
Species Richness, Endemism, and the Choice of Areas for Conservation

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Abstract: *Although large reserve networks will be integral components in successful biodiversity conservation, implementation of such systems is hindered by the confusion over the relative importance of endemism and species richness. There is evidence (Prendergast et al. 1993) that regions with high richness for a taxon tend to be different from those with high endemism. I tested this finding using distribution and richness data for 368 species from Mammalia, Lasioglossum, Plusiinae, and Papilionidae. The study area, subdivided into 336 quadrats, was the continuous area of North America north of Mexico. I also tested the hypothesis that the study taxa exhibit similar diversity patterns in North America. I found that endemism and richness patterns within taxa were generally similar. Therefore, the controversy over the relative importance of endemism and species richness may not be necessary if an individual taxon were the target of conservation efforts. I also found, however, that richness and endemism patterns were not generally similar between taxa. Therefore, centering nature reserves around areas that are important for mammal diversity (the umbrella species concept) may lead to large gaps in the overall protection of biodiversity because the diversity and endemism of other taxa tend to be concentrated elsewhere. I investigated this further by selecting four regions in North America that might form the basis of a hypothetical reserve system for Carnivora. I analyzed the distribution of the invertebrate taxa relative to these regions and found that this preliminary carnivore reserve system did not provide significantly different protection for these invertebrates than randomly selected quadrats. I conclude that the use of Carnivora as an umbrella taxon is an unreliable method for invertebrate conservation.*

Riqueza de Especies, Endemismo y Selección de Areas para Conservación

Resumen: *Aunque grandes redes de reservas serán los componentes integrales de la conservación exitosa de la biodiversidad, la implementación de tales sistemas esta limitada por la confusión sobre la importancia relativa del endemismo y la riqueza de especies. Existe evidencia (Prendergast et al. 1993) de que las regiones con alta riqueza de especies para un taxón tienden a ser diferentes de aquellas con endemismo alto. Probé lo anterior utilizando datos de distribución y riqueza de 368 especies de Mammalia, Lasioglossum, Plusiinae y Papilionidae. El área de estudio, subdividida en 336 cuadrantes, fue el área continua de Norte América al norte de México. También probé la hipótesis de que los taxa estudiados presentan patrones de diversidad en Norte América similares. Encontré que los patrones de endemismo y de riqueza de especies intra-taxa generalmente eran similares. Por tanto, puede que la controversia sobre la importancia relativa del endemismo y de la riqueza de especies no sea necesaria si los esfuerzos de conservación estuvieran orientados a un taxón individual. Sin embargo, también encontré que los patrones de endemismo y de riqueza generalmente no eran similares entre taxa. Por tanto, ubicar reservas naturales alrededor de áreas importantes para la diversidad de mamíferos (concepto de especie sombrilla) puede conducir a grandes huecos en la protección integral de la biodiversidad porque la diversidad y el endemismo de otros taxa tienden a estar concentrados en otros sitios. Investigué esto más profundamente seleccionando cuatro regiones en Norte América que podrían ser la base de un sistema hipotético de reservas para Carnivora. Analicé la distribución de taxa de invertebrados presentes en esas regiones y encontré que este sistema preliminar de reservas para carnívoros no proporcionó protección significativamente diferente a los invertebrados que la proporcionada en*

Paper submitted March 24, 1996; revised manuscript accepted December 2, 1996.

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cuadrantes seleccionados aleatoriamente. Concluyo que el uso de Carnivora como un taxón sombrilla es un método no confiable para la conservación de invertebrados.

Introduction

Most biologists agree that national or international reserve systems will be central to biodiversity conservation in an era of increasing human environmental impacts (Soulé 1991; McNeely 1994; Miller 1994; Kerr & Currie 1995). Central to the success of reserve strategies is an understanding of regional biodiversity patterns (Scott et al. 1987; Margules et al. 1988; Scott et al. 1990; Westoby 1993). Reserve selection algorithms (e.g., Vane-Wright et al. 1991; Pressey et al. 1993; Pressey et al. 1994) are largely useless without a good, working knowledge of species distributions that permit the prioritization of areas for conservation.

The difficulties faced by the conservation community in recommending reserve sites are compounded by debate over the relative importance of regions with high biodiversity and endemism. Some have argued that regions of high endemism should receive priority (Myers 1988, 1990; Bibby 1994), whereas others have suggested that aggregate biodiversity levels are more important (Dinerstein & Wikramanayake 1993; Pressey et al. 1993). The picture is further complicated by Prendergast et al. (1993) who suggest that areas of high endemism do not correspond with those of high species richness. Their results, however, were based on richness patterns in the United Kingdom and may not be applicable to larger, non-insular areas.

