

Some general propositions about the study of spatial patterns of species richness¹

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Abstract: Spatial patterns of species richness are very well studied, yet there is surprisingly little consensus about what factors or processes control those patterns. Hypotheses have accumulated in the literature, rather than being tested and replaced by better ones. We argue that this is because most studies are not designed to test hypotheses about what controls patterns of richness. Many hypotheses are weak (often because of non-operational variables) or badly formulated (often because they do not make mutually exclusive predictions). Support for many existing hypotheses is largely *post hoc*. In contrast, correlations have been used to test general hypotheses. The clearest general patterns over broad spatial scales in polar to temperate areas are that richness is related to variations in climate. At smaller spatial scales, richness is most consistently related to productivity. Mechanistic hypotheses that predict more than just patterns of richness would be desirable, but simple correlative hypotheses that make testable predictions about patterns of richness in nature are better than elegant mechanistic hypotheses that, in practice, make no predictions.

Keywords: diversity, species richness, hypothesis testing, spatial patterns.

Résumé : Bien que les patrons spatiaux de diversité spécifique soient très bien étudiés, une vive discussion se poursuit actuellement à propos des facteurs qui les ont engendrés. Des hypothèses explicatives s'accumulent dans la littérature scientifique au lieu d'être testées et remplacées par de meilleures hypothèses. Nous croyons que ceci n'est guère surprenant : la grande majorité des études ne vise pas à tester des hypothèses générales. Beaucoup d'hypothèses sont trop faibles (souvent à cause des variables non-opérationnelles) ou trop mal formulées (car elles ne permettent pas de prédictions mutuellement exclusives) pour être testée. D'ailleurs, les preuves appuyant plusieurs hypothèses sont en grande partie *post hoc*. On a déjà utilisé des corrélations pour tester des hypothèses générales. La corrélation la plus évidente s'observe à grande échelle : la variabilité de la diversité est fortement corrélée avec le climat. À plus petite échelle, la diversité est reliée le plus fréquemment à la productivité. Bien entendu, des hypothèses mécanistes qui prédiraient plus que les patrons de diversité seraient appréciées. Pourtant une hypothèse correlative simple qui fait des prédictions testables des patrons de diversité sur le terrain vaut beaucoup plus qu'une hypothèse mécaniste élégante qui n'en fait pas du tout.

Mots-clés : diversité, richesse en espèces, test d'hypothèses, patrons spatiaux.

Introduction

The numbers of different species in a given area, *i.e.*, species richness, varies enormously from place to place. Gradients of species richness are obvious and well documented on several spatial scales. Then why do some places have more species than others? This question is a fundamental one, since the variety of species that comprise a species assemblage is one of its most basic characteristics. Variation in richness is also a matter of increasing practical concern to conservation biologists and planners, insofar as human activities may affect patterns of richness (Heywood & Watson, 1995), with potentially serious consequences for ecosystem functioning (Schulze & Mooney, 1993; Heywood & Watson, 1995).

In what follows, we criticize the state of knowledge regarding spatial patterns of species richness in nature and the factors that give rise to them. We focus on spatial patterns of richness because explanation of the natural variability in richness is a prerequisite to discussion of issues such as human influences on richness. Although species richness

varies through time as well as through space, the present review will concentrate only on spatial patterns. We focus mainly on reviews rather than the primary literature itself, because these reviews presumably represent the current consensus regarding the state of knowledge of the field.

We present our meta-review as a series of general propositions (in capitals below). Some of these are empirical and can be regarded as hypotheses. Other propositions are philosophical (or non-empirical); we present these at the outset to make our biases clear. Finally, some of the propositions can be construed as a critique of the field, in the spirit of Peters (1991). Whatever their nature, all are offered as starting points for debate.

A philosophical prelude

FUNDAMENTALLY, SCIENTISTS, INCLUDING ECOLOGISTS, ARE IN THE BUSINESS OF MAKING PREDICTIONS.

