

The echo pattern of species diversity: pattern and processes

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Ecologists need not despair of discovering the mechanisms that lead to large scale patterns. The search for process at higher scales has already led to enhanced confidence in the patterns and to improvements in their description. For example, species-area relationships turn out to form not one, but three patterns. Each is controlled by gain-loss dynamics at its own scale. At the macroscale, origination and global extinction reign. At the archipelagic scale, immigration and island extinction determine the results. At the local scale, metapopulation processes do. The three scales exhibit species-area curves with systematically different slopes in logarithmic space. We use the three scales of species-area to illuminate the relationship between local and regional diversity. Algebra shows that the latter pattern is an echo of species-area curves, and that those echoes ought to be nearly linear. So, we call the relationship of local and regional diversity, the Echo pattern. Ecology has long known that species-area curves within a region reflect the accumulation of habitat variety. Thus, their connection to Echo patterns argues against concluding that local diversity has little or nothing to do with population interactions. To obtain a pure Echo pattern, one should draw data from independent regions rather than separate islands. The independence allows natural selection to adjust the fundamental niches of species to diversity. Theory suggests that higher diversity should shrink niches, allowing the coexistence of more species locally. Hence, independence should tend to produce the straightest Echoes. However, archipelagic species-area curves predict that even when different islands are used as the regions, the Echoes should show only very gentle curvatures. Flouting theory, some archipelagic Echoes approach an asymptote as regional diversity increases. These must have logarithmic slopes that increase with regional pool size. We do not understand why.

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Terborgh and Faaborg (1980) originated the examination of local species diversity as a function of regional species diversity. The pattern they observed was asymptotic: local diversity reached a fairly constant level after only a modest pool of regional diversity became available to it.

Since then, ecology has learned that the asymptotic pattern is unusual (Lawton 1999). Much more often, local diversity keeps rising – with no evident limit – as the size of the regional pool grows. Sometimes this growth appears virtually linear. In other cases, it exhibits a slight convex-upward curvature.

In looking at this pattern, Terborgh and Faaborg wanted to test a hypothesis. Is there a fairly constant value of tolerable niche overlap – called limiting similarity – that sets a limit to local diversity, a limit that is independent of regional diversity? They interpreted the asymptotes they found as support for the concept of limiting similarity. Naturally enough, once people began finding patterns lacking asymptotes, those people interpreted them to mean that we ought to prefer other hypotheses. Cornell (1993) thought they could mean that ecological interactions do not determine local diversities, but that instead, local assemblages may con-

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sist of random sub-assemblages of regionally available species. Ricklefs (1987) offered the conclusion that linear and near linear patterns mean that regional pool sizes set local diversities. The principal difference between them is Ricklefs' use of the concept of determinism vs Cornell's preference for randomness. Lawton's minireview in this series (1999) continues and elaborates his and Cornell's concern that these patterns could mean many different things (Cornell and Lawton 1992). But he concludes that, most probably, the linear and near linear patterns at least signal the futility of trying to understand the interactive processes that shape local communities.

Where are we? In this minireview, we shall try to expose the theoretical roots of the interpretations. None of them turn out to be very substantial. But the patterns are real enough. Using simple algebra, we shall show that local-regional diversity relationships echo species-area relationships (SPARs). So, we will call the pattern of local species diversity vs regional species diversity, the Echo pattern. The connection between SPARs and Echoes has an added consequence. It argues for enhanced precision in defining the regional pool, i.e., the x-axis of Echo patterns.

Ecology does understand quite a lot about the mechanisms that lead to SPARs. This knowledge of process informs our interpretations of Echo patterns. And, going in the opposite direction, the Echo patterns indicate deficiencies in our understanding of the processes that lead to SPARs. Based on what we have learned about SPARs and Echoes, we shall suggest profitable directions for further inquiry into community ecology.

Pattern and mechanism in ecology

First, we address a matter of considerable general importance in ecology. Is the investigation of mechanism scale-limited, or is it relevant at all scales of ecological investigation? Some definitions may help.

A **pattern** is a set of data points of two or more variables such that the values of the variables show some relationship to each other. None is statistically independent of another, although the nature of the dependence may range from simple linearity through complex nonlinear chaos.

A **mechanism** is the dynamic interplay of variables leading to a system's state. A mechanism explains the variables of a pattern as the outcome of differential equations. Those equations may be quite cryptic. In ecology, they may even be impossible to write down explicitly.

A **phenomenon** is a pattern without a mechanism. The elucidation of phenomena is called phenomenology in other sciences. We ecologists could do worse

than emulate that standard usage, although, more often, we tend to use the word 'rule' instead of 'phenomenon'. That is acceptable among friends, but we must not go so far as to use the word 'law'. We need law for the next category of patterns.

A **law** is a pattern explained by a mechanism. Ecology is science, of course, so the explanation may be half-baked, incomplete, provisional or even wrong.

A **theory** is a hypothesis produced, at least in part, by deductive logic operating on a set of assumptions. The logic of a theory may be cryptic – generated by computer algorithms because our brains cannot manage closed-form, analytical solutions. Any component of a theory may be wrong, not just its hypothesis. But a bad theory is still a theory.

What does all this peremptory philosophizing have to do with Echo patterns? Two things. First, without an explanation, Echoes are phenomena, not laws. When Terborgh and Faaborg first sought them, they were testing a theory, the theory of limiting similarity. When they found what they were looking for, their combination of pattern and theory became a law. When, however, Cornell (Cornell 1985) found a linear Echo, the pattern lost its explanation and thus its status as a law. Surmising that it stems from a random selection of regional species pools does not restore that status – it merely links two phenomena. Similarly, our demonstration (below) that Echoes and SPARs are two sides of the same coin would also merely link two phenomena, unless we could explain one of them mechanically. Then they would both become laws. In fact, we will argue that SPARs and near-linear Echoes do constitute a single ecological law, albeit one needing much improvement.

Second, during the past two decades, ecology has suffered from a chronic loss of heart. Our early baby steps in devising laws led to disappointing pratfalls. Grand theories failed. Careful analysts took our field work to task for pseudo-replication.

Seeing that explanations of what we wanted to explain would at least cost dearly in time and effort, and might never succeed, many ecologists of the generation that matured in the 1980's stepped away. They replaced the grand questions with questions on a much smaller scale. They asked about diets and behavior. They asked about the ecology of single species. They looked at ecophysiology. They retreated to laboratories where variables could be more carefully controlled and experiments more easily replicated. Their revolt was not cowardice but a longing for achievement. They wanted to taste successful mechanical explanations even if they were not answering the questions that had initially attracted them to ecology. "Study mechanism" became a sort of motto, if not a battle cry.

