

## THE RELATIONSHIP BETWEEN LOCAL AND REGIONAL DIVERSITY

M. JULIAN CALEY<sup>1</sup> AND DOLPH SCHLUTER<sup>2</sup>

<sup>1</sup>*Department of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia*

<sup>2</sup>*Department of Zoology and Center for Biodiversity, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada, V6T 1Z4*

**Abstract.** The extent to which species richness in local communities is determined by regional and historical processes is not well understood. An increasingly popular way to investigate these large-scale processes is through regressions of local on regional species richness. We sampled local and regional species richness in a broad array of taxa from around the world to address five questions. First, is the relationship between local and regional species richness linear, or does local richness accumulate more slowly at progressively higher regional diversities, suggesting local saturation of species diversity? Second, do these relationships vary with locality size? Third, do taxa and continents differ in the form of relationships between local and regional diversity? Fourth, do relationships between local and regional diversity depart from that expected from a null model in which all individuals of a locality are randomly sampled from a regional pool of species whose abundances have a canonical log-normal distribution? Fifth, using this same null model, how does the expected relationship between local and regional species richness depend on the sampling intensity within localities? We used distribution maps to ensure that diversity was sampled in a consistent manner across diverse taxa. Each region was  $500 \times 500$  km, and localities were 1% and 10% of the region size.

There was no evidence of local species saturation, as local species richness was strongly and linearly related to regional richness at both spatial scales. Between scales, local diversity accumulated faster as a function of regional diversity at the larger spatial scale. The slope of this relationship between local and regional diversity was the same among taxa across continents, and between Australia and North America across taxa. In other words, at each spatial scale one relationship between local and regional diversity describes most cases very well. The null model showed that approximately linear relationships between local and regional diversity are expected when regional species abundances are log-normal and when the number of individuals sampled within localities is large (roughly 200 times the number of species in the most species-rich region examined). However, empirical slopes were less than expected from the null model, which we interpret as an effect of spatial turnover of species (beta diversity). Since these slopes were nevertheless similar among taxa and between regions, rates of spatial turnover must be approximately the same among these taxa and regions. The log-normal model also showed that nonlinear (concave down) relationships between local and regional diversity are expected under random sampling when sample size is small relative to regional diversity. Therefore, nonlinear relationships are not necessarily indicative of saturation. Our results suggest that at the scales investigated here local communities are unsaturated and that their diversities are strongly limited by species richness of the surrounding regions. Similarity between taxa and continents in the form of the local-regional diversity relationship implies that “rules” governing the assembly of local communities may be widely consistent. If so, understanding species diversity in local assemblages will require knowledge of processes acting at larger spatial scales, including determinants of regional species richness and spatial turnover of species.

*Key words:* biodiversity; community saturation; community structure; log-normal distribution; sampling methodology; spatial scale; species abundance; species diversity, local and regional; species richness among taxa; species richness between continents; species richness, local *cf.* regional.

### INTRODUCTION

The role of regional and historical processes in determining local patterns of species richness has recently regained prominence in the ecological literature (Ricklefs 1987, Cornell and Lawton 1992, Cornell 1993,

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Ricklefs and Schluter 1993, Westoby 1993). These processes, operating on large temporal and spatial scales, are likely to be important determinants of local patterns of diversity because they will determine the characteristics of the species pools from which local communities can be assembled, and because they set the upper limit on local species richness. However, a range of relationships between local and regional species

richness is possible, from those in which local species richness is dependent on regional species richness to those in which it is not. Communities in which local diversity is linearly dependent on regional diversity over the entire range of regional diversities have been referred to as “unsaturated” or “Type I” communities (Cornell 1985a, Cornell and Lawton 1992). Alternatively, as regional richness increases, local diversity might reach a ceiling above which it does not rise despite further increases in regional diversity. In this case, local communities are said to be “saturated” with species and are referred to as “Type II” communities (Cornell 1985a, Cornell and Lawton 1992).

A variety of community-organization models predict that local species richness can be either saturated or unsaturated (Cornell and Lawton 1992, Caswell and Cohen 1993, Cornell 1993). For instance, biotic interactions in limited niche space (MacArthur and Levins 1964, Levin 1970, Armstrong and McGehee 1980, Caswell and Cohen 1993), disturbance (Huston 1979), and limited dispersal capabilities (i.e., pool exhaustion, Cornell 1993) might limit the number of species coexisting locally irrespective of regional diversity. Alternatively, models of noninteractive community structure (Caswell 1976), lottery competition for space (Sale 1977), random colonization and extinction (Hubbell and Foster 1986), specialist predators (Jansen 1970, Armstrong 1989), and disruption of competitive exclusion by disturbance (Caswell and Cohen 1993) suggest that local species richness might be positively related to regional species richness across its range of values. It is also possible that in natural communities a variety of such processes could interact, resulting in a complex array of outcomes. Therefore, no simple and consistent predictions arise as to the relationship expected between patterns of local and regional species richness.

In spite of a lack of consistent predictions from theoretical studies, empirical studies of saturation in natural communities have in general not detected local species saturation (Cornell 1985a, b, Stevens 1986, Ricklefs 1987, Wiens 1989, Hawkins and Compton 1992, Hugueny and Paugy 1995, Shorrocks and Sevenster 1995, Cornell and Karlson 1996; but see Aho and Bush 1993). Such studies, however, have examined the relationship between local and regional richness for a limited range of taxa and regional diversities, and over relatively small geographical ranges.

In this report, we examine the relationship between local and regional species richness across a broad range of taxa worldwide. Our primary objective is to determine whether the relationship is linear across disparate taxa, distant continents, and large differences in regional species diversities, or whether the relationship is nonlinear and suggests species saturation. A second goal is to see whether the relationship between local and regional diversity varies with locality size. Third, we determine if patterns of saturation and nonsaturation are consistent across taxa and between continents.

Fourth, we compare observed relationships with those expected from a simple null model in which all individuals in a locality constitute a random sample from a region having canonical log-normal species abundances. Finally, we examine whether the shape (i.e., linear vs. curvilinear) of the expected relationship between local and regional species richness is independent of local sampling intensity.