Popper (1958) and many others (Magee, 1973; Peters, 1991; Rigler & Peters, 1995; Chitty, 1996; Popper, 1990) propose that science consists of the process of posing hypotheses, deriving predictions from them, testing those

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predictions, and eliminating hypotheses whose predictions do not conform with empirical observations. It has often been argued that fields of science that consistently derive critical predictions to test their central hypotheses progress more rapidly than fields that do not (Platt, 1964; Peters, 1991; Rigler *et al.*, 1995). “Predictive power [is] the strongest evidence that the natural sciences have an objective grip on reality” (Gottfried & Wilson, 1997).

Strong hypotheses make predictions that clearly indicate which conceivable states of the universe are likely to be observed, and which are not (Rigler & Peters, 1995). For example, in the case of richness, a strong hypothesis would specify how many species should be observed under stated conditions. Explicit predictions make these hypotheses easy to test. In contrast, hypotheses that provide *post hoc* explanations of phenomena but no new testable predictions are weak at best, and untestable and non-scientific at worst (even if they happen to be true). Peters (1991) has argued that progress in ecology has been slowed by a preponderance of weak or untestable hypotheses.

The notion that predictive ability is the criterion by which science is judged has interesting corollaries. The measure of “understanding” is the extent to which one can make predictions that are consistent with observations. Some mechanistic hypotheses may make no predictions whatsoever (*e.g.*, the hypothesis that the number of available niches limits species richness). Further, some simple correlative hypotheses whose mechanisms remain obscure may nonetheless make strong predictions (*e.g.*, the hypothesis that regional species richness is a function of temperature). Unlike correlative hypotheses, mechanistic hypotheses have the potential to make predictions about novel phenomena outside the range of conditions that are currently observed. However, mechanisms are but a means to generate new and more powerful predictions. If they fail to do that, then their utility is limited to inspiring other new (and hopefully predictive) hypotheses.

MUCH OF THE VARIABILITY IN THE BEHAVIOR OF NATURAL SYSTEMS (INCLUDING PATTERNS OF SPECIES RICHNESS) CAN BE ACCOUNTED FOR BY A TRACTABLY SMALL NUMBER OF FACTORS OR GENERAL PROCESSES.

This is a pragmatic assumption – a statement of belief – that observations of nature need not be explained on a case-by-case basis. Rather, they represent specific instances of a few general laws. It is quite possible that the tractably small number of factors may only be able to account for natural phenomena in a statistical sense. Popper (1990), in one of his last works, argued that nearly all natural phenomena are influenced by webs of interactions far too complex to untangle. The best one can do is to determine the “propensity” (Popper’s word) of systems to behave in particular ways, as functions of state variables, and to recognize that these propensities are probabilistic.

In the case of patterns of species richness, this proposition means that one should be able to account statistically for much of the variance in observed patterns of richness, and to predict richness in as-yet-unobserved situations, as functions of a relatively small number of ecosystem characteristics. In all likelihood, some variation in richness is related to conditions that occur rather infrequently, so that one cannot statistically detect their influence.

Patterns of species richness

Patterns of diversity, and factors that are related to them, are extremely well studied. In their books dealing with biodiversity, Ricklefs & Schluter (1993) and Huston (1994) each cite roughly 2000 primary studies! While some of these studies are undoubtedly peripheral, it would be difficult to argue that ecologists have not already had a good crack at this issue. Reviews of the subject also abound (Pianka, 1966; MacArthur, 1972; Ricklefs, 1987; Rohde, 1992; Rosenzweig, 1992; Schluter & Ricklefs, 1993; Krebs, 1994; Huston, 1994; Rosenzweig, 1992; Rosenzweig, 1995; Begon, Harper & Townsend, 1996; Gaston, 1996).

VARIATIONS OF RICHNESS THROUGH SPACE ARE THE FUNDAMENTAL PATTERNS THAT REQUIRE EXPLANATION. THEY EXIST AT MANY SPATIAL SCALES. CORRELATIONS WITH METRICS OF SPACE (SUCH AS LATITUDE OR AREA) ARE NOT PARTICULARLY INFORMATIVE, SINCE THEY REFLECT THE COLINEARITIES OF OTHER UNSPECIFIED VARIABLES WITH SPACE.

At least since the time of Wallace (1878), ecologists have noted variation of richness through space. Gradients of richness have been described relative to many metrics of space such as latitude, longitude, altitude, distance from a water line on lake or sea shores, depth in water bodies, etc. (Huston, 1994: Table II.1).