Unfortunately, this motto had one undesirable effect. Somehow ecologists accepted the false idea that

mechanism and this new scale of approach were identical, that study at any other scale abandoned mechanism. We do not accept the limitation of mechanistic inquiry to small, local scales. Inquiry into mechanism applies at all scales of science. Moreover, to limit mechanistic questions to one or two scales of ecology will impede our progress toward explanations at larger scales in space and time. If, for example, we take it for granted that macro-scale patterns are not subject to mechanistic explanations, we will never search for them. We will never be able to transform Echoes from phenomena to laws. We will never even demand of them the descriptive precision that will convince us of their generality.

Ecology should never be satisfied with the mere description of macroecological patterns. All scientists know that the world is full of chance, and replete with meaningless correlations. So, until we understand the mechanisms behind macroecological patterns, we cannot even be sure that they reflect meaningful relationships between ecological variables.

But can ecology ever learn how to predict large-scale pattern from small-scale processes? Can we ever predict (say) the abundance distribution of the beetle species in Borneo from considering their physiologies and morphologies against the background of their biotic environment? We agree with the unspoken premise of this question. Ecology will not deliver such a success. But it is not the right question. Tacitly, it accepts the premise that small scales contain all the mechanisms in ecology. No. To predict the abundance distribution of Borneo's beetles, we should not rely on studies of beetle physiology and the like. Instead, we should focus on the dynamics of beetle speciation and extinction, on the coevolution of beetle niche widths and overlaps, and on the energetics of beetle communities in the Bornean milieu. If it turns out that regional diversities control local diversities, then we should also ask about the mechanisms of community assembly.

Richard Levins once pointed out that road maps conveyed information at a limited range of scales. Looking at them with a microscope would obliterate their information. Looking down on them from a jet liner would also obscure them. He was warning us that models have restricted scales of usefulness. The same is true of mechanisms. Mechanisms help us to go from one scale to another, not from sub-atomic particle physics to the structure of the universe.

Many examples show that one person's mechanism is another person's pattern. For example, in studying competition, we will want to measure the effect that individuals of one species have on the net reproductive rate of individuals of another. We do not study the endocrine system to do that. Such reproductive effects (a mechanism not reduced to still smaller scales of explanation) lead to patterns of species' abundances, co-occurrences, and extinctions. They also have dy-

namic consequences (another sort of pattern). Now, reaching up, the landscape ecologist may use the emergent patterns of competition as mechanisms leading to habitat-patch patterns. Reaching down, the behavioral ecologist seeks to understand competitive effects of individuals by studying the mechanical components of physiology and foraging. She may study the endocrine system to do it. So what if the subatomic particle physicist – not understanding the true import of natural selection – would label us all phenomenologists (all of us, even the biochemists among us). Oh, how wrong he would be!

Large-scale ecological patterns very often deal with the number of species. In his recent minireview, Lawton (1999) has summarized several of them: 1) latitudinal gradients in species diversity, 2) SPARs, 3) species-productivity relationships, 4) species-abundance relationships, 5) Echo patterns. Ecologists have long labored not only to describe these patterns, but also to elucidate the mechanisms that produce them. This is actually evident in Lawton's own paper and in many of his references. For example, he mentions the disagreement among ecologists as to the causes of the latitudinal gradient. No one disagrees about the existence of the pattern. And the whole point of the MacArthur-Wilson revolution called island biogeography was to explain diversity patterns as the outcome of two dynamic processes, the mechanisms of extinction and immigration.

In our essay, we will explore the interaction between pattern and mechanism in the study of SPARs and the Echo pattern of species diversity. We begin by asking how considerations of mechanism help us to sort out the several scales of SPAR. Then we move on to ask what these several scales of SPAR have to say about the relationship between regional and local diversity. And then we examine various proposed explanations of Echo patterns.

Scale and mechanisms of species-area relationships

When, some 80 years ago, species-area relationships were first fitted to quantitative models, the principal topic of discussion became which model fit SPARs best. Should we use semi-log plots or log-log plots? As data accumulated, this question was joined by another set relating to the slopes of log-log plots. Why do these seem to be so similar regardless of taxon? Why do they also seem so similar from continent to continent? And why are the slopes that one obtains from islands of different area consistently higher than those obtained from varying sample area on a nearby mainland?

Today we know that perfect statistical sampling of mainland patches will produce sigmoid SPARs in log-log space (Leitner and Rosenzweig 1997). That makes

both biological and theoretical sense. As sample areas get very small, the all-knowing ecologist should be seeing all species of a single habitat. As areas get even smaller, all the species of that habitat will still be able to live there. Given enough of a sampling effort, they will all turn up.

In log-log space, the semi-log formula exhibits curvature opposite to that of a sigmoid curve – its left side has negative second derivatives. The semi-log formula therefore reflects the relatively poorly known small samples that are uncorrected for the bias of small sample sizes. And SPARs that are linear in log-log space are those that lack both the very small samples and the very large ones. They have been taken from the middle of the sigmoid curve, which is approximately linear.

The slopes of those log-log plots are another matter. As long as we ecologists treated them merely as the results of our curve fitting, we made no progress. Connor and McCoy (1979) labeled their variance ‘statistical noise’. But once we turned our attention to mechanism, the puzzle fell into place. (We herein ignore those species-area curves caused solely by variation in sample size. We understand them too, but they are statistical artifacts without a biological cause.)

The macro-scale: extinction and speciation are the mechanisms that determine diversity at the largest scale, that of entire biogeographical provinces. SPARs at this scale have slopes near unity. So do SPARs obtained by comparing entities not generally recognized as biogeographical provinces, but whose diversities are set primarily by extinction and speciation (such as those of isolated archipelagoes with high endemism) (Rosenzweig 1995). We recently collected a most dramatic example of such SPARs deep in time. The data come from tree fossils of the northern Hemisphere during the eleven times in the history of plants when paleontologists have good knowledge of the extent of land in the hemisphere, and a good fossil record of trees (Tiffney and Niklas 1990). The shallow seas ebbed and flowed across the land, altering its extent by a factor of two. Tree diversity followed along as exhibited in Fig. 1. The most remarkable feature of this graph is its shape. It is straight, indicating a logarithmic slope of unity. Tiffney and Niklas’ points are just as evolutionarily independent as the diversities of different continents, but they are separated by time instead of space.

The archipelagic scale: immigration and extinction on islands determine SPARs in archipelagos (MacArthur and Wilson 1967). Archipelagic logarithmic slopes range from ca 0.25–0.55 (Rosenzweig 1995).

The local scale: local population dynamics determine SPARs in local sample areas of a mainland. Thus, the list of species in such a local area includes some that are maintained therein only by dint of metapopulation processes. These are sink species locally and cannot be sustained by the much lower immigration rates to islands.