It would be desirable to use a single, higher level taxon as an indicator of overall biodiversity at a regional scale (Noss 1990; Pearson & Cassola 1992) in order to accelerate assessment of local biodiversity levels and help select areas for conservation. However, the climatic and physical factors that most closely relate to vertebrate richness patterns (Wright 1993; Currie 1991; Kerr & Packer 1997) are different from the factors that correlate with plant richness in North America (Currie & Paquin 1987; Adams & Woodward 1989). Invertebrates, in turn, vary in their richness distribution patterns between taxa. Therefore, it may not be possible to consistently use any single taxon as an indicator of overall biodiversity. Further basic research into factors that correlate with biodiversity patterns is needed before this issue can be addressed comprehensively. Although patterns of endemism are less well understood than large scale variation in species richness patterns, there is little reason to predict that endemism patterns between taxa will covary extensively. Some taxa, however, may exhibit similar patterns of richness and endemism, and an investigation of the

extent to which this is true would be useful in conservation planning.

Consequently, I determined the extent to which patterns of species richness in four higher taxa parallel their respective endemism patterns in North America. If richness patterns of an individual taxon are similar to its endemism patterns, the question of whether taxon-specific conservation efforts should be directed toward centers of endemism or high species richness becomes moot. I used four taxa—Mammalia (a vertebrate class), *Lasioglossum* (a bee genus), Plusiinae (a moth subfamily), and Papilionidae (a butterfly family)—to test whether endemism and richness patterns are similar within a taxon. I continued this analysis at a practical level by investigating the extent to which the mammalian order Carnivora can be used as an umbrella taxon for invertebrates, exemplified by *Lasioglossum*, Plusiinae, and Papilionidae because adequate protection of taxa with large home ranges, such as carnivores, has been hypothesized to lead to the successful protection of smaller organisms (Shafer 1990).

Methods

I collected data on the distributions of terrestrial Mammalia (D. J. Currie, personal communication), Plusiinae (Lafontaine & Poole 1991), *Lasioglossum* (McGinley 1986), and Papilionidae (Tyler et al. 1994) to produce species richness totals on a 336-quadrat map covering North America north of Mexico. These quadrats were 2.5° × 2.5° south of 50°N, and 2.5° × 5° north of 50°N. There were 254 mammal, 69 Plusiinae, 27 *Lasioglossum*, and 18 Papilionidae species. This large scale approach to biodiversity analysis, in particular, is essential because this is the scale at which reserve planning should begin if protection of biodiversity is the goal (Ceballos & Brown 1995).

Following the conceptual methodology of Usher (1986 in Williams 1993), I calculated endemism by counting the number of quadrats in which each species occurred, taking its inverse, and summing the total for each quadrat, as follows:

$$Endemism = \sum_{i=1}^S Q^{-1}, \quad (1)$$

where S is the total number of species in the taxon under consideration (for example, Chiroptera, Papilionidae, etc...), and Q is the total number of quadrats in-

cluded within each species' range. Thus, species with very narrow distributions have higher endemism scores, with the most restricted species (occurring in one quadrat only) scoring 1.0 on the endemism scale. A common taxon will contribute relatively little to the overall endemism score of each quadrat in which it occurs, whereas a rare species will contribute more but to fewer quadrats. This intuitive measure provides an estimation of geographical distribution of rarity for each taxon considered. Quadrats containing a high proportion of geographically restricted taxa will have higher endemism scores than quadrats containing principally wide-ranging species, but similar species richness levels. Quadrats with no species for a given taxon were assigned an endemism value of zero. The final data matrix, therefore, consisted of endemism and species richness scores for each taxa for 336 quadrats.

I examined bivariate plots of species richness and endemism patterns for each taxon to determine the nature of the relationships between these variables. Endemism variables were $\log(x + 1)$ transformed. Pearson correlations and linear or polynomial regression were used to investigate the richness-endemism relationship for each taxon more thoroughly. I further subdivided class Mammalia into its respective orders and analyzed them individually, except for Marsupiala, which has only one North American species and was excluded from the order-level analysis. I used the same approach to compare the richness and endemism patterns exhibited by different taxa to determine whether large scale convergence of biodiversity patterns existed in these groups. For clarity, I did not divide class Mammalia into constituent orders when comparing the species richness and endemism gradients in this group with those of *Lasioglossum*, Papilionidae, and Plusiinae.