Studies that correlate richness directly with spatial coordinates are not particularly informative. Spatial coordinates are arbitrary constructs. If richness correlates with them, it is because those coordinates are colinear with characteristics of the environment. However, spatial coordinates can be colinear with many environmental variables, and those colinearities often change among regions. The oft-cited latitudinal gradient of richness is a prime example. Any hypothesis that predicts that richness should covary with latitude cannot be distinguished from the multitude of other hypotheses that make the same prediction. Latitude (or any other spatial coordinate) is thus a poor surrogate to test the influence of other variables on richness.

Moreover, richness clearly varies in a complex manner through space: consider any map of the spatial variation in richness (Simpson, 1964; Currie, 1991). The variation of richness along a given transect is likely to depend strongly on where that transect is situated (Figure 1), and single transects need not be representative of general trends. For example, although mid-latitude peaks of richness have sometimes been considered exceptional (Janzen, 1981; Huston, 1995: Chapter 2), gradients of many shapes can occur, depending on where one looks (Figure 1).

Unidimensional gradients produced by integrating richness over other dimensions can disguise important variation in richness. For example, richness is sometimes tallied in latitudinal bands across continents. However, in so doing, one integrates over radically different sets of physical conditions in different latitudinal bands. There is plenty of evidence that richness depends upon climatic (Currie, 1991) and topographic (Kerr & Packer, 1997) factors. Consequently, while richness may be summed across a latitudinal band to show a general trend of richness varying with latitude (Kaufman, 1995), the analysis hides the fact

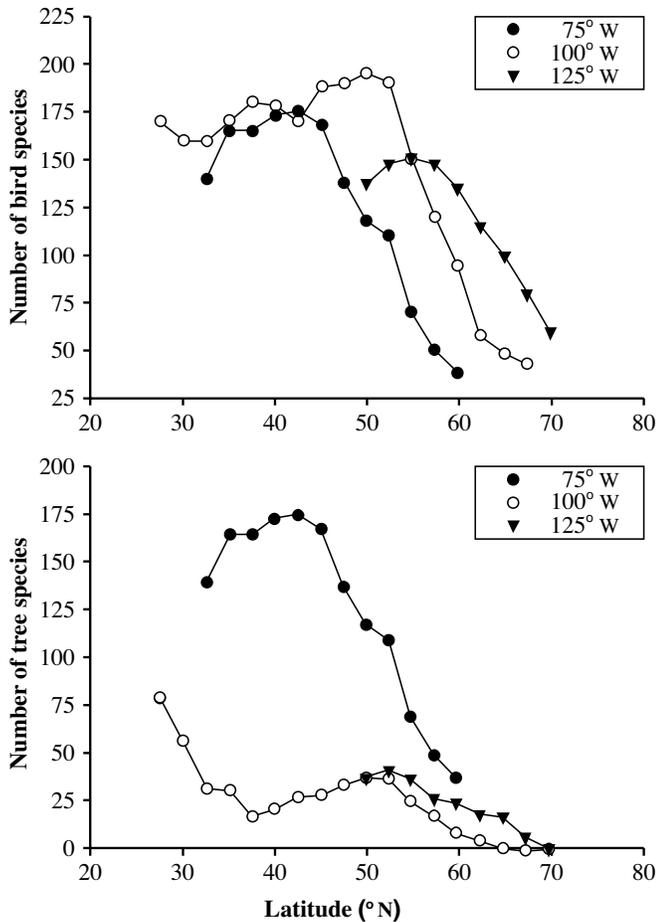


FIGURE 1. The number of species of birds (upper panel) and of trees (lower panel) in 2.5° by 2.5° quadrats at various longitudes in North America. There is no single, uniform trend in the variation of richness with latitude.

that longitudinal variance in richness is much greater in some latitudinal bands than at others (Figure 2). Moreover, mean richness in a band will depend upon which topographic features happen to be included therein.