So, an island must have fewer species than a similar-sized mainland patch. And a similar-sized biogeographical province must have fewer still because it relies on the much slower process of speciation to add to its total. These process-based relationships constrain SPARs geometrically. The mainland curve must lie atop them all and have the gentlest slope. The inter-provincial curve must be the steepest. Mirabile dictu, the data agree (Rosenzweig 1995).

Of course, many problems relating to the species area relationship remain. We cannot yet predict the value of the slope for even one of the three mechanism-based SPARs. But, at least, we know now where to look.

More important, we can use what we already do know to link species-area relationships to other ecological rules. Lawton (1999) already cited the Hanski pattern – larger ranging species tend to be locally more abundant than species that are more geographically restricted. This has been connected to SPARs at two scales. Hanski and Gyllenberg (1997) did it from a metapopulation standpoint. They assumed that all species can occur everywhere, but that some are much more patchily distributed than others. Leitner and Rosenzweig (1997) did it at the provincial scale, where range maps are most commonly drawn. Their species have very variable range sizes and population densities, but each occurs everywhere within its range.

We shall not overlook the opportunity to mention the close relationship of SPARs to the latitudinal gradient (Rosenzweig 1995, Rosenzweig and Sandlin 1997).

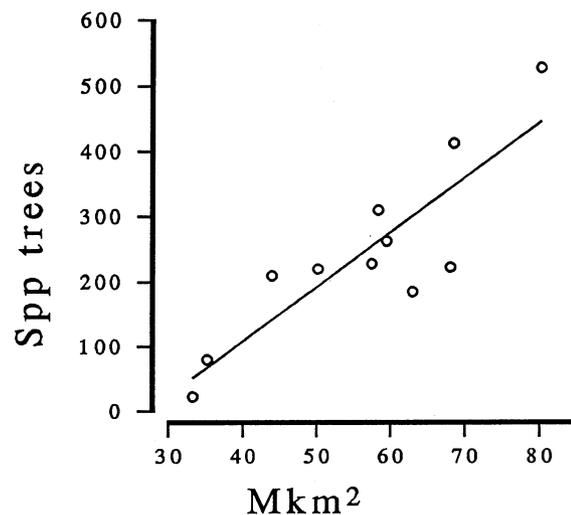


Fig. 1. The interprovincial species-area curve for northern hemisphere tree fossils. As shallow seas ebbed and flowed altering the extent of the land, tree diversity kept pace. We plotted this graph in arithmetic space to emphasize its straight shape. The linearity indicates a logarithmic slope of unity. The data come from the eleven times in the past 400 my when we have some confidence in our knowledge of the extent of land in the hemisphere, and a good fossil record of trees. Data from Tiffney and Niklas (1990).

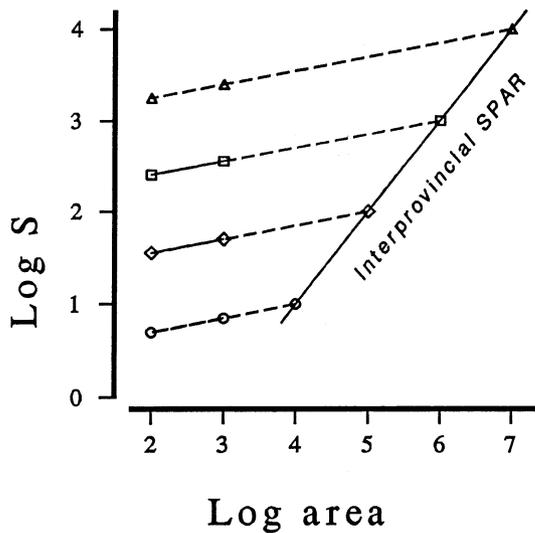


Fig. 2. The species-area relationships (SPARs) at the root of local-regional diversity relationships (Echo patterns). The regional diversities (solid line) are the pools of species from which the local species emanate. They lie on a typical interprovincial SPAR with slope unity. We mimic the ideal data set by measuring local diversity in a fixed area. We show these at two such areas, 2 and 3 arbitrary logarithmic units. The dashed lines – connecting the local diversities to their region of origin – constitute “mainland” SPARs. For mathematical convenience, we drew these as parallel lines, and data suggest that they are nearly so.

Lawton (1999) is correct to point out that most ecologists feel unsure of this connection. But we predict their students will not be, because the connection is based on pattern and mechanism both.

SPARs determine Echoes

Now, we will point out a new link between rules: the smallest and largest scales of SPAR already contain the pattern that relates regional and local diversity. In Fig. 2, we graph the regional diversities as the pools of species from which the local species emanate. We also graph the local diversities as “mainland” SPARs. We drew these as parallel lines. Although we suspect that they may not be strictly parallel at all scales (evidence is inadequate to decide this), data indicate that they are nearly so. Making them parallel greatly simplifies the math and provides another example of Lawton’s principal advice: “Step back and look at the grand pattern.”

We need some symbols: S is the number of species; A is area (in arbitrary units); R will be a subscript to indicate “regional”; L will be a subscript to indicate “local”; z is the slope of the mainland species-area curve in log-log space; δ is the slope of the interprovincial species-area curve in log-log space. So, we write the familiar equation for the mainland SPAR:

$$\log S_L = \log k_L + z \log A_L$$

And the interprovincial SPAR:

$$\log S_R = \log k_R + \delta \log A_R$$

Now we determine z as a function of the parameters of the regional SPAR. Notice that a unit area of a province has k_L species. That fixes one point. We find a second point by noticing that the area and diversity values for the whole province also lie on the mainland curve. That sets the point $(\log A_R, \log S_R)$. Hence, two points on the mainland curve must be $(0, \log k_L)$ and $(\log A_R, \log k_R + \delta \log A_R)$. Because two points determine the slope of a straight line, these points allow us to find the value of z with the standard algebraic method:

$$z = \{(\log k_R + \delta \log A_R) - \log k_L\} / \log A_R$$

If you examine this equation for z , you will see that it contains k_L , the expression for local diversity in any arbitrary unit area. The unit may be any measure of area – a square meter, a hectare, a square kilometer or any measure. We do have to specify the measure of local area and keep to it. Values of constants will change depending on the unit chosen, but not curve shapes. So, we solve the equation for local diversity of a unit area (i.e., k_L):

$$\log k_L = \log k_R + (\delta - z) \log A_R$$

We substitute for $\log A_R$ using the basic equation for interprovincial SPARs:

$$\log A_R = (\log S_R - \log k_R) / \delta$$

The result is the equation for the local vs regional diversity pattern:

$$\log k_L = \log k_R + \{(\delta - z) (\log S_R - \log k_R) / \delta\}$$

Once we gather its terms and convert it to its arithmetic form, this equation becomes a simple power curve:

$$k_L = \{(k_R)^{(z/\delta)}\} \{(S_R)^{(1 - (z/\delta))}\}$$

or, simplifying by replacing $\{(k_R)^{(z/\delta)}\}$ with c , and $(1 - (z/\delta))$ with κ :

$$k_L = c S_R^\kappa$$

In sum, the mapping of regional diversity into local diversity is a logical, quantitative consequence of species-area relationships. That is why we have called the local-regional pattern, the Echo pattern.