We apply a standard method for testing species saturation in local communities (e.g., Terborgh and Faaborg 1980, Cornell 1985a, b, Stevens 1986, Ricklefs 1987, Aho 1990, Hawkins and Compton 1992, Aho and Bush 1993, Dawah et al. 1995, Hugueny and Paugy 1995, Cornell and Karlson 1996). Typically, small, replicate local communities are sampled in regions that vary in total species richness and the relationship between local and regional species richness is examined. A strong linear relationship is taken as evidence that local communities are unsaturated and results from proportional sampling of the regional species pool (reviews by Cornell and Lawton 1992, Cornell 1993; but see *Discussion*, below). This relationship will have slope 1 in communities in which all species in the regional species pool are present at all localities. More commonly, turnover of species among habitats (beta diversity) or incomplete sampling within habitats will result in a linear relationship between local and regional richness that is less steep. Alternatively, either no relationship or a concave-down, curvilinear relationship between local and regional species richness is used as evidence of local species saturation.

Our survey attempts to correct a number of potential problems of interpretation arising from this curve-fitting approach. The first problem is that, while the size of sampled localities within studies has generally been held constant, region size has often been allowed to vary in order to sample a range of regional richness (e.g., Lawton 1982, Cornell 1985a, b, Ricklefs 1987, Aho 1990, Aho and Bush 1993). Strong regional species-area relationships have been reported in many of these studies (e.g., Aho 1990, Aho and Bush 1993), or associated studies of the same system (Cornell and Washburn 1979). Therefore, as region size increases independent of locality size, localities sample a decreasing proportion of larger and more species-rich regions. Sampling in this way increases the probability of detecting a curvilinear relationship, and such a relationship could be incorrectly interpreted as evidence of local saturation.

To avoid this problem, we fix locality and region size for all estimates of species richness for surveys at a particular spatial scale. Locality size can then be varied between surveys while keeping region size fixed, enabling comparisons of relationships between local and regional richness at different spatial scales. We compare relationships between local and regional diversity at two scales, one in which locality area is 1% of the region area and the other in which the locality is 10%

of the region area. The 1% scale is closer to what most would regard as "local," but a dependence of local diversity on regional diversity is expected at all spatial scales (Ricklefs and Schluter 1993). Localities at the 10% scale are expected to include more environmental heterogeneity than smaller localities. Our goal was to see how these different levels of heterogeneity might affect the form of the local–regional relationship, and whether different taxa respond similarly to this increased variation.

A second problem is that sampling methods have varied, making it difficult to compare the relationship between local and regional diversity among taxa. For instance, even if region sizes were uniform among studies, localities defined as individual oak trees for sampling cynipid wasps (Cornell 1985*a, b*), transects for sampling West Indian birds (Terborgh and Faaborg 1980), and water bodies or parts of water bodies for sampling helminth parasites of herpetofauna (Aho 1990) all sample different proportions of the area used to estimate regional species richness. Therefore, to date no attempts to explore any general relationship between local and regional species richness among taxa have been possible. Here we use the same sampling protocol for all taxa, which enables us to examine the relationship between local and regional richness across taxa.

A third problem is that abundances vary among species, and common species are more likely to be sampled in a locality than are rare ones. We are aware of only two studies that explore the effect of relative abundance on the relationship between local and regional diversity (i.e., Cornell 1985*a*, Aho 1990). In both studies, relationships between local and regional richness were examined for common and rare species separately. No clear differences between rare and common species were reported in either study. However, because rare and common species within regions and localities contribute to patterns exhibited at both spatial scales, it may be better to account for a more complete range in variation in relative abundances within communities rather than relying on a dichotomous division of species into rare vs. common.

We account for differences in abundance among species using a simple neutral model that predicts the relationship between local and regional diversity where species abundances are canonical log-normally distributed. This model is neutral in that it incorporates no spatial structure (i.e., beta diversity) or biotic interactions that could cause local saturation. We compare the predictions of this model to distributional data for a range of taxa to ask whether and how empirical local–regional relationships depart from random expectation. We also explore the shape of the local–regional relationship under proportional sampling and a range of sampling intensities.

#### METHODS

##### *Natural regions and localities*

We tested the relationship between local and regional species richness in the wild using published distribu-

tion maps for a variety of taxa throughout the world. These data were collected from biogeographical monographs (e.g., Veron 1993) and field guides. A region was arbitrarily defined as an area 500 km on a side. A locality was defined as either 1% or 10% of the region area. For each taxon (e.g., birds) at a particular locality size, only a single region per continent was sampled. This was done to maximize the independence of observations (i.e., each is from a different continent). Regions within continents were located by the random selection of a latitude and a longitude marking its center, under the constraint that the entire region fell within the boundaries of a particular continent. Within a continent, and again to maximize independence of observations, different regions of 500 × 500 km were used for each taxon considered (e.g., mammals and reptiles of Australia). Local diversity was estimated for a single locality at the center of each region sampled.

All taxa for which field guides were available to us were included in our survey (see Appendix). For these taxa, species richness within regions and localities was estimated by enumerating the species whose distributions overlapped the selected region and locality, respectively. Species distributions that were in any way in question (e.g., *Tinamus major*, Hilty and Brown 1986) were excluded from our analyses. Similarly, species with temporally disjunct distributions (i.e., migratory birds) were excluded if their migratory path crossed the locality or region of interest but they were otherwise nonresident in those areas.

Field guides that depicted species distributions using dot maps were not used. While dot maps may convey accurate information regarding where a species has been either collected or observed, we felt unjustified in assuming the extent of the distribution of species from such maps without having any first-hand experience of these species. For instance, collections of a particular species may have been made along two roads separated by uniform habitat. A specialist of this species would be much better able than we are to decide whether the species is likely to be found in the intervening habitat. If, however, our locality fell between these two roads, a dot map of collecting sites would underestimate local species richness.