Similarly, richness increases as a function of the area sampled (MacArthur & Wilson, 1967). As with latitude, many habitat characteristics are colinear with area sampled: the variability of physical conditions (and perhaps thereby the number of habitats) represented in a sample increases with area, immigration rates may increase with area (MacArthur *et al.*, 1967), speciation rates may increase (Rosenzweig, 1992), etc. Because area is colinear with many environmental attributes, it is often, but not always (Gilbert, 1980), a good predictor of richness. Also because of these colinearities, correlations between richness and area are a very poor way to test any particular hypothesis predicting that correlation (such as speciation rate: Rosenzweig, 1992).

SPATIAL VARIATIONS IN RICHNESS ARE CORRELATED WITH MANY OTHER VARIABLES. THESE CORRELATIONS DIFFER WITH SPATIAL SCALE. SOME ARE STRONG, REPEATABLE, AND STATISTICALLY ACCOUNT FOR MUCH OF THE SPATIAL VARIABILITY IN RICHNESS. THESE CORRELATIONS PERMIT FIRST ORDER PREDICTIONS OF PATTERNS OF RICHNESS

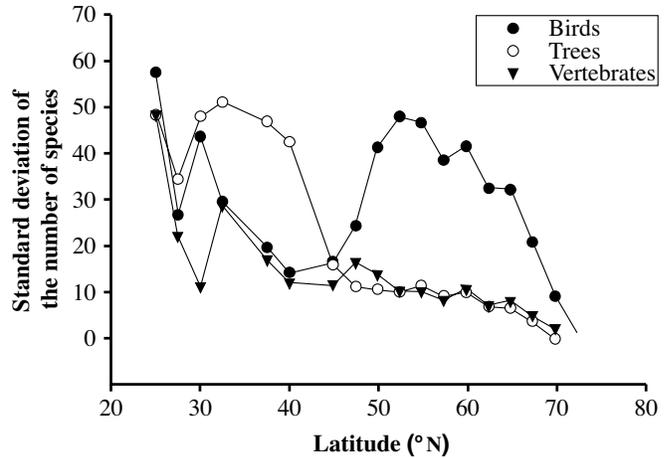


FIGURE 2. The standard deviation of the number of species in 2.5° by 2.5° quadrats in latitudinal bands covering North America. The trends are shown for bird species, tree species, and terrestrial vertebrates. These curves show that richness varies within latitudinal bands to a much greater extent at some latitudes than others, and that these trends differ among taxonomic groups.

A vast number of studies have documented correlations between richness and a wide variety of environmental characteristics (Wright, Currie & Maurer, 1993). We are now carrying out a meta-analysis of published correlations between species richness and environmental characteristics. Until the quantitative analysis is completed, we offer the following qualitative generalizations:

Across temperate to polar areas, broad-scale patterns of animal richness (within orders and classes) correlate consistently and strongly with measures of annual heat (Currie, 1991; Roy *et al.*, 1998). Plant richness covaries with the joint availability of heat and water (Wright, 1983; Adams & Woodward, 1989). Statistical models allow predictions of richness as a function of climate. Statistical models developed in one geographical area (*e.g.*, a continent) generally make reasonably good predictions about richness on other continents (Adams & Woodward, 1989; Francis & Currie, 1998), although there remain unexplained differences among broad regions (Latham & Ricklefs, 1993; Fraser & Currie, 1996).

In studies of broad spatial extent in warm-temperate to sub-tropical regions, relationships between richness and measures of heat typically become weak or weakly negative, while relationships with water, or the combination of water and heat become stronger (Schall & Pianka, 1978; Owen, 1988).

Broad-scale patterns of richness in the tropics are poorly characterized (Voss & Emmons, 1996). Disturbance may play an important role (Phillips & Gentry, 1994), but the evidence is still preliminary.

On local to regional scales, patterns of richness are nearly always related to surrogate measures of productivity, but the strength and forms of the relationships are highly variable (Rosenzweig, 1995: Chapter 12). Richness at these scales is also related to a hodge-podge of variables that suggest an effect of habitat diversity.

Local richness is related to regional richness (Caley & Schluter, 1997).