Fortunately, many have studied SPARs, and have provided real parameter values to insert in the Echo pattern. The parameter z varies from ca 0.09 to 0.20. The parameter δ varies from ca 0.65 to 1.5. Hence, the exponent of the Echo pattern may vary from 0.94 to 0.69.

Typical values may be even more constrained. Our experience has been that values of z are often ca 0.18 for such taxa as green plants or birds, and that these taxa have δ -values close to unity. Such a combination yields an exponent of 0.82. On the other hand, invertebrate taxa often show the lower z -values. These also tend to have smaller δ -values. A combination of 0.09 and 0.75 would not be extraordinary. It results in a power of 0.88.

Ecology cannot distinguish powers so close to unity from unity itself. As an example, we plot the values for the exponent 0.82 in Fig. 3. In practice, who would choose anything but a linear model to fit these points? But, in fact, they fit a power curve perfectly. Now add a little of the usual noise that comes with ecological data, and you will agree that we have no hope of detecting the curvilinearity.

We obtained the exponent values so far by assuming evolutionarily independent regional pools. However, many examples of Echo patterns come, not from such independent pools, but from separate islands that draw most of their species from a common mainland pool (e.g., Terborgh and Faaborg 1980, Ricklefs 1987, Hugueny and Paugy 1995). We have not done an exhaustive search for all cases of this misapprehension

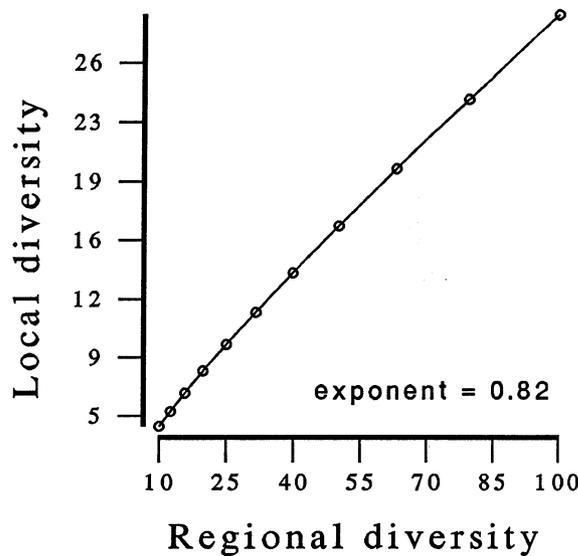


Fig. 3. The Echo pattern that results from assuming typical logarithmic slopes for mainland and interprovincial SPARs. Here, we set the value of z at 0.18 and the value of δ (the interprovincial slope) at unity. Such a combination yields an Echo with an exponent of 0.82, i.e., one virtually impossible to distinguish from a straight line.

– i.e., that the biotas of separate islands may be treated as independent species pools – but we suspect that many more cases exist in our literature. Islands are much more common than biogeographical provinces, and it is therefore tempting – until you connect pattern with mechanism – to turn to them as independent species pools. Does it matter? What difference does it make to Echo patterns if their regional pools are separate islands rather than separate provinces?

The islands of a typical archipelago exhibit a SPAR with a much lower value than unity. Archipelagic SPARs usually have z -values between 0.25 and 0.55. Birds of the West Indies show a slightly lower z -value of 0.23 (Wright 1981). The fishes in the ten island-like river drainages of the Ivory Coast – which all belong to a single biogeographical province, the Eburneo-Ghananian (Hugueny and Lévêque 1994) – have a z -value that we calculated to be 0.306. Notice that this value is analogous to the interprovincial value, which we labeled δ above.

What should one expect of an Echo pattern within an island system like the West Indies or the Ivoirian rivers? To answer this by applying equation y , we also needed the average “mainland” z -value, i.e., the value obtained from sampling different areas of a single island. Although these data are rare, we could estimate them for the Ivoirian fishes. Hugueny and Paugy had been extremely careful about taking adequate samples using the same method of gill netting and always for two consecutive nights. Based on the minimum areas they sampled (0.1 km²), we assigned a value of 0.1 km² to all the local areas. Then we calculated the z -values with the two-point method. The results had typical mainland slope values and averaged 0.106.

Now we substitute our values for δ and z (0.306 and 0.106 respectively) into the same equation used for separate provinces. The Echo pattern with these values has a power of 0.65, reflecting very gentle curvature indeed. The Echo is definitely not asymptotic. This result, based on an archipelago with typical SPARs, should thus typify Echoes of island-based data. So, we conclude that, if they follow the rules of SPARs, even sets of islands ought not to exhibit asymptotic Echo patterns.

Having linked the Echo pattern to SPARs, we can now muster the data that gave us SPARs and apply them to the Echo problem. All those data that led us to our conclusions about SPARs, perforce agree with the generalization that Echo patterns are predominantly linear or weakly curvilinear. Thus, the linkage gives us bolstered confidence in the rule.

We need to sum up this pivotal section. Multi-scale SPARs predict near-linear Echo patterns. This is true whether the regional pools come from evolutionarily independent biogeographical provinces or separate islands. Hence, an asymptotic Echo pattern in some way breaks the rules of SPARs. Later, we will reconstruct the pattern of those rule violations.

Interpreting linear and near-linear Echo patterns

Both Lawton and Cornell (Cornell and Lawton 1992, Lawton 1999) declare that a linear Echo pattern usually should be interpreted to mean that local diversity reflects mere random sampling from the regional species pool. For them, saturation requires that the local diversity approach an asymptote as regional diversity rises.

What is saturation? Cornell (1993, p. 243) defines it in terms of the Echo pattern itself. Saturation is “an upper limit to local richness that is independent of the size of the regional colonization pool.”

If we define saturation as a pattern, it could have an infinite number of explanations and still hold true. However, in his very next sentence, Cornell exhibits strong signs of being dissatisfied with the definition of saturation as a pattern. He writes, “Such a limit must result from species interactions in local habitats.”

Evidently, Cornell is looking for something meatier than a mere pattern. Indeed, in tabulating which theories lead to saturation (p. 244), he lists only those that incorporate species interactions. Thus, Cornell subtly reverses his line of interpretation. He goes from, “saturation means significant interspecific interactions”, to, “significant interspecific interactions mean saturation”. Cornell, does not take an inflexible position, however. On p. 245 he writes: “Interactive communities can show the (proportional sampling) pattern.”