I performed a coarse gap analysis on North American carnivores, a group perhaps most likely to serve as an umbrella taxon due to large home range requirements and the consequent need to protect large tracts of territory to maintain population viability (Eisenberg 1980; East 1981; Eisenberg & Harris 1989; but see Murphy & Wilcox 1986). I separated the most species-rich quadrat first, eliminated all carnivore taxa in this quadrat from the database and then identified successively less important quadrats until all carnivores had been included at least once. All carnivore species can be found in just four quadrats. These four quadrats represent a hypothetical initial system of reserves for this taxon, not a completed carnivore conservation system. I then examined *Lasioglossum*, Papilionidae, and Plusiinae richness in these four quadrats and determined the number of species in each invertebrate taxon that would be missed by targeting carnivores exclusively in reserve planning (species that fall through the "gaps" in the system). I randomly selected 10 sets of four quadrats, counted the number of invertebrate species included by this ap-

proach, and compared the number of insect species found to that using Carnivora as an umbrella taxon. This approach is conservative in assessing the conservation status of the study taxa because any species that occurs anywhere in a quadrat that is selected for "conservation" is considered to have been successfully protected despite the relative enormity of the study quadrats in comparison with most parks.

Results

In general, there was a strong positive correlation between species richness and endemism within the taxa I studied (Table 1; Pearson $r = 0.703-0.851$, $p < 0.0001$). This correlation was similar for Mammalia, *Lasioglossum*, Papilionidae, and Plusiinae (Fig. 1). Regions with high species richness tended also to contain a large number of geographically restricted taxa. Individually, most mammal orders also showed a powerful richness-endemism relationship (Table 1; Pearson $r = 0.384-0.814$, $p < 0.0001$). I did find, however, that Carnivora and Insectivora richness and endemism patterns are only weakly correlated. These results are not consistent with those of Prendergast et al. (1993), who found little geographical convergence between endemism and species richness in the United Kingdom.

In contrast, I observed generally weak correlations in between-taxa comparisons of species richness and endemism patterns. Mammalian species richness patterns were similar to those of *Lasioglossum* and Papilionidae (Fig. 2), however. There were no strong correlations between endemism patterns of different taxa. Other correlations were significant but weak. Although these results do show a general correspondence between the richness and endemism patterns of individual taxa, there appears to be little basis for the use of a single taxon as an indicator of other groups' diversity or endemism levels at this scale.

Despite some general similarity in trends of species richness in North America between mammals and some

Table 1. Pearson correlations between patterns of species richness and endemism among 10 taxa in the conterminous United States and Canada.

<i>Species richness</i>	<i>Correlation with endemism*</i>
All Mammalia	0.807
Artiodactyla	0.807
Carnivora	0.384
Chiroptera	0.814
Insectivora	0.523
Lagomorpha	0.665
Rodentia	0.773
<i>Lasioglossum</i>	0.851
Papilionidae	0.703
Plusiinae	0.772

*All correlations are significant at $p < 0.001$, and endemism is $\log(x + 1)$ transformed.