Hypotheses and tests

Many hypotheses have been proposed to account for patterns of species richness. What controls these variations of richness? Most reviews (Pianka, 1966), and textbooks (Krebs, 1994; Begon, Harper & Townsend, 1996) present long lists of factors hypothesized to affect patterns of richness. For example, these include: Habitat age: older habitats have evolved more species. Habitat heterogeneity: spatially heterogeneous habitats can accommodate more species. Habitat area: habitat types that extend over larger areas have had more opportunity to evolve species. Climatic harshness: fewer species can tolerate climatic extremes. Climatic stability: stable environments allow niche diversification and thus more species. Productivity: more productive habitats have more individuals, and hence more species have enough individuals to avoid extinction. Competition: areas in which competition is more intense have more finely divided niches, and hence more species. The inverse has also been argued: in areas of intense competition, competitive exclusion reduces species richness. Predation: predation reduces competition, and therefore allows more species to co-exist. Disturbance: habitats of intermediate disturbance have maximal richness. Immigration and extinction: equilibrium of these processes leads to a given level of richness. History: species originated in specific areas and dispersed elsewhere. Centers of origin have more species than elsewhere.

More generally, many of the hypotheses propose that richness is limited, in some sense, by particular characteristics of the environment. Their basic prediction is that spatial variation in richness should correlate with variation in the quantity of the limiting attribute. Other hypotheses propose that variation in richness reflects variation in the rates at which species are added to, and removed from, given areas. These hypotheses predict that richness patterns should be related to variation in these rates.

EVIDENCE CONSISTENT WITH ALL OF THESE HYPOTHESES HAS BEEN CITED, AT LEAST IN SPECIFIC CIRCUMSTANCES. REVIEWS TYPICALLY CONCLUDE THAT MANY FACTORS CAN POTENTIALLY INFLUENCE DIVERSITY. UNFORTUNATELY, FEW ATTEMPTS HAVE BEEN MADE TO TEST AND ELIMINATE HYPOTHESES, OR TO DETERMINE WHICH ARE GENERAL, IMPORTANT INFLUENCES ON RICHNESS, AND WHICH ARE MINOR.

Pianka's (1966) review concludes by suggesting that all of the mechanisms he lists operate at some spatial scales. Krebs's (1994) textbook review, nearly thirty years later and a couple of thousand studies later, concludes that all of these hypotheses operate in some situations, but that history, climate and disturbance "seem most important." He did not, however, indicate on what grounds he reached this assessment. Begon, Harper & Townsend (1996) simply concluded that, "for most of these generalizations important exceptions can be found, and for most of them current explanations are not entirely adequate."

In the editors' paper summarizing the largest multi-authored review of this field, Schluter & Ricklefs (1993) reach the following, rather broad, conclusions: (i) "Diversity is itself poorly characterized geographically, taxonomically, and ecologically." (ii) "[Local] diversity appears to vary in direct proportion to regional diversity." (iii)

"Ecologists should use historical, biogeographical, and systematic data to reconstruct the development of species assemblages." (iv) "Ecologists should take a more active role in investigating the processes of species production and extinction." (v) "Ecologists should join with physiologists, functional morphologists, and evolutionists in studying adaptive radiation." Conclusion (i), if true, is a sad comment, given the number of studies that have been produced in recent decades. Conclusion (ii) is the only empirical conclusion about patterns of richness. It is not clear how the three remaining conclusions would contribute to the question of what determines patterns of richness.

The inability of reviews to reach conclusions is mirrored in the primary literature by the plethora of factors postulated (or assumed) to be the main controls of richness. Denslow (1995), for example, builds a model of richness beginning with the assumption that richness depends on the number of individuals in the area. Roberts & Gilliam (1995), in a review of hypotheses pertinent to the management of forests, concluded that, "maximum diversity would occur under the historic (natural) disturbance regime." Mönkkönen (1994), comparing nearctic and palaeartic bird assemblages, says that richness patterns are "driven by ... life history traits of species that occupy an area and the physical patterns of the landscape." Rohde (1992) concludes that rates of evolutionary speed determine richness gradients. Hacker & Gaines (1997) develop a conceptual model of richness in marshes assuming that richness gradients are the result of the interaction of gradients of mortality and of positive interactions.