Far from being a defect, Cornell's de facto reversal adds considerably to the value of the whole investigation. With Cornell, we recall that Terborgh and Faaborg (1980) originated the examination of Echoes to understand the functioning of communities. If they had merely been searching for an asymptotic pattern, we would have cared much less.

So, “saturation” means something like “the local diversity of species is set by strong population interactions”. But there is more. There is the idea of capacity – but not the trivial sort of capacity you learn about when you fall asleep while pouring coffee into your 200 ml cup. This capacity is a dynamic capacity: adding species to a highly interactive system must eventually lead to a steady state. Unsaturated communities have fewer than their steady-state number of species. “Non-saturation goes hand in hand with community openness.” (Hugueny and Paugy 1995, p. 167)

A chemical analogy may help us explain what this steady state is and what it is not. Let us analogize our local area to a beaker of NaCl in water. At a fixed temperature, the water can hold only a limited amount of salt in the form of ions in solution. At that concentration, the water is saturated. It does not matter whether we observe the beaker in South Africa or South America or South Georgia. Water is water and salt is salt. But a saturated solution is dynamic: at

saturation, salt molecules go into solution at the same rate as they precipitate out. A saturated solution is a steady state.

In some ways, local diversity resembles the salt solution. The local area is like the beaker; the species living there are like the sodium and chlorine ions held in the solution. The dynamic processes of species loss and species gain determine the number of species.

The analogy becomes really useful, however, when we ask how local diversity differs from the concentration of ions in a solution. Suppose the two systems – salt solution and ecosystem – were exactly alike. Then it would be reasonable to posit a saturation level that depended only on the size of the local area: a fixed area, like a beaker of a certain volume, can hold no more than a fixed number of species. Were salt solution and ecosystem exactly alike, Cornell's and Lawton's interpretation of the linear Echo pattern would have to be accurate.

But species are not salt crystals. Species coevolve. In particular, they adapt their niches to the presence of other species. Evidence, both empirical and theoretical, strongly suggests that niches become narrower in the presence of competitors. Hence, if there are more species in the regional pool, there should be more at the local level. We should not expect saturation to lead to an asymptote when comparing species from different pool sizes. And we should not view linear and near-linear Echo patterns as evidence against the importance of interactions in determining local diversities.

Ricklefs (1987) was on the mark. He set the notion of inflexible niches against that of niches whose breadth evolves in response to diversity. So, for Ricklefs, an asymptotic Echo pattern means that species have the same set of niche breadths regardless of where they live, and a linear Echo pattern means that their niches are narrower in regions with higher diversities. The issue for Ricklefs is not whether interactions play an important role. It is rather whether they play that role predominantly at the local or at the regional level. Ricklefs does associate the regional scale hypothesis with the word “history.” But he does not pursue that association. Supporting it would mean demonstrating that regional diversity differences have arisen as historical accidents, something Ricklefs does not try to do.

Our own view recognizes a hierarchy of causes. The most influential, at the largest scale – that of the biotic province in which the pool exists – are the forces of speciation and global extinction (Rosenzweig 1995). Speciation and global extinction have rates determined mostly by non-ecological variables. How rapidly are geographical isolates formed? How quickly can their life histories and genomes respond to such isolation? (The latter involve such matters as life span and the probability of beneficial mutations.) The extent of the geographical range plays a large part in setting these rates and the rates of extinction. That is how provincial

area helps to determine diversity. Compared to more narrowly distributed species, species living in larger areas of a biome type should form isolates faster, have a higher probability of beneficial mutation, and suffer extinction at a lower rate. The forces of speciation and global extinction determine, to a first approximation, how many species will form the steady state of the regional pool. These forces may have probabilistic components, but their overall effect follows patterns that clearly do not match what one would expect of the traces of capricious history.

Once speciation and global extinction set the steady-state diversity, coevolution refines the initial set of fundamental niches as follows. Individuals respond to competitive differences by confining their activities to a fraction of their fundamental niches. That is one of the overwhelmingly important results obtained from studies of optimal density-dependent foraging. This restriction subjects them to a new selective environment. In the presence of trade-offs, natural selection will reduce their ability to live in places and to perform tasks which they normally avoid. They evolve to increase their degree of specialization. We say this even in light of the lucid study of Joshi and Thompson (1995) that emphasizes how cautious an evolutionary ecologist must be in testing the hypothesis of niche-breadth trade-off using real organisms.

What should be the result of a coevolutionary decrease in niche breadth? More species should be able to coexist in local areas. Morton and Law (1997) confirm that conclusion for their computer-based species pools. Yet, when we read about their confirmation, we merely nodded our heads and smiled. Is there an ecologist who would have questioned the positive correlation? All of us seem to believe it to be common sense. The steady-state diversity of a set of specialists surely must be greater than that of a set of generalists.

The position we take synthesizes a considerable amount of research that began with the seminal investigations of Robert H. MacArthur in the 1960's. MacArthur walked three separate paths toward understanding the ecological world. He looked at biogeographical patterns, at population dynamics and at optimal behavior of individuals. Sadly, he did not live to combine them all nor to see them merging as they are in fact doing today. One can only wonder how much more we would understand had he lived.

MacArthur first approached ecology by studying population interactions and their consequences. He looked at both predation and competition, and the former studies form a crucial underpinning of the equations he used in the latter work. In particular (as he once pointed out to M.L.R.), his competition equations deliberately incorporate vertical predator isoclines. With Richard Levins', he asked and addressed the question of limiting similarity (MacArthur and Levins 1967). How similar can the niches of species be before

they suffer competitive exclusion. He was trying to make Gause's principle quantitative enough to be both interesting and testable. But, to everyone's amazement, he and May and MacArthur (1972) discovered that, in a deterministic world, limiting similarity is zero. That helps to explain why they spent so much of their paper exploring the effects of stochasticity. However, Turelli (Turelli 1978a, b, 1980) showed that even stochasticity does not rescue limiting similarity. Thus, the number of species in a regional pool would seem to be unbounded. This conclusion has been extended and well defended (Abrams 1975, 1976, 1983, 1996, Turelli 1981).

Now it is certainly true that as diversity climbs in a region, average population size must shrink. And it is also clear that populations with sizes approaching zero cannot be viable. However, the effect of shrinking population sizes differs from the postulated effect of limiting similarity. The latter predicts extinction once adjacent species' niches overlap too much, regardless of overall diversity and the abundance of those species.

It is also undeniable that increased overlap of adjacent species' niches reduces the abundances of those species. That explains why morphologically and behaviorally relevant features tend to get hyperdispersed in phenotypic space (e.g., Moulton and Pimm 1987). But, again, the enhanced extinction rates have to do with reduced abundance rather than the overlap per se.