In one case, local and regional species richnesses were estimated from species lists. Veron (1993: Table 2) provides species lists of hermatypic corals of coastal Western Australia. Reef areas for Ashmore Reef, Scott Reef, Rowley Shoals, the Dampier Archipelago, Ningaloo Reefs, and the Houtman Abrolhos Islands were digitized (map scale = 1:2.5 × 10<sup>6</sup>). All species from these six areas were used to estimate regional species richness, while the species of Rowley Shoals were used to estimate local species richness. Reef area of Rowley Shoals was ≈8% of the total reef area of the six areas combined. Furthermore, Rowley Shoals is centrally located among these areas, and therefore its use as a locality best approximates our use of distribution maps.

Introduced species whose ranges overlapped our localities and regions were included in estimates of local and regional diversity, respectively. Most introduced species recorded in field guides have persisted for a number of generations, and species extinctions that would occur because of such introductions may have already taken place. Inclusion of exotic species, therefore, should provide the most appropriate estimate of current patterns of local and regional species coexistence. If exotic species included here are causing extinctions that are not yet complete, or not yet recorded on range maps, our data will underestimate the importance of local species saturation. This bias, however, should be small because exotic species constitute a relatively small portion of the regional faunas sampled here.

Locations of regions were rerandomized at each spatial scale (but note that the regions used for the freshwater fishes of New Guinea overlapped almost completely at the two spatial scales; see Appendix). No species list of corals was available for any reef in Western Australia with an area  $\approx 1\%$  of the regional area. Therefore, corals were excluded from comparisons at this smaller scale. Analyses at even finer spatial scales were not done because of insufficient resolution available from the distribution maps we used. Furthermore, distribution maps are likely to adequately sample the presence of rare species at the large spatial scales we have examined here. For instance, at least one individual of all rare species whose ranges overlap a sampled locality is likely to occur in a large locality. At smaller spatial scales this is less likely to be true.

At the spatial scales used here, local species richness at the smaller scale may be slightly overestimated relative to local species richness at the larger scale. Overestimation would occur if a discontinuity of a species' distribution coincides with the locality sampled and if such a discontinuity is not illustrated on that species' range map. Small discontinuities are less likely to be illustrated on range maps than are larger ones. Therefore, between-scale differences in the relationship between local and regional diversity may be underestimated. Such discontinuities are unlikely to systematically bias comparisons between taxa and continents, but they may increase residual error around the relationship between local and regional richness. Scale differences among maps from which local and regional diversity were estimated may also increase residual error around this relationship.

*Analysis.*—When regional diversity is zero, so too is local diversity. Therefore, regression through the origin is a logical choice of method for describing this relationship. The most serious potential drawback of this approach is that pseudosaturation may be detected if samples of local diversity are insufficient to detect rare species in species-rich regions (Hawkins and Compton 1992). Because regression through the origin may overestimate curvature, caution should be exer-

cised in interpreting results from such regressions as evidence of saturation. These same regressions, however, provide a conservative test of linearity. All regressions and ANCOVAs reported here are through the origin.

Relationships between local and regional diversity were examined for curvilinearity by comparing linear and curvilinear (second-order polynomial) regressions calculated at each scale. The linear model is nested within the second-order polynomial model. Therefore, the relative fits of the two models were compared by testing for a significant contribution of the quadratic term to the linear regression. The slopes of linear relationships were also compared between spatial scales. Where sufficient data were available, we used ANCOVA to compare the relationship between local and regional richness between continents and among taxa. The local-regional relationships within continents were also examined for curvature, as above, at both spatial scales. Too few estimates of local and regional richness were available to test for curvature of this relationship within taxa.

*Proportional sampling, sample size, and log-normally-distributed abundances*

What is the expected relationship between local and regional species richness under proportional sampling when abundance among species and the number of individuals sampled within a locality varies? To answer this question, we constructed a model that randomly sampled individuals to simulate a locality from a sampling universe that simulated a region. Species abundances within this sampling universe varied from rare to common, and local species richness was calculated as the expected species richness given a particular locality size and regional species richness. This model contained no spatial structure (and therefore no beta diversity) and no means by which local species richness could saturate due to interspecific interactions. By varying the number of individuals sampled and regional richness within the range sampled from field guides we were able to generate expected relationships between local and regional species richness at a variety of sampling intensities.

Species–abundance relationships in ecological communities tend to be log-normally distributed (May 1975, Sugihara 1980). Therefore, we simulated regions with log-normally distributed abundances. The number of species per abundance category, or octave, was determined using the formula

$$S(R) = S_0 \exp(-a^2 R^2) \quad (1)$$

where  $S(R)$  = the number of species in the  $R$ th octave (abundance class) to the right or left ( $R = \dots, -2, -1, 0, 1, 2, \dots$ ) of the modal octave (the abundance class containing the greatest number of species);  $S_0$  = the number of species in the modal octave;  $a$  = the inverse of the width of the distribution. We used abun-

dance classes of  $\log_2$ . Therefore, the abundance of a species within a particular octave was double that of species in the class with the next least abundant species. The number of species representing the lowest and highest octaves was set to 1, thereby truncating the log-normal distribution. Empirical species–abundance relationships tend to be canonical log-normal (i.e.,  $a \approx 0.2$ ; May 1981). Therefore,  $a = 0.2$  was used in all our simulations. Simulated regions with species richness values that spanned empirical values taken from the literature were created by varying  $S_0$ .

The size of the sampling universe (or region size) was preset at  $10^7$  individuals and the exact abundance of each species given a particular regional richness was back calculated using the relation:

$$N(R) = I_r 2^R / \sum_{R=1}^m S(R) 2^R \quad (2)$$

where  $N(R)$  = the abundance of species in the  $R$ th octave rounded to an integer value;  $I_r$  = the total abundance summed across species (this way region size is expressed as the total number of individuals in an area, not the area per se); and  $S(R)$  = the species richness of the  $R$ th octave. Note that now the octave containing the rarest species is denoted  $R = 1$  to the most abundant  $R = m$  (cf. Eq. 1). The size of the sampling universe was set at  $10^7$  to satisfy the criterion that the rarest species in the most speciose region was represented by at least one individual. This was done so that rounding to integer values would not lead to rare species with 0 abundance. The presence of such 0-abundance classes would have effectively caused the left-hand side of the log-normal distributions of species abundances to be truncated.