In sum, lists of hypotheses grow ever longer: Pianka (1966) presented six hypotheses, Currie (1991) eight, Rohde (1992) twenty-three, and Palmer (1994) one hundred and twenty. There is little indication whether these hypotheses have been shown to explain much variance or only a little, whether they have been rigorously tested or have only *post hoc* support, or whether the hypotheses can be applied broadly or only in selected cases.

HYPOTHESES ABOUT PATTERNS OF RICHNESS IN NATURE CAN BE TESTED BY DETERMINING WHETHER THE CORRELATIONS THEY PREDICT EXIST, BY TESTING FOR COLINEARITIES, AND THEN BY MANIPULATING THOSE CORRELATIONS.

A test of the general hypothesis that factor *x* influences patterns of richness in nature requires several things. First, one must specify the spatial scale over which the hypothesis applies. The two main predictions of the hypothesis must be tested at that scale. The first prediction is that species richness covaries with *x* in nature. One must show that the correlation is repeatable, *i.e.*, that it occurs in other locations and under other conditions. One must also show that the correlation is unlikely to be due to colinearities. To do this, one must simultaneously test competing factors that might be responsible for the covariation of richness and *x*. Since many factors are known to covary with spatial variations in richness, it is most efficient to simultaneously compare the patterns of richness predicted by multiple hypotheses. Finally, one must show that modifying *x* leads to a change in richness at that spatial scale.

Few studies have attempted to do this systematically. A good example of the first part of the process is the study of

Roy *et al.* (1998). These authors considered four hypotheses proposed to explain latitudinal patterns of richness, and they derived the predicted correlations between richness and habitat characteristics for each one. They tested the predictions relative to the global variation in richness of marine gastropods, and they showed that patterns were not consistent with hypotheses citing area or historical effects, whereas the patterns are consistent with the hypothesis that energy availability influences richness.

If the patterns predicted by a particular hypothesis are not observed, or if they consistently reflect colinearities, then the hypothesis can be regarded as provisionally falsified. On the other hand, if the correlations predicted by a particular hypothesis prove to be repeatable within the domain of the hypothesis, then the next question is whether manipulation of that factor causes richness to change. A classic example of the manipulation stage is Simberloff & Wilson's (1970) experimental defaunation of mangrove islets to determine if recolonization was consistent with MacArthur and Wilson's (1967) island biogeography theory, which presented correlative evidence.

Although manipulations may not be possible at the global scale, "natural experiments" (*sensu* Diamond, 1986) may serve a similar purpose. For example, Huston's (1993) hypothesis that broad-scale patterns of richness depend upon soil fertility predicts that losses of soil fertility should lead to increases in richness. This could be tested by testing whether historical losses of soil fertility have led to changes in richness. Similarly, the hypothesis that climate determines broad-scale patterns of richness (Wright, Currie & Maurer, 1993) could be tested by examining changes in richness during the Quaternary climate changes.

Why have so few hypotheses been tested and eliminated?

MANY STUDIES PROVIDE POST HOC SUPPORT FOR HYPOTHESES, RATHER THAN TESTING THEM. EVIDENCE SUPPORTING, AS OPPOSED TO TESTING, AN HYPOTHESIS IS NOT PARTICULARLY VALUABLE.

Studies often conclude that they have produced support for the hypothesis that factor *x* influences patterns of richness. The evidence may be a correlation between richness and *x*, or it may be the result of experiments showing that manipulation of *x* changes richness. Either way, evidence consistent with the hypothesis is often inferred to mean that *x* does influence richness gradients. This is an example of the classical logical fallacy of *post hoc, ergo propter hoc*. Although data may be consistent with the hypothesis in question, they may be equally consistent with many other hypotheses as well.

As many others have pointed out, evidence consistent with an hypothesis does not increase the probability that a hypothesis is true (Popper & Miller, 1983). "For until corroborated by [tests of] risky predictions, favorable evidence must always be mistrusted, especially if it is your own" (Chitty, 1996).