In sum, despite some impressive theoretical evidence of Mitchell (which we will discuss in a moment), we do agree with Abrams, Turelli, Lawton and others about the soundest position for an ecologist to have today: competition sets no intrinsic limit to the number of species in a province – at least none that we can deduce from the concept of limiting similarity.

But the niches in theories of limiting similarity are far too inert to have satisfied Robert MacArthur for long. They are too much like salt molecules. They do coevolve in the sense that they jockey for position along niche axes. But they do not change shape. In other words, theories of limiting similarity do not allow for the evolution of specialization or generalization. To study this question, MacArthur turned with MacArthur and Pianka (1966) to the study of optimal realized niches. Independently, Emlen (1966) also invented this approach.

The mathematics of optimality proved daunting for awhile. Most studies focused on the behavior of individuals and ignored even intraspecific competition let alone interspecific. But Fretwell and Lucas (1970) showed how intraspecific competition expands the realized niche (Fryxell and Lundberg 1998). And we have explored with several colleagues how interspecific competition often constricts it (Pimm and Rosenzweig 1981, Brown and Rosenzweig 1986, Ziv et al. 1995, Rosenzweig and Abramsky 1997). Many older studies showed that island birds use a diversity of habitats that corre-

lates inversely to their species diversity (e.g., Crowell 1962, Keast 1970, Terborgh and Faaborg 1973, Gorman 1975, Terborgh and Weske 1975, Cox and Ricklefs 1977, Diamond 1978, Wunderle 1985). Gorman (1979) also studied the perches used by lizards, *Anolis sagrei*, on islands in the West Indies. The fewer the species of congener, the greater the variety of perch heights used by *A. sagrei*.

David Lack pioneered such studies (Lack and Southern 1949, Lack 1969). He also exposed the most extreme case, the Gough Island bunting, *Rowettia goughensis*. *Rowettia* is a finch, the only perching bird of Gough Island, in the South Atlantic. Despite its isolation, Gough has five distinct terrestrial habitats – tussock grass, fern bush, wet heathland, montane vegetation and peat bog – in addition to its beaches and its tiny human outpost (Wace 1961). *Rowettia* uses every one of these habitats. It even feeds in the intertidal. It eats seeds and fruit. It eats flies, moth larvae, spiders and amphipods. It eats vertebrate carrion. And – a true bird of the millennium – it scavenges in garbage cans. As Lack said, *Rowettia* is “the ultimate, all-purpose bird”.

Ecology has also investigated the link between predation and optimal habitat use (Sih 1987, Schwinning and Rosenzweig 1990, Rosenzweig 1991). Recently we have turned our attention to empirical tests of the effects of predation threat on the realized niche (Abramsky et al. 1998). We were able to use these optimality experiments to test and confirm an old prediction of population dynamical theory, thus further intertwining two of the MacArthurian threads. (The prediction: at low population densities, potential victims are, dynamically speaking, intraspecific mutualists although they may not cooperate in any way.)

But all of this work – whether it deals with competition or predation or both – all of it begins by assuming that natural selection has already perfected the fundamental niches of the individuals we study and the species they belong to. They may adapt to the conditions we set up, but they do not evolve.

A case from the literature will help us to explain what is usually missing (Grant 1986 and references therein). On Espanola Island, *Geospiza conirostris*, one of Darwin’s finches, occupies two niches – a cactus finch niche and a large ground finch niche. On Genovesa Island, however, in the presence of *G. magnirostris*, *G. conirostris* uses only the cactus finch niche. Were this restriction merely behavioral, it would not differ from other examples we have cited above. But *G. conirostris* on Espanola is also morphologically different. Its fundamental niche has shrunk in correlation with the presence of a competitor.

Some theories do follow the hypothesis of Cody (1975) and allow niche shapes (especially breadths) to evolve in response to diversity. Optimal responses of individuals can set the stage for the evolution of spe-

cialists (Rosenzweig 1987, Brown 1990). Brown and Pavlovic (1992) also examined the effect of migration on niche coevolution. They showed that a single species could get stuck in an adaptive valley only to be replaced by two other species with more specialized niches. Holt and his colleagues, in a distinguished series of contributions (Holt and Gaines 1992, Holt 1996a, b, 1997, in press, Holt and Gomulkiewicz 1997), has also investigated the evolution of the fundamental niche. He has been especially interested in what freezes niche shapes, i.e., what circumstances inhibit selection from altering them. Other important contributions to this growing literature include those of van Tienderen (1991) and Kawecki (1995, Kawecki et al. 1997). Finally, we mention Whitlock (1996) who looks at the trade-offs between evolutionary rate and niche breadth. Whitlock finds that – quite counterintuitively – narrower niches actually speed evolution. If Whitlock’s conclusion proves robust, then diversity could lead to a self-enhancing spiral in specialization!

Mitchell (1999) has produced an optimality theory of coevolution and coexistence on a continuous niche axis. It threatens the conclusion that competition sets no upper limit to the number of species. Mitchell’s species coevolve along their niche axis and occupy a deterministically predictable number of discrete, stable niches. This number varies with certain ecological properties of the virtual “region”. But it is never infinity (the prediction that others made). Yet, Mitchell does not seek nor does he find a fixed amount of niche overlap that will, if exceeded, cause competitive extinction. The individuals that his model produces have niche shapes and niche overlaps that very much depend on ecological conditions. Mitchell’s theory gives no comfort to proponents of limiting similarity.

The work has only begun, but has already taught some general lessons: 1) individuals must behave a certain way to optimize the fitness of the phenotype they have. 2) Their very behavior can change the selective regime so that future individuals will have to behave differently. 3) Some of those differences will arise because future individuals will have altered fundamental niche shapes. 4) And, finally, adding species sometimes sets in motion the behaviors that will lead to the evolution of narrower niches, both fundamental and realized. Such things are not often said of salt molecules.

MacArthur’s third path, and most famous set of researches, focused on patterns of species diversity. Can competition and niche relationships account for species-abundance distributions? Can species-area curves on islands emerge from the dynamics of species arrival and disappearance?

Of course, we all know the positive answers he and MacArthur and Wilson (1963) offered to the latter question. They have stood up in part because they are so simple and so robust. We may be able to refine

them, but it is hard to imagine replacing them. Some have mistakenly concluded that because they are so powerful, they must be trivial (Lack 1976, Williamson 1981). When M.L.R. was a high school student, he remembers thinking the same thing about Dalton's atomic theory. As Lawton has made so clear, science needs big, general, not-too-fussy rules. Ecology is no exception. It's a good thing Dalton did not have to contend with his colleagues crying, "Yeah, but what about isotopes?" Or, an even more trenchant criticism: "Rubbish! Atoms can be split." Despite isotopes, the concept of an element retains significance. And if atoms were not recognized, how could we have learned to split them?