The relationship between local and regional species richness was examined by sampling localities from these simulated regions with canonical log-normal species abundances. A locality was defined as some fixed number of randomly selected individuals making up a region. Expected species richness within localities,  $E(S_l)$ , was estimated by rarefaction (Hurlbert 1971, Simberloff 1972):

$$E(S_l) = S - \left(\frac{I_r}{I}\right)^{-1} \sum_{j=1}^s \left(\frac{I_r - I_j}{I}\right) \quad (3)$$

where  $S$  = total number of species in the region;  $I_r$  = total number of individuals in the region;  $I_j$  = the number of individuals of species  $j$  in the region, and  $I$  = number of individuals in the locality. This procedure of estimating expected local species richness was repeated for a particular sample size across a range of species richnesses, with a maximum of 500 species per region.

The relationship between local and regional species richness and sampling intensity within locations was examined using samples of  $10^6$ ,  $10^5$ ,  $10^4$ , and  $10^3$  individuals sampled from a region of  $10^7$  individuals. The

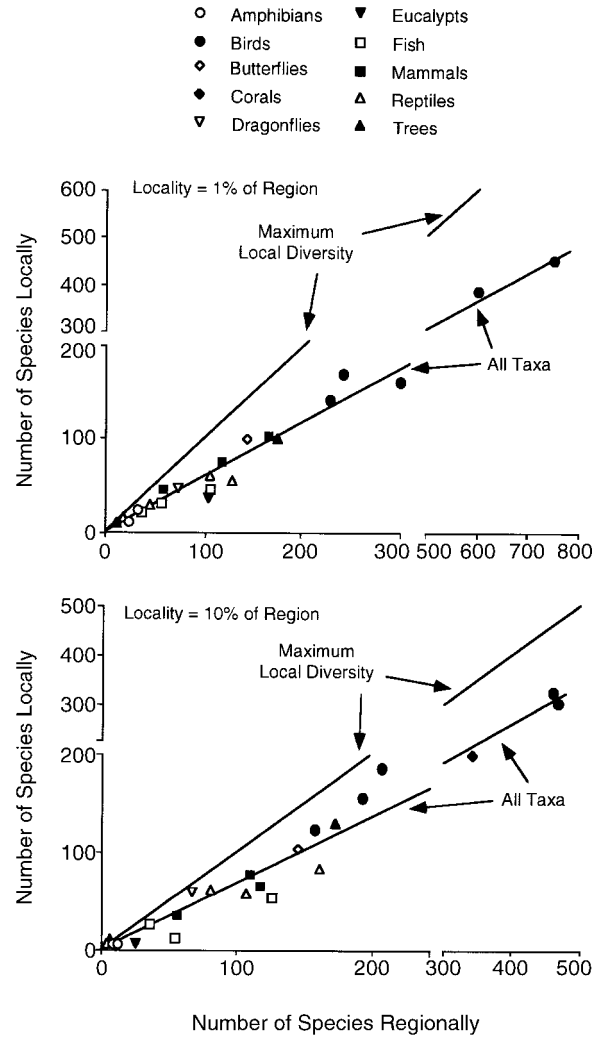


FIG. 1. Observed relationships between local and regional species richness for localities of two sizes. For locality size = 1% of region, 22 taxa were sampled; for locality size = 10% of region, 23 taxa were sampled. Estimates of local and regional species richness are illustrated for each taxon sampled, as are least-squares regressions fitted through the origin that include all taxa sampled. These relationships are contrasted with the curve for maximum local diversity. Locations of regions sampled, estimated values of local and regional species richness, and the sources of data used to sample diversity are provided in the Appendix.

degree of curvature in the relationships between local and regional species richness at different sampling intensities was examined visually.

RESULTS

*Natural regions and localities*

We sampled local and regional species richness of 22 taxa with locality size equal to 1% of regions and 23 taxa with locality size equal to 10% of regions (Fig. 1). Taxa were sampled from regions distributed among

TABLE 1. Linear and curvilinear (second-order polynomial) regressions through the origin of local and regional species richness at two spatial scales. Results are presented for local and regional species richness for all taxa sampled worldwide and for Australia and North America separately.

Region	Locality size (% of region)	Regression term	<i>P</i>	Best regression	<i>R</i> <sup>2</sup>
Worldwide	1	Linear	<0.001	$y = 0.61x$	0.99
		Quadratic	0.77		
	10	Linear	<0.001	$y = 0.68x$	0.98
		Quadratic	0.79		
Australia	1	Linear	<0.001	$y = 0.59x$	0.97
		Quadratic	0.29		
	10	Linear	<0.001	$y = 0.62x$	0.93
		Quadratic	0.47		
North Amer- ica	1	Linear	<0.001	$y = 0.58x$	0.99
		Quadratic	0.06†		
	10	Linear	<0.001		
		Quadratic	0.014	$y = 0.41x + 0.002x^2$	0.99

† Coefficient =  $-4.6 \times 10^{-4}$ .

Australia (including coastal Western Australia), Africa, Europe, North and South America, and Papua New Guinea. At both locality sizes there was a strong linear relationship between local and regional species richness (Table 1). The slope of this relationship was greater for larger localities than for smaller ones (ANCOVA:  $F_{1,41} = 6.0$ ,  $P < 0.02$ ; note, this comparison excludes corals because data were only available for corals at a single spatial scale [see *Methods: Natural regions and localities*]).

Intercontinental comparisons of local and regional species richness were possible for North America and Australia (Australia:  $n = 6$  taxa; North America:  $n = 8$  taxa). In two of four tests (two continents  $\times$  two spatial scales) for curvature in this relationship, linearity clearly described the relationship better (Table 1). In a third test, curvilinearity was marginally significant but the coefficient of the quadratic term was effectively zero (Table 1). In the final test, curvilinearity described the relationship better (Table 1) but was concave up, not down as expected in the presence of species saturation. Therefore, in comparisons of slope between continents, linear relationships were used.