Hypotheses are often presented with exactly this sort of *post hoc* supporting evidence. Consider a textbook example. Regarding the influence of history, Krebs (1994: pp. 524-525) writes, "... communities diversify in time, and older

communities consequently have more species than younger ones." He continues, "Lake Baikal ... is a particularly striking illustration of the role of time in generating species diversity. Baikal is an ancient lake ... [and it] contains a very diverse fauna." But clearly, the reasons that Baikal has a diverse fauna may have nothing to do with history. Moreover, if Baikal did not have a diverse fauna, that fact would not refute the hypothesis that historical factors influence patterns of diversity, for one could propose ancillary explanations as to why Baikal should have low richness. In other words, the evidence cited by Krebs does nothing to test the hypothesis he cites.

Thus, adding evidence in support of hypotheses is a sterile exercise. It is far more useful (but seldom practiced) to attempt to eliminate competing hypotheses and to determine which ones permit the best predictions of patterns of diversity. Several hypotheses may prove to be necessary to completely account for patterns of richness. If so, their relative importance, and the conditions under which they apply, must form part of the final explanation of richness patterns.

MANY HYPOTHESES ABOUT RICHNESS MAKE PREDICTIONS THAT ARE TOO WEAK TO BE TESTED RIGOROUSLY, AND MANY MAKE NO PREDICTIONS BEYOND THE QUALITATIVE PATTERN (LATITUDINAL GRADIENTS) THAT GAVE RISE TO THEM. HYPOTHESES THAT DO NOT MAKE MUTUALLY EXCLUSIVE PREDICTIONS CANNOT BE DISTINGUISHED.

Consider, for example, the hypothesis that high species richness in the tropics is due to greater intensities of biotic interactions (competition, predation, mutualism, etc.). If the prediction of this hypothesis is simply that there should generally be more species in the tropics than in temperate zones, then it is not difficult *post hoc* to find examples of higher richness in the tropics than elsewhere. However, there are also low richness areas in the tropics (Hart, 1990). A much more appropriate test of the hypothesis, at the appropriate scale, would require a metric of the intensity of biotic interactions and a test of whether the variation in richness across temperate and tropical zones correlates with it. In the absence of such a metric, the hypothesis is very weak. If such a metric were constructed and if richness did not correlate with it, then one might even conclude that the metric did not measure interaction intensity after all, rather than concluding that the hypothesis is false. This would render the hypothesis circular and untestable. It is possible that a testable version of this hypothesis might one day be constructed, but the existing hypothesis is weak enough to not merit serious consideration.

Another example of a weak hypothesis is the hypothesis that patterns of richness reflect the historical processes of speciation and extinction (Rohde, 1992; Latham & Ricklefs, 1993). By definition, these two processes alter global species richness. This does not imply, however, that contemporary patterns of richness at finer scales resulted from differing rates of speciation and extinction. Dispersal, local limits to richness, biotic interactions, etc., could all modify patterns created by speciation and extinction. To test the hypothesis that different rates of speciation and extinction generated patterns of richness, one would need to be able to specify which patterns one would expect historical processes to generate, and then determine to what extent current spatial

variation in richness is consistent with expectation. We are aware of only one instance in which an historical hypothesis has been tested this way (Stehli & Wells, 1971). More often, historical factors are cited *post hoc* to explain differences in richness among regions (Latham & Ricklefs, 1993; Oberdorff, Guégan & Hugué, 1995). However plausible such explanations may be, they remain conjectural if they make no testable predictions.

A third example of a weak hypothesis is Huston's (1979; 1994) general hypothesis of diversity. According to this hypothesis, diversity is the result of two interacting processes: the rates of population growth and competitive exclusion *versus* the disturbance rate. Richness is postulated to vary as a peaked function of both of these rates (Huston, 1994; Chapter 5). The strongest evidence supporting this hypothesis comes from experimentally created gradients of disturbance and growth rates (Huston, 1994: Figure 5.9).

However, can Huston's theory account for the spatial variation of richness in nature? The fundamental difficulty with the hypothesis is that disturbance rate and rate of competitive exclusion are difficult, or impossible, to measure. Additionally, the hypothesis postulates that richness is a peaked function of these variables, but without parameterizing the function. Consequently, nearly any relationship between richness and disturbance (or richness and the rate of competitive exclusion) – positive, negative, flat, or peaked – could represent a segment of the predicted relationship. Because of the practical difficulty of comparing the predictions of the hypothesis with observations in nature, its actual power is very limited (but see Death & Winterbourn, 1995; Pollock, Naiman & Hanley, 1998).