Yet, the rules and processes of island biogeography are far from a complete explanation for species-area curves. Island biogeography does not concern itself with any scale other than that between islands. And it does not even attempt a prediction of the shape and slope of archipelagic SPARs. In his defense, we point out that MacArthur thought the matter settled by Frank Preston (1962), papers that purported to derive species-area curves from canonical lognormal species-abundance distributions. Ecology would be far more advanced if only that had turned out to be true.

Instead, Leitner and Rosenzweig (1997) found serious problems with the Preston explanation, as well as its distinguished companion (May 1975). First, data do not agree. Preston predicted z -values ca 0.26, May about the same. Many island values come close to that value, but those of interprovincial curves are much larger and those of mainlands are smaller. Second, both "proofs" have mathematical problems. Crucial to their arguments is a tacit (and false) assumption: the canonical lognormal abundance distribution is self-similar. (That is to say, what is canonical lognormal at one scale will also be at every other scale.) Third, computer simulation that follows canonical lognormality produces a z -value of 0.77.

Too bad. As we have shown here, the relationship of local to regional diversity is an echo of the mainland and interprovincial species-area curves. If we could predict those as consequences of the biological and geological processes that produce them, we would have the Echo pattern too. But so far we cannot, and recent work has not yet addressed the issue. Like this paper, it has been concerned with relating different patterns to each other. Ritchie and Olff (1999) and Harte et al. (1999), for example, derive mainland SPARs from assumptions of self-similarity. But self-similarity is a pattern. What mechanism generates the self-similarity? Leitner and Rosenzweig connect SPAR to a combination of species-abundance distributions and species-range – population-density distributions. But Leitner and Rosenzweig offer no mechanical explanation of either sort of distribution. Hanski and Gyllenberg (1997) come closest to an attempt. Using metapopula-

tion dynamics, they generate the relationship between population density and percent-sites occupied. Then they tie the latter distribution to SPAR. But the scale is so small as to ignore the principal explanation for local SPARs, i.e., larger areas have more habitat types (Williams 1943, Rosenzweig 1995). All of Hanski and Gyllenberg's virtual species live in a world of a single habitat. So, Hanski and Gyllenberg actually explained an unrecorded pattern. Similarly, Harte et al. (1999) assume spatial homogeneity in their model region, and therefore, that all species can live anywhere within it. These are substantive assumptions for the success of their proof. Thus, they too have answered a question with problematic relevance to biology. Does anyone think that species ranges have wholly accidental borders?

Obviously, we believe that having successful theories of SPARs as outcomes of biological and geological processes would clear up a large number of diversity patterns, especially Echoes. But these theories elude us. The only collector's curve with such a theory is the one that accumulates species over long periods of evolutionary time (Rosenzweig 1998). This curve is straight in arithmetic space, and therefore has a slope of unity in log-log space. That is consistent with the prediction of long-term steady states in provincial species diversity, a prediction that derives from considering the effect of provincial area and diversity on speciation and extinction rates (Rosenzweig 1995).

What does the Echo pattern imply about population interactions and community ecology? Is our understanding of SPARs so embryonic that, even having linked them to the Echo pattern, we are no better off? Actually, we believe the opposite.

Yes, the model of Caswell (1976), which assembles species randomly from a regional pool, would lead to a linear Echo pattern. But it would have other consequences too. It would lead to a hodgepodge of species assemblages from which all traces of morphological overdispersion (such as in body size) would disappear. It would obliterate the identity of habitats as places where we can expect to observe certain species and not others. Thus, it cannot hold in a world where local SPARs reflect the accumulation of habitat types in space. It is a fine null hypothesis, but useless as a notion of what is really going on. So, connecting SPARs to Echoes makes it clear that Echoes do not emanate from a blind proportional sorting of regional pools. Does that mean Echoes reflect interaction? Perhaps so.

Local SPARs partially reveal the outcomes of regional coevolution. If the monotonic increase in local diversity with regional diversity does not come from a Caswellian random sorting of species pools, then it must reflect finer and finer coevolutionary outcomes in larger regional pools. But these outcomes derive in part from the interactive effects of increased diversities. So,

we suggest that interactions do produce the local diversities, at least indirectly. Natural selection may sometimes have turned those interactions into ghosts, making them quite difficult to measure at a local scale. But even ghosts can get busted by patient science (Rosenzweig and Abramsky 1997, Morris 1999).

And ghosts are far from necessary. Morton and Law's (1997) theory postulates a variable pool size set by regional forces. The local assemblages they generate, however, experience intense interspecific interactions. Yet, the more species in the pool, the more in the local assemblage. So, setting the species pool size at the regional level does not preclude strong interactions at the local level. Not only that, but Morton and Law's final assemblages were all "completely invasion resistant" (p. 325), and in all their results, in the 1997 paper and others, each pool resulted in only one or a small number of final, permanent sets of species. Such results almost give the appearance of determinism.

Morton and Law's simulation curves do not follow the Echo pattern we derived above. Theirs are quite curvilinear (and may even be asymptotic). But that was to be expected. They explore the effect of pool diversity at a fixed value of specialization. Thus, their work becomes another indication of the importance of modeling specialization as a co-variate of diversity in the regional pool. The precise form of the Echo pattern in the real world has much to teach us.

Interpreting asymptotic Echo patterns

Undeniably, some Echo patterns are asymptotic, for example, the one generated by West Indian birds. These patterns break the rules of SPARs. And we don't need them to demonstrate the existence of strong interactions. What do they mean?

At first we guessed that asymptotic Echoes might be typical of studies done with islands as regions. Islands have not enjoyed the evolutionary independence that forces species to adjust their fundamental niche breadths to different pool diversities. If species from different geographical regions all live in the same evolutionary region, their diversities might face a common saturation point. Island pools would follow an island SPAR (with a δ -value between 0.25 and 0.55) and have an asymptotic Echo pattern. In contrast, independent pools would follow an interprovincial SPAR (with a δ -value near unity) and have a straight Echo pattern.

Perhaps separate provinces always do obey those rules, but islands generally do not. Islands with island-like δ -values sometimes have straight Echo patterns. Consider the case of the Ivory Coast fishes (Hugueny and Paugy 1995). Although the drainages in which they live are islands, their Echo pattern is insignificantly different from a straight line. The power equation that fits it has an exponent of 0.92.

Moreover, theory showed (above) that island systems, too, should generate near-linear Echo patterns, albeit with power values much less than unity. Recall that the Echo pattern that we calculated from typical archipelagic slopes had a power of 0.65, reflecting very gentle curvature.