The slope of the relationship between local and regional species richness did not differ between continents at either scale (Fig. 2; ANCOVA: locality = 1% of region,  $F_{1,11} = 0.86$ ,  $P > 0.37$ ; locality = 10% of region,  $F_{1,11} = 1.29$ ,  $P > 0.27$ , slope of linear regression for North America = 0.78; see Table 1 for slopes for other continents and scales). Similar to intercontinental comparisons, no clear differences in the slopes of the relationships between local and regional richness among taxa were evident (Fig. 3; ANCOVA: locality = 1% of region,  $F_{3,8} = 0.31$ ,  $P > 0.81$ ; slopes: birds = 0.62, fish = 0.45, mammals = 0.61, reptiles = 0.49, other taxa = 0.59; locality = 10% of region,  $F_{3,8} = 0.59$ ,  $P > 0.63$ ; slopes: birds = 0.71, fish = 0.42, mammals = 0.63, reptiles = 0.55, other taxa = 0.63). Within taxa, local richness increased with regional rich-

ness for all taxa for which estimates were available from more than one continent (Fig. 3).

#### *Proportional sampling, sample size, and log-normally distributed abundances*

Our null model revealed that expected relationships between local and regional richness are generally curvilinear when regional species abundances have a canonical log-normal distribution (Fig. 4). The expected relationship is approximately linear only when sample size is large ( $\approx 200$  times the number of species in the richest region), and in this case the expected slope approaches 1. This expected slope is substantially higher than observed slopes (locality = 1% of region: slope  $\pm 95\%$ ,  $CI = 0.61 \pm 0.02$ ; locality = 10% of region: slope  $\pm 95\%$ ,  $CI = 0.68 \pm 0.04$ ).

## DISCUSSION

### *Local and regional richness*

In answer to our first two questions, local species richness was unsaturated at both spatial scales, but the observed rate at which localities accumulated species when regional richness varied was less when locality size was smaller. Irrespective of differences in the rates of local accumulation of species, regional species richness was a very good predictor of local species richness at both these scales. In answer to our third question, almost all the variation in local diversity among regions was accounted for by regional richness regardless of taxon or continent.

The strength of these relationships is impressive given the taxonomic and geographic breadth of the taxa examined and the range of life histories encompassed therein. The cause of this apparent uniformity among and within taxa and regions remains unknown and requires further investigation (1) to increase the statistical power of our taxonomic and geographic comparisons

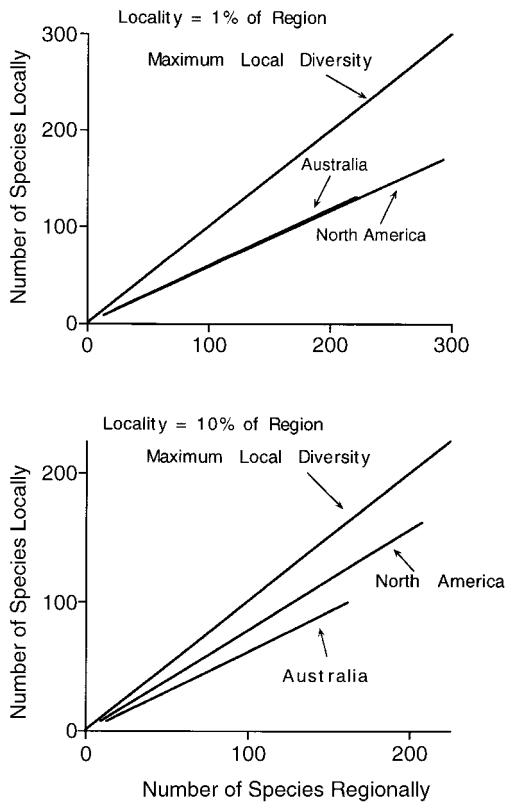


FIG. 2. Intercontinental comparisons of relationships between local and regional species richness for localities of two sizes. Curves are least-squares regressions fitted through the origin and include all taxa sampled for a particular continent (number of taxa sampled: Australia,  $n = 6$ ; North America,  $n = 8$ ). These relationships are contrasted with the curve for maximum local diversity.

and (2) to investigate if these relationships hold across a greater range of taxa and regional diversities. Irrespective of the outcome of future studies, however, local diversity of the taxa examined here clearly bears the imprint of diversity at larger spatial scales, and we will not fully understand the basis of local-regional diversity relationships until we understand the causes of regional diversity.

In answer to our fourth question, the observed rate at which localities accumulated species when regional richness varied was less than the rate expected were individuals randomly sampled from a regional pool of species having a canonical log-normal distribution of species abundances. Under random sampling a slope  $\approx 1$  is expected if sample sizes are sufficiently large. Instead, observed slopes were in the range of 0.6 to 0.7, depending on locality size. There are at least two possible explanations for these differences between the observed and expected relationships.

The most likely explanation is spatial variation in environmental conditions leading to species turnover among habitats (i.e., beta diversity) and a consequent reduction in the slopes of observed local-regional re-

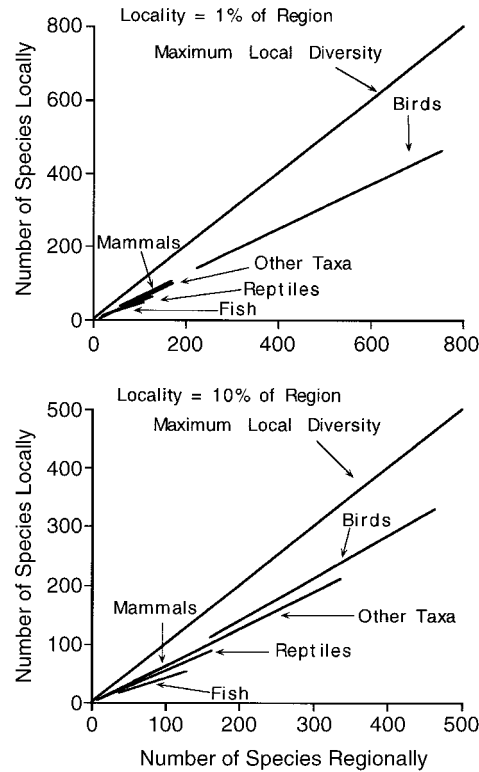


FIG. 3. Intertaxon comparisons of relationships between local and regional species richness for localities of two sizes. Least-squares regressions fitted through the origin are presented for each taxon sampled in three or more regions (number of regions sampled: birds,  $n = 5$ ; fish,  $n = 3$ ; mammals,  $n = 3$ ; reptiles,  $n = 4$ ; other taxa,  $n = 7$ ). Taxa sampled in fewer regions are pooled in "Other Taxa." These relationships are contrasted with the curve for maximum local diversity.