Ideally, hypotheses that account for (*i.e.*, predict) patterns of richness should make predictions about other phenomena as well. Consider, for example, the species richness-energy hypothesis (Brown, 1981; Wright, Currie & Maurer, 1993). This hypothesis postulates that energy (or productivity) determines the number of individuals in a region, which in turn determines how many species can coexist. The prediction therefore is that numbers of individuals should be related to energy. Tilman & Pacala (1993) argue that this prediction is probably incorrect. If so, the mechanism thought to give rise to the richness-energy correlation is incorrect.

THE FACTORS THAT DETERMINE PATTERNS OF RICHNESS ARE LIKELY TO DEPEND STRONGLY ON SPATIAL, TEMPORAL, AND TAXONOMIC SCALE. THE SCALE AT WHICH PARTICULAR FACTORS INFLUENCE PATTERNS OF RICHNESS IS RARELY MADE EXPLICIT.

The factors controlling ecological processes are unlikely to be scale-invariant. Consider, for example, the factors that control primary productivity in lakes. The global variation in aquatic primary productivity is strongly related to total annual insolation (Brylinsky & Mann, 1973) because growing season length is highly variable globally. If one considers only temperate zone lakes, growing season length varies little. Rather, the variation in primary productivity is related to differences in nutrient concentrations (Schindler, 1977). Within particular lakes, nutrient concentrations vary little, and the variation in primary productivity is related to light penetration.

Experimental evidence about species richness (or most other ecological phenomena) is almost invariably at small scales for practical reasons. There is no reason to believe

that this evidence can be extrapolated to larger scales. For example, experimental manipulation of starfish abundance in the intertidal zone has shown that predation can influence the richness of prey species in small quadrats (Paine, 1966; Lubchenco, 1978). Yet, examined over larger areas, predation is not always important (Menge *et al.*, 1994). Moreover, the results of manipulation of a predator depend upon the scale of the experimental manipulation (Carpenter, 1996; Sarnelle, 1997). Although one may be able to create systems in which predators influence prey diversity, this in no way means that, at larger spatial scales, variation in predator abundance is responsible for significant amounts of variation in prey diversity.

Taxonomic scale also remains poorly considered in studies of species richness patterns. The distributions of individual species depend strongly upon their specific biological requirements (Root, 1988) and accidents of history. Thus, patterns of richness within low taxonomic levels (*e.g.*, genera) can be expected to reflect mainly the idiosyncrasies of the biology of the species involved. At progressively higher taxonomic levels (families, classes, orders), increasingly large numbers of species can potentially occur in any given environment, such that the total number of species that do co-occur can become dependent upon other factors. Empirically, relationships between richness and environmental characteristics are not constant across levels of taxonomic aggregation (Currie, 1991), and there is no reason to expect that a single explanation of patterns of richness should be taxonomic scale-invariant.

Conclusions

Hypotheses about patterns of species richness have been accumulating over recent decades because: (*i*) many of the hypotheses are too weak to actually be tested, (*ii*) evidence presented in apparent support of the hypotheses does nothing to test them, and (*iii*) the evidence is at the wrong spatial scale.

Correlations can be, and have been, used to test hypotheses about the determinants of patterns of richness at the appropriate spatial scales. However, correlations serve little purpose if they are not used to test hypotheses.

The bewildering variety of extant correlations needs to be sifted and applied to hypotheses. Which correlations are general and repeatable? Which simply reflect colinearities? A preliminary answer is that, at broad spatial scales, patterns of richness in polar to temperate areas are consistently correlated with climate. At smaller scales, richness is usually correlated with productivity.

Once general correlations are identified, manipulation of the correlation is called for to determine if the link with richness is direct. There is little point in doing experiments to study the effect of some factor *x* on richness if the spatial scale differs from that of the spatial variation of richness (which is usually the case!).

Mechanistic hypotheses that predict more than already observed patterns of richness would be desirable. However, simple correlative hypotheses that make testable predictions about patterns of richness in nature are better than elegant mechanistic hypotheses that make none.

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