So then, what rules of SPAR do asymptotic Echo patterns follow? Let us reverse-engineer the question. We begin with a set of complete regional pools from different provinces. Let these follow a standard SPAR with a z -value of unity. Next, we imagine a set of local samples taken from each one. For this set of SPARs to result in an asymptotic Echo, the samples cannot all fall on typical mainland SPARs with a z -value of 0.15. (Above, we showed that would lead to nearly linear Echoes.) To get an asymptotic Echo, z -values must increase with provincial area. We have drawn Fig. 4 as a model example. The same pattern of variation in z -values should exist among islands when they are used as the regional pools.

We are unaware of any systematically non-parallel set of mainland SPARs in the literature. However, although within-island SPARs are rarely reported, we found two data sets from which we extracted empirical examples. We re-examined Wilson's ant data (Wilson 1961) and found some evidence of an asymptotic Echo and z -values that increase as island diversity rises (Fig. 5). Yet, when we looked at the Ivoirian fish data, which has a linear Echo, we actually saw the reverse relationship (z declines as pool diversity grows) (Fig. 6). Perhaps this way of looking at the data may help to clarify the question.

What mechanism generates asymptotic Echo patterns? We do not know. Perhaps they will turn out to be the true reflection of history in community ecology? Or perhaps they originate from a sampling problem of some sort? Does the model of Morton and Law (1997) contain the relevant mechanism? Does a restricted set of circumstances actually exist to which one can apply the old idea of a fixed limit to niche overlap? We shall await Oikos's 60th anniversary essays and hope that one of them contains the answer. Meanwhile, we note the great usefulness of linking patterns, and of linking pattern with mechanism. Now, at least we know that the asymptotic pattern requires an improved explanation, and that SPARs and Echoes need to be explained together.

A future for community ecology

Community ecology will flourish from the realization that larger scales help to determine the attributes of communities. It should encourage community ecologists to target new questions in novel ways. Echo patterns already have taught us to ask about the peck

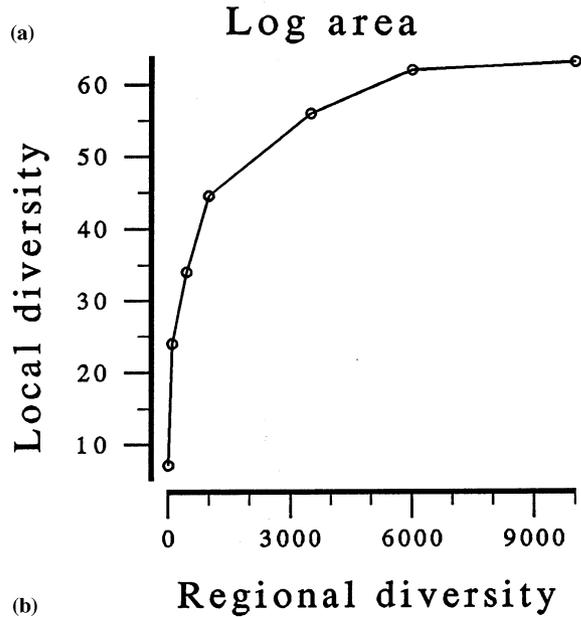
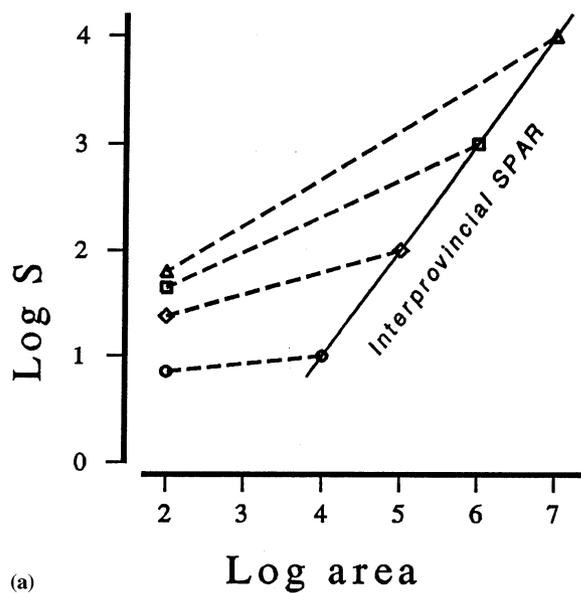


Fig. 4. a) Rules of SPAR that asymptotic Echo patterns adhere to. The pools from different provinces in this model example follow a standard SPAR with a z -value of unity. We took two local samples from each pool, one at 2 log area units, the other at 3 units. The SPARs result in an asymptotic Echo because we made the z -values increase with provincial area. b) The Echo pattern generated by 4a. Note: For clarity, we graphed fewer points on 4a's logarithmic axes than on 4b's arithmetic axes. But all points come from the same table of values and their range is the same in both graphs.

order of scales and causes. But we believe the most important issues will focus on niche coevolution.

As exciting as is the prospect, we do not suggest that a focus on niche coevolution refers to the expounding of a general theory for niche breadths and shapes as functions of diversity. Such a theory will tell us only a little about the properties of ecological communities.

We mean something much more elusive. We refer to local and regional properties whose patterns – let alone mechanisms – remain poorly described.

MacArthur (1964) noted that a community's species manage to co-occur for one of three reasons. They may subdivide space, or time, or resources. We believe that to be an inclusive list (although non-theoreticians sometimes choke on recognizing that predators can be resources for species that adeptly avoid exploitation). SPARs show us that there are regular patterns that characterize the subdivision of space. Accordingly, many have noted the close relationship of SPAR slopes to β -diversity. The temporal counterpart to SPAR is the species-time curve (SPTI) originated by Frank Preston (1960). Although a small amount of preliminary

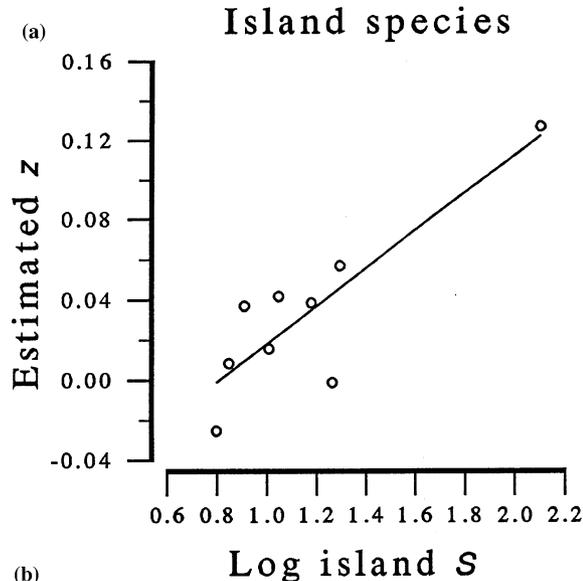