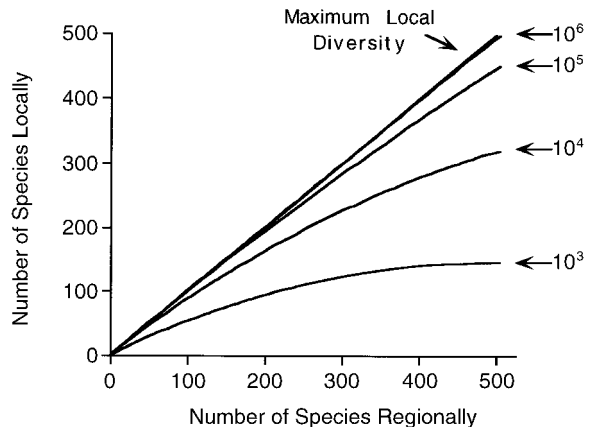


FIG. 4. The expected relationships between local and regional species richness with canonical log-normal distributions of species abundances. Relationships are presented for four sample sizes:  $10^6$ ,  $10^5$ ,  $10^4$ , and  $10^3$  randomly selected individuals. The boundary condition at which local diversity equals regional diversity is also illustrated (the "maximum local diversity" curve).

lations. For example, the addition of a species to a region does not increase local species richness in all habitats. In this case, the rate of species accumulation locally is less than the rate expected from our simple model, which incorporates no habitat variation. In support of this interpretation, the slope of the regression of local diversity on regional diversity was higher for localities of size = 10% of regions than for localities of 1%; smaller localities should sample fewer of the habitats within regions.

Given the presence of spatial turnover of species across regions, it is all the more remarkable that slopes of regressions of local diversity on regional diversity should remain similar in different taxa and between continents. This finding implies that the relationship between spatial turnover of species (beta diversity) and regional species richness is also similar across a broad range of taxa worldwide and between these taxa in North America and Australia.

Second, inadequate sample sizes may have reduced the chances of sampling the rarest species. This explanation is unlikely because our use of distribution maps should have sampled rare species adequately. Distribution maps are usually constructed from collection and observation data accumulated over many years. They thus sample rare species through time and are, therefore, likely to reduce or eliminate the chances of missing rare species (see Magurran 1988 for an example of how one year of sampling of reef fish diversity revealed the entire log-normal distribution). Also, inadequate sample sizes produce curvilinear relationships between local and regional diversity (Fig. 4), whereas the empirical relationships were linear.

The locality sizes used in this study are large compared to all those used in previous studies of saturation. Such large localities were necessary to enable us to examine patterns of local and regional diversity across taxa and to examine the scale dependence of these patterns. By using these large areas we have incorporated much habitat heterogeneity. How relationships between local and regional diversity at smaller spatial scales are affected by patterns of habitat heterogeneity is unknown. Intertaxon differences, however, may appear at smaller spatial scales. For instance, habitat heterogeneity on the scale of tens of meters may be important to the relationship between local and regional diversity for cynipid wasps but may not be for West Indian birds.

#### *Tests of saturation*

Cornell and Lawton (1992) and Cornell (1993) review the methodology used to detect species saturation in local communities and the accumulated evidence for and against local saturation. Independence of local and regional species richness or the presence of a curvilinear relationship between these two parameters has been the main diagnostic tool used to detect the presence of saturation. From the use of these methods, the majority of evidence to date suggests that local species richness

is not saturated (reviews by Cornell and Lawton 1992 and Cornell 1993; Dawah et al. 1995, Hugueny and Paugy 1995, Shorrocks and Sevenster 1995, Cornell and Karlson 1996). In contrast, however, asymptotic relationships between local and regional species richness for parasite communities of amphibians (Aho 1990) and fishes (Aho and Bush 1993) have been reported and interpreted as evidence of local saturation (Aho and Bush 1993, Cornell 1993).

In studies of saturation it has been common to standardize plot size when estimating local species richness; to incorporate variation in regional species richness, region size has been allowed to vary, often by orders of magnitude (e.g., Lawton 1982, Cornell 1985*a, b*, Ricklefs 1987, Aho 1990, Aho and Bush 1993). If by allowing region size to increase more habitats are incorporated in larger, more diverse regions, a constant locality size will sample fewer habitats in more diverse regions. Therefore, as locality size decreases relative to region size, accumulation of species locally may slow relative to the accumulation of species regionally. The resulting curvilinear relationship, however, is not evidence of local saturation. It is the result of a systematic sampling bias.

In studies of parasite communities where asymptotic relationships have been reported, regional diversity was either estimated across host ranges of variable size (Aho and Bush 1993) or summed from a sample of host populations (Aho 1990). It is not clear how much habitat heterogeneity might have varied among regions in these studies. This variation, however, may have been sufficient to result in asymptotic relationships between local and regional diversity due to a sampling bias of the type described above. Alternatively, these local communities may indeed be saturated with species. Further study will be required to choose between these possibilities.

Curvilinearity may also be detected where sample size is limited and held constant among regions because a smaller and smaller average number of individuals per species will be sampled as regional diversity increases (Hawkins and Compton 1992, and this study). In this case, as diversity rises the rate at which the expected number of local species increases will diminish, and a curvilinear relationship between local and regional species richness may result in the absence of local saturation. A log-normal distribution of species abundances will exaggerate this effect because as species richness rises, more and more species become relatively rare. This effect of pseudosaturation was minimized in our simulations when sample size within a locality approached 200 times the number of species in the richness region (i.e., 500 species in our simulations). Therefore, the answer to our final question is that the form of the expected relationship between local and regional species richness does depend on sampling intensity within localities.