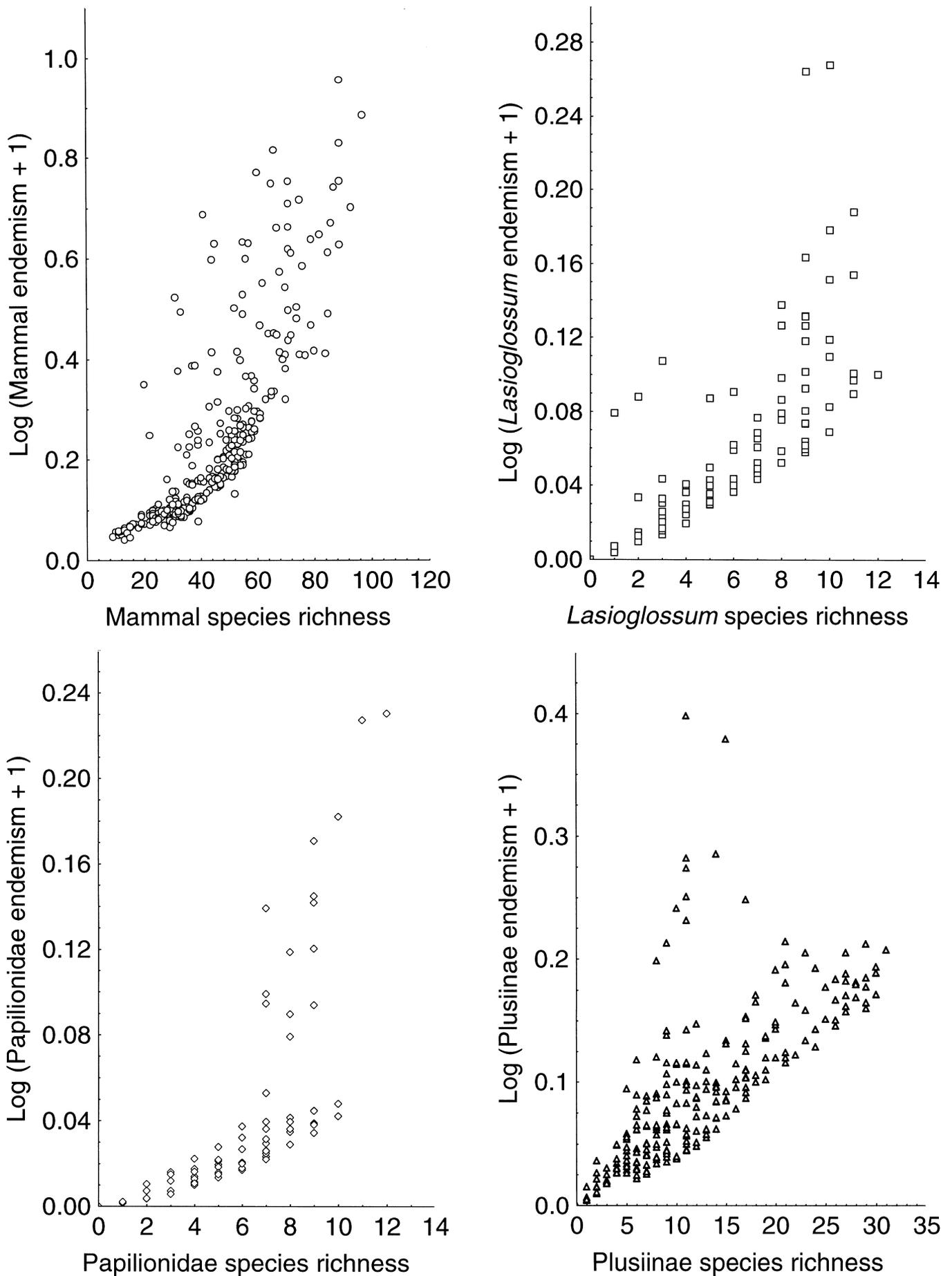


Figure 1. Plots of endemism versus species richness for several taxa in mainland North America north of Mexico. Endemism variables are $\log(x + 1)$ transformed.

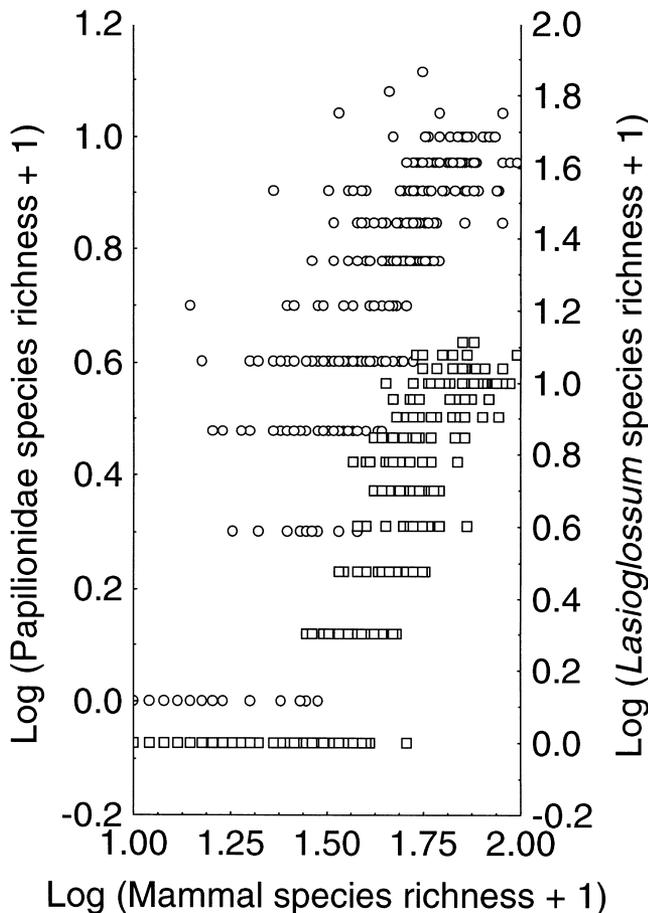


Figure 2. *Lasioglossum* and *Papilionidae* species richness plotted against mammal species richness in North America north of Mexico. *Lasioglossum* are represented by open squares and *Papilionidae* by open circles. All variables are $\log(x + 1)$ transformed to stabilize residual variance.

invertebrates, gap analysis based on carnivore distributions revealed that a large proportion of invertebrates would be missed if reserves were designated based on the use of Carnivora as an umbrella taxon. The quadrats required to find all carnivore species at least once were central Arizona, northeast Manitoba, southwest Texas, and central Wyoming in decreasing order of importance. However, if these quadrats were completely protected, only 14 out of 27 *Lasioglossum* species (51.9%), 14 out of 18 *Papilionidae* species (77.8%), and 22 out of 70 *Plusiinae* species (31.4%) would also receive protection. When all invertebrate species were considered together, a gap analysis that targeted carnivores as an umbrella taxon would successfully conserve only 50 out of 115 species, or about 43.5% of the total invertebrate diversity in this study. This was not significantly different from the random quadrat selection approach (mean = 0.390 or 39%, $t = 0.690$, $p = 0.508$). Obviously, carni-

vores might be more successful as umbrella species if other invertebrate taxa were considered, but this does not alter the fundamental conclusion from this analysis: there is little reason to believe that conservation efforts directed toward carnivores will incidentally conserve most invertebrates.

Discussion

Within taxa the broadly similar patterns of endemism and richness suggest that networks of protected areas designated to protect centers of richness for one taxon will also tend to encompass a high proportion of that taxon's geographically-restricted species. These findings may facilitate the initial prioritization of sites for reserve selection if individual taxa are the focus of conservation efforts, although finer scale information on species distributions and habitat preferences will remain an important component in reserve planning.

The weak correlations I observed in richness patterns between taxa suggest that national networks of protected areas will need to be designed carefully if large gaps in biodiversity protection are to be avoided. Furthermore, these comparisons show that centers of species richness for one taxon are frequently not diverse for another (Table 2). Conservation efforts in the past have tended to focus on large, charismatic species, based in part on the umbrella species concept (Wilcox 1984; Shafer 1995). To protect viable populations of such large organisms, large areas need to be set aside (Newmark 1987). These reserves also serve to protect the species-rich but relatively poorly known invertebrate taxa, whose individual area requirements are less. Whereas large reserves may successfully protect viable populations of these less noticeable taxa, my results show that targeting mammals for reserve protection will not generally conserve centers of invertebrate species richness.

Table 2. Pearson correlations of richness and endemism between different taxa in the conterminous U.S. and Canada.*

	Species richness		
	Mammal	<i>Lasioglossum</i>	<i>Papilionidae</i>
<i>Lasioglossum</i>	0.833		
<i>Papilionidae</i>	0.831	0.676	
<i>Plusiinae</i>	0.514	0.610	0.376
	Endemism		
	Mammal	<i>Lasioglossum</i>	<i>Papilionidae</i>
<i>Lasioglossum</i>	0.805		
<i>Papilionidae</i>	0.594	0.341	
<i>Plusiinae</i>	0.459	0.516	0.238

*All correlations are significant at $p < 0.0001$, and all variables measuring endemism have been $\log(x + 1)$ transformed.

Extensive reliance on the umbrella species concept, therefore, is likely to lead to inadequate biodiversity protection. Smaller reserves that are designated principally for invertebrate or plant taxa may be necessary in order to maintain these organisms in an increasingly degraded landscape (Shafer 1995), provided population viability issues are addressed adequately in such areas (Soulé 1987). An obvious difficulty with this proposition is that because richness patterns of invertebrate taxa in this study are not strongly correlated (Table 2), protection of a major proportion of invertebrate diversity may require more reserves than current conservation funding or political resolve will permit.

A limitation of this broad-scale approach to conservation planning is that local detail in habitat and species distributions remains unresolved. However, this method permits the selection of high priority regions for conservation based on the general convergence, within individual taxa, between endemism and richness patterns. Although it is not possible to make generalizations with respect to richness patterns in North America, these findings underline the need for further basic research into factors controlling biodiversity. Reserve networks incorporating appropriate design strategies (Harris 1984; Shafer 1990) may then be established in these areas. Overcoming the obstacles to adequate nature conservation at this scale remains one of the fundamental challenges in conservation.

Acknowledgments

I am grateful to the Natural Science and Engineering Research Council of Canada (NSERC) for post-graduate scholarship support. This research was supported by an NSERC grant to L. Packer, for whose helpful comments I am grateful. Thanks also to D. Currie who provided the mammal database and helped me considerably in our discussions of biodiversity and conservation, and M. De Giusti who provided support in assembling the invertebrate databases.

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