidopteran species richness) ^{1/2}	PET & PET ²	2	—	—	0.61	< 0.001	101
8		Holdridge life zone	3	—	—	0.25	< 0.001	101
9		Holdridge zone	3	0.03	0.34	0.62	< 0.001	101
		PET & PET ²	2	0.49	< 0.001			
10	(Forest lepidopteran species richness) ^{1/2}	PET & PET ²	2	—	—	0.69	< 0.001	103
11		Ecozone	8	—	—	0.48	< 0.001	103
12		Ecozone	8	0.26	< 0.001	0.77	< 0.001	103
		PET & PET ²	2	0.56	< 0.001			

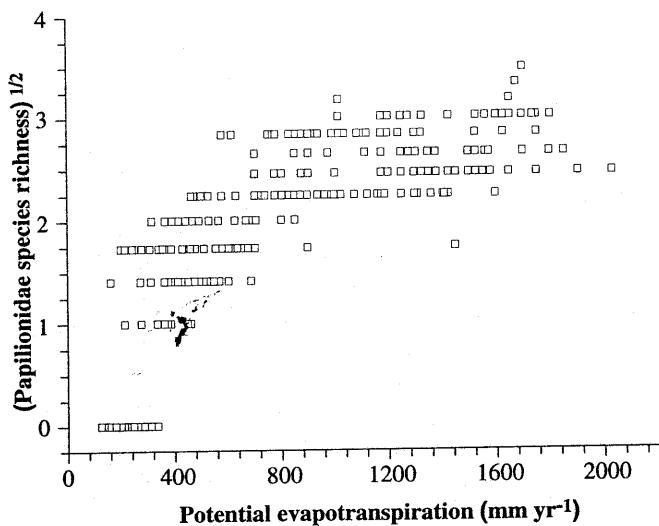


FIGURE 4. The square root of Papilionidae species richness as a function of potential evapotranspiration in North America.

are the strengths of the correlations. These results are consistent with the hypothesis that patterns of richness in North American animals in general are determined by energy. In the specific case of lepidopterans, Turner, Gatehouse & Corey (1987) showed that patterns of lepidopteran richness in Britain are related to solar radiation; this study is the first evidence that the same patterns exist on the continental scale, using the same environmental variable (PET) most closely related to patterns of vertebrate richness.

Why might energy limit species richness? There is some evidence suggesting that factors relating to climatic energy availability, such as winter temperature patterns, limit bird species distributions due to metabolic considerations (Root, 1988). In low energy regions, fewer organisms

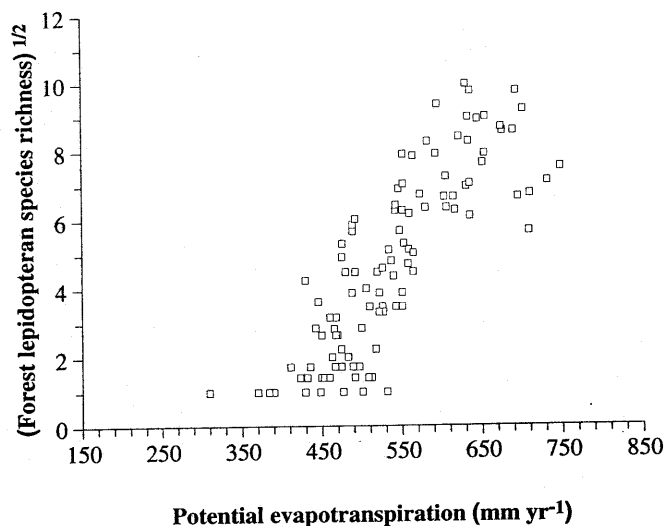


FIGURE 5. The square root of the number of forest Lepidoptera species as a function of potential evapotranspiration in Canada. Note that this data set represented a random subset of 30% of all of the taxa observed. Thus, total richness is 3.3 times higher than the figures shown here.

are able to maintain viable populations because of the persistently large demands on their metabolic processes to thermoregulate as well as forage and reproduce successfully. A similar mechanism can be proposed for insect diversity patterns (Kukal, Ayres & Scriber, 1991). A dependence on external thermal conditions, rather than a direct reliance on food abundance or other ecological factors, may provide the major limit to diversity in the temperate or cold regions of North America.

For both Papilionidae and forest Lepidoptera, richness remains strongly related to PET even after controlling for differences among biomes. In other words, richness is

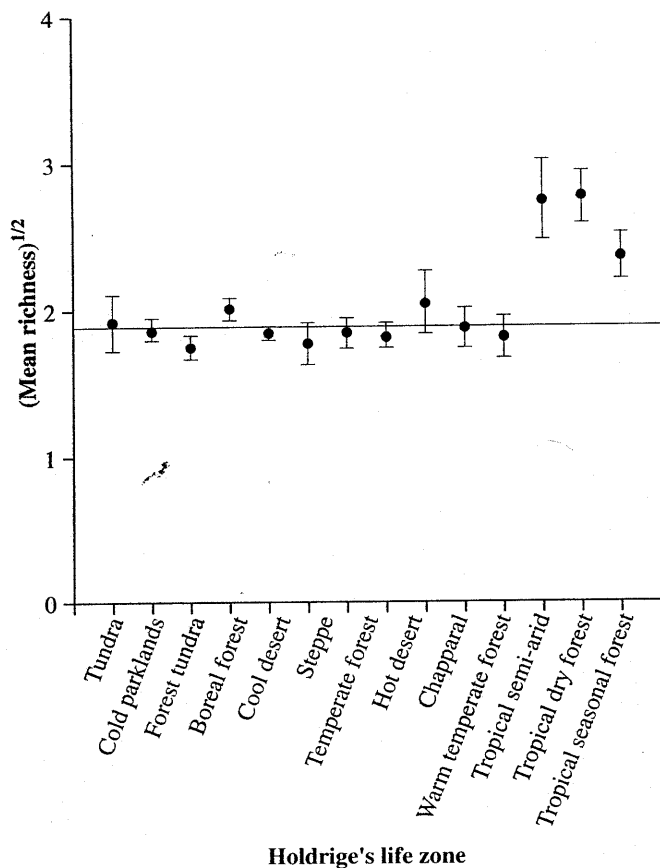


FIGURE 6. Residual variation in the square root of Papilionidae species among Holdridge life zones in North America, after controlling for differences of potential evapotranspiration and elevation among zones. Variation is shown around an overall mean value of 1.89. Error bars show ± 1 standard error. This figure shows that, after accounting for climate and elevation, richness does not vary significantly among northern and temperate life zones. In other words, climate and elevation accounts for the differences among life zones seen in Figure 1. However, life zones designated by Holdridge as tropical have more species than PET and elevation would predict.

related to PET within biomes, as well as among biomes. This means that continental-scale richness-energy relationships are not simply an artefact of differences of richness among biomes (Latham & Ricklefs, 1993).

There are taxa whose richness does not covary neatly with PET. Penguins, gadid codfish, ichneumonid wasps, sawflies, and bees have all been observed to show richness peaks at high or intermediate latitudes (reviewed by Gaston & Williams, 1996). However, such patterns are atypical, usually associated with particular geographic areas and/or taxa with specialized ecological requirements (Gaston & Williams, 1996). Currie (1991) found that the strength of richness-PET correlations among vertebrates typically increased with the level of taxonomic aggregation. Richness of higher-level taxa (classes and phyla) was strongly related to PET, whereas the richness of lower-level taxa (families) sometimes showed similar patterns, and sometimes not. The general pattern appears to be that overall richness covaries with PET, but the richness within particular groups may depend upon other local conditions.

In temperate and arctic areas, after one statistically accounts for PET and topography, there are no differences

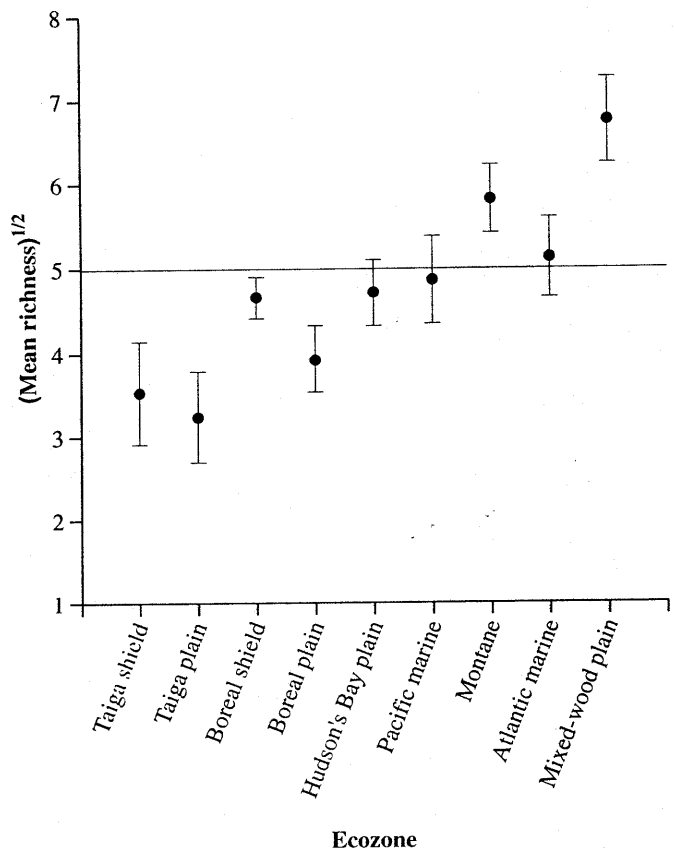


FIGURE 7. Residual variation in the square root of forest lepidopteran species among Canadian ecozones, after controlling for differences of potential evapotranspiration and elevation among zones. Variation is shown around an overall mean value of 5.04. Error bars show ± 1 standard error. The Mixed-wood Plain ecozone has significantly more species than Taiga zones. These differences seem likely to be artefacts (see Discussion).

in richness among biomes. In other words, differences of climate and topography can completely account for among-biome differences in richness. However, areas designated by Holdridge (1967) as tropical (in this case, the Gulf coast of the United States, and the Atlantic coast south of the Carolinas) do have higher species richness than PET and elevation would predict (Figure 6). It is not clear why this is the case. Perhaps reduced seasonality and/or a greater complexity of biotic interactions permit greater numbers of species to coexist (Huston, 1995). These questions are being addressed in current work.

The observed differences in richness among ecozones in the Canadian forest lepidopteran data (Table II) seem likely to be artefacts. The Forest Insect Survey was carried out principally for economic reasons. Northern ecozones had fewer sample sites than ecozones in more heavily forested (and populated) areas. Thus, species are more likely to have been overlooked in the North. The inverse situation holds in the Mixed-Wood Plains ecozone (in southern Ontario), the most highly populated area in Canada. It is also possible that some environmental difference not included in this study might account for the residual variability (after controlling for PET) in richness.

In conclusion, on the continental scale, patterns of lepidopteran richness are very similar to those of vertebrates. In

all these cases, most of the spatial variability in richness can be statistically related to simple climatic and topographic variables. These relationships hold within biomes as well as among them. These observations are consistent with the hypothesis that, at least in cooler parts of North America, energy may limit total regional species richness. Only small amounts of residual variability remain that might be attributed to other factors such as history. Our results suggest that the richness-energy hypothesis probably applies generally to all higher taxa terrestrial animals in cold and temperate habitats.

Acknowledgements

We would like to thank D. L. Wagner for valuable comments on an earlier draft of the manuscript. J. T. Kerr gratefully acknowledges doctoral scholarship support from the Natural Sciences and Engineering Research Council of Canada (NSERC). This work was supported by NSERC research grants to D. J. Currie and to L. Packer.

Literature cited

- Adams, J. M. & F. I. Woodward, 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature*, 339: 699-701.
- Bird, P. M. & D. J. Rapport, 1986. State of the Environment Report for Canada. Environment Canada, Ottawa, Ontario.
- Currie, D. J. & V. Paquin, 1987. Large-scale biogeographic patterns of species richness of trees. *Nature*, 329: 326-27.
- Currie, D. J., 1991. Energy and large-scale patterns of animal and plant species richness. *American Naturalist*, 137: 27-49.
- Gaston, K. J. & P. H. Williams, 1996. Spatial patterns in taxonomic diversity. Pages 202-229 in K. J. Gaston (ed.). *Biodiversity*. Blackwell Science, Oxford.
- Holdridge, L. R., 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.
- Hubbell, S. P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203: 1299-1309.
- Huston, M. A., 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Janzen, D. H., 1970. Herbivores and the number of tree species in the tropics. *American Naturalist*, 104: 501-28.
- Kerr, J. T. & L. Packer, 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385: 252-254.
- Kukal, O., M. P. Ayres & J. M. Scriber, 1991. Cold tolerance of the pupae in relation to the distribution of swallowtail butterflies. *Canadian Journal of Zoology*, 69: 3028-37.
- Latham, R. E. & R. E. Ricklefs, 1993. Global patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. *Oikos*, 67: 325-33.
- May, R. M., 1988. How many species are there on Earth? *Science*, 241: 1441-49.
- McGugan, B. M., 1958. Forest Lepidoptera of Canada Recorded by the Forest Insect Survey, Volume 1. Papilionidae to Arctiidae. Forest Biology Division, Department of Agriculture, Ottawa, Ontario.
- Prentice, R. M., 1958-1965. Forest Lepidoptera of Canada Recorded by the Forest Insect Survey, Volumes 2-4. Forest Biology Division, Department of Agriculture, Ottawa, Ontario.
- Randolph, J. C., 1973. Ecological energetics of a homeothermic predator, the short-tailed shrew. *Ecology*, 54: 1166-1187.
- Ricklefs, R. E. & D. Schluter, 1993. Species diversity: Regional and historical influences. Pages 350-363 in R. E. Ricklefs & D. Schluter (ed.). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, Illinois.
- Rohde, K., 1992. Latitudinal gradients in species diversity: The search for the primary cause. *Oikos*, 65: 514-27.
- Root, T., 1988. Energy constraints on avian distributions and abundances. *Ecology*, 69: 330-339.
- Shmida, A. & M. V. Wilson, 1985. Biological determinants of species diversity. *Journal of Biogeography*, 12: 1-20.
- Stevens, G. C., 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. *American Naturalist*, 143: 240-256.
- Turner, J. R. G., C. M. Gatehouse & C. A. Corey, 1987. Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, 48: 195-205.
- Tyler, H. A., K. S. Brown & K. H. Wilson, 1994. *Swallowtail Butterflies of the Americas*. Scientific Publishers, Gainesville, Florida.
- Wallace, A. R., 1878. *Tropical Nature and Other Essays*. Macmillan, New York.
- Wilson, E. O., 1987. The little things that run the world. *Conservation Biology*, 1: 344-346.
- Wright, D. H., 1983. Species-energy theory: An extension of species-area theory. *Oikos*, 41: 496-506.
- Wright, D. H., Currie, D. J. & B. A. Maurer, 1993. Energy supply and patterns of species richness on local and regional scales. Pages 66-74 in R. E. Ricklefs & D. Schluter (ed.). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, Illinois.