In addition to the potential problems considered



above, further problems of interpretation can arise in investigations of local–regional diversity relationships. First, analyses of the shapes of relationships between local and regional richness are correlative tests, and thus detection of curvilinearity provides no evidence of the cause(s) of saturation (Cornell and Lawton 1992). Second, species within communities may vary in the strengths of their competitive interactions. If so, some species may saturate locally, while others may not (Cornell and Lawton 1992, Hawkins and Compton 1992). If noncompetitive species outnumber competitive species, local richness of the entire community may appear unsaturated while a subset of the community is indeed saturated. In this case, one process affecting local species richness has been obscured.

Third, tests of species saturation that examine relationships between local and regional species richness assume that variation in local diversity is determined by variation in regional diversity. Alternatively, localities from different regions may differ greatly in the number of species they can sustain with each locality at or near its saturation point. In this case, regional diversity may be determined by local diversity (Cornell 1993). We regard this alternative hypothesis as unlikely, but cannot rule it out with presently available data. Further tests are necessary. One such test would be to examine sites on different continents whose environmental characteristics are closely matched. If local diversity determines regional diversity, instead of the reverse, sites with closely matched environmental characteristics should contain similar numbers of species. Earlier studies have commonly shown disparities in local species diversity between matched sites on different continents (Schluter and Ricklefs 1993), suggesting that local diversity is often not saturated. It could be argued, however, that such sites are not identical. Another test would be to examine the consequences for local diversity of temporal changes in regional species richness caused by such external factors as the appearance (or removal) of dispersal bridges between previously unconnected (or connected) regions or by the introduction of exotic species.

If some of the methodology previously used in studies of local saturation is potentially flawed, how then might local saturation be detected? We agree with Cornell (1993) that deviations from expected relationships between local and regional diversity may be the best initial indicator of species richness patterns consistent with local saturation. Our work here, however, suggests that these expected relationships are not necessarily linear. Where the expected relationship between local and regional species richness is curvilinear, deviations from expected relationships can still be tested.

Alternatively, sampling programs may be designed to minimize the curvature in the expected relationship between local and regional diversity. For instance, expected curvature from our sampling model was minimal once a sampling ratio of 200 individuals per spe-

cies in the richest region was reached (Fig. 4). For a taxon that is not locally saturated, sampled at this minimum intensity, and sampled with error it is unlikely that curvature could be detected. Therefore, when sampling at this intensity, detection of curvilinearity would be evidence of saturation.

Note, however, that in cases where a linear expected relationship between local and regional diversity is desirable, a sampling intensity of 200 individuals per species in the richest region is a minimum rule of thumb. It is appropriate only where individuals can be randomly sampled. Often, random sampling will not be possible due to clumped distributions of individuals within species. Where spatial distributions within species are clumped it will be necessary to increase sampling effort further. The required increase in sampling effort could be determined from a neutral model such as the one presented here but that incorporates an appropriate spatial structure.

In not all cases will it be possible or desirable for logistical reasons to sample at these intensities. For instance, where maximum regional richness is 500 species, the sampling rule would dictate a minimum sample size of  $10 \times 10^5$  randomly selected individuals. If the locality size of interest is small, localities may not contain enough individuals to accommodate sampling at this intensity. In such a situation, curvature would be expected from proportional sampling, and tests of saturation would need to test for departures from this expected curvature. Similarly, where sampling at this intensity is not feasible for logistical reasons, deviations from a curvilinear expected relationship could be used as evidence of species saturation. Alternatively, curvature could be minimized by using a constant ratio of individuals sampled in a locality to the number of species in the region in which each locality is embedded. Therefore, a number of alternative sampling regimes are available for tests of species saturation, but in designing such tests it is important to know the shape of the expected relationship between local and regional diversity in order to construct meaningful tests of saturation using these relationships.

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#### LITERATURE CITED

- Aho, J. M. 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. Pages 157–196 in G. W. Esch, A. O. Bush,

- and J. M. Aho, editors. *Parasite communities: patterns and processes*. Chapman and Hall, London.
- Aho, J. M., and A. O. Bush. 1993. Community richness in parasites of some freshwater fishes from North America. Pages 185–193 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Allen, G. R. 1989. *Freshwater fishes of Australia*. T.F.H. Publications, Neptune City, New Jersey, USA.
- . 1991. *Field guide to the freshwater fishes of New Guinea*. Christensen Research Institute, Madang, Papua New Guinea.
- Armstrong, R. A. 1989. Competition, seed predation and species coexistence. *Journal of Theoretical Biology* **141**: 191–194.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* **115**:151–170.
- Askew, R. R. 1988. *The dragonflies of Europe*. Harley, Colchester, England.
- Behler, J. L., and F. W. King. 1979. *The Audubon Society field guide to North American reptiles and amphibians*. Alfred A. Knopf, New York, New York, USA.
- Branch, B. 1988. *Field guide to the snakes and other reptiles of Southern Africa*. Struik, Cape Town, South Africa.
- Brooker, M. I. H., and D. A. Kleinig. 1990. *Field guide to Eucalypts*. Volume 2. Inkata, Melbourne, Australia.
- Campbell, J. A., and W. W. Lamar. 1989. *The venomous reptiles of Latin America*. Cornell University Press, Ithaca, New York, USA.
- Caswell, H. 1976. Community structure: a neutral model analysis. *Ecological Monographs* **46**:327–354.
- Caswell, H., and J. E. Cohen. 1993. Local and regional regulation of species–area relations: a patch-occupancy model. Pages 99–107 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Cogger, H. G. 1992. *Reptiles and amphibians of Australia*. Fifth edition. Reed, Sydney, Australia.
- Cornell, H. V. 1985a. Local and regional richness of cynipine gall wasps on California oaks. *Ecology* **66**:1247–1260.
- . 1985b. Species assemblages of cynipine gall wasps are not saturated. *American Naturalist* **126**:565–569.
- . 1993. Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness. Pages 243–252 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Cornell, H. V., and R. H. Karlson. 1996. Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* **65**:233–241.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**:1–12.
- Cornell, H. V., and J. O. Washburn. 1979. Evolution of the richness–area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas. *Evolution* **33**: 257–274.
- Dawah, H. A., B. A. Hawkins, and M. F. Claridge. 1995. Structure of the parasitoid communities of grass-feeding chalcid wasps. *Journal of Animal Ecology* **64**:708–720.
- Hall, E. R., and K. R. Kelson. 1959. *The mammals of North America*. Ronald Press, New York, New York, USA.
- Hawkins, B. A., and S. G. Compton. 1992. African fig wasp communities: undersaturation and latitudinal gradients in species richness. *Journal of Animal Ecology* **61**:631–372.
- Heinzel, H., R. Fitter, and J. Parslow. 1979. *The birds of Britain and Europe*. Fourth edition. William Collins & Sons, London, England.
- Hilty, S. L., and W. L. Brown. 1986. *A guide to the birds of Columbia*. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–329 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Hugueny, B., and D. Paugy. 1995. Unsaturated fish communities in African rivers. *American Naturalist* **146**:162–169.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**:577–586.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Jansen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501–528.
- Lawton, J. H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *Journal of Animal Ecology* **51**:573–595.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* **104**:413–423.
- Little, E. L. 1980. *The Audubon Society field guide to North American trees, Eastern region*. Alfred A. Knopf, New York, New York, USA.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences (USA)* **51**:1207–1210.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Croom Helm, London, England.
- May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- . 1981. Patterns in multispecies communities. Pages 197–227 in R. M. May, editor. *Theoretical ecology: principles and applications*. Blackwell, Oxford, England.
- National Geographic Society. 1987. *Field guide to the birds of North America*. National Geographic Society, Washington, D.C., USA.
- Newman, K. 1991. *Birds of Southern Africa*. Third edition. Harper Collins, London, England.
- Opler, P. A., and V. Malikul. 1992. *A field guide to Eastern butterflies*. Houghton Mifflin, Boston, Massachusetts, USA.
- Page, L. M., and B. M. Burr. 1991. *A field guide to freshwater fishes*. Houghton Mifflin, Boston, Massachusetts, USA.
- Pizzey, G. 1980. *A field guide to the birds of Australia*. Collins, Sydney, Australia.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity: regional and historical influences. Pages 350–363 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**: 337–359.
- Schluter, D., and R. E. Ricklefs. 1993. Convergence and the regional component of species diversity. Pages 230–240 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Shorrocks, B., and J. G. Sevenster. 1995. Explaining local species diversity. *Proceedings of the Royal Society, London B* **260**:305–309.
- Simberloff, D. S. 1972. Properties of the rarefaction diversity measurement. *American Naturalist* **106**: 414–418.

- Stevens, G. C. 1986. Dissection of the species-area relationship among wood-boring insects and their host plants. *American Naturalist* **128**:35–46.
- Strahan, R., editor. 1983. Complete book of Australian mammals. Angus and Robertson, Sydney, Australia.
- Stuart, C., and T. Stuart. 1988. Field guide to the mammals of Southern Africa. Struik, Cape Town, South Africa.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. *American Naturalist* **116**:770–787.
- Terborgh, J. W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. *American Naturalist* **116**:178–195.
- Veron, J. E. N. 1993. A biogeographic database of hermatypic corals. Monograph Series Volume 10. Australian Institute of Marine Science, Townsville, Australia.
- Westoby, M. 1993. Biodiversity in Australia compared with other continents. Pages 170–177 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.
- Wiens, J. A. 1989. The ecology of bird communities. Volume 1. Cambridge University Press, Cambridge, England.

## APPENDIX

Locations of regions and taxa sampled, estimated values of local and regional species richness, and the sources of these estimates used in examinations of observed relationships between local (L) and regional (R) species richness.

Taxon	Geographic region	Spatial scale						Source
		Locality = 1% of region		Locality = 10% of region		Region coordinates	Species richness	
		Region coordinates	Species richness		L			
Amphibians	Australia North America	19° S, 138° E 34° N, 94° W	10 22	23 34	28° S, 122° E 47° N, 108° W	7 6	12 9	Cogger 1992 Behler and King 1979
Birds	Africa Australia Europe North America South America	20° S, 28° E 18° S, 131° E 49° N, 12° E 34° N, 100° W 5° N, 73° W	386 141 170 161 447	600 222 236 293 751	21° S, 30° E 21° S, 132° E 60° N, 54° E 33° N, 94° W 1° N, 72° W	322 125 157 187 300	455 158 192 207 461	Newman 1991 Pizzey 1980 Heinzel et al. 1979 National Geographic Society 1987 Hilty and Brown 1986
Butterflies	North America	35° N, 88° W	99	141	40° N, 96° W	103	145	Opler and Malikul 1992
Corals†	Coastal Western Australia	...	...	...	17° S, 119° E	193	335	Veron 1993
Dragonflies	Europe	51° N, 15° E	47	72	49° N, 26° E	62	67	Askew 1988
Eucalypts	Australia	32° S, 118° E	39	102	29° S, 128° E	8	25	Brooker and Kleinig 1990
Freshwater fishes	Australia New Guinea North America	35° S, 146° E 5° S, 142° E 49° N, 114° W	20 44 29	36 106 56	19° S, 144° E 6° S, 141° E 42° N, 114° W	13 54 26	54 126 36	Allen 1989 Allen 1991 Page and Burr 1991
Mammals	Africa Australia North America	25° S, 28° E 26° S, 128° E 52° N, 74° W	99 45 73	169 58 116	20° S, 17° E 28° S, 143° E 39° N, 103° W	77 36 66	110 56 117	Stuart and Stuart 1988 Strahan 1983 Hall and Kelson 1959
Reptiles	Africa Australia North America	23° S, 26° E 27° S, 144° E 38° N, 82° W	53 57 27	126 104 44	26° S, 18° E 18° S, 127° E 34° N, 93° W	57 81 59	107 161 80	Branch 1988 Cogger 1992 Behler and King 1979
Reptiles (venomous snakes only)	South America	0° N, 69° W	13	17	17° S, 64° W	4	6	Campbell and Lamar 1989
Trees (angiosperms)	North America	32° N, 83° W	99	170	33° N, 88° W	130	172	Little 1980
Trees (gymnosperms)	North America	47° N, 77° W	8	13	46° N, 95° W	9	11	Little 1980

† Data were available for corals only at a single intermediate spatial scale (see *Methods: Natural regions and localities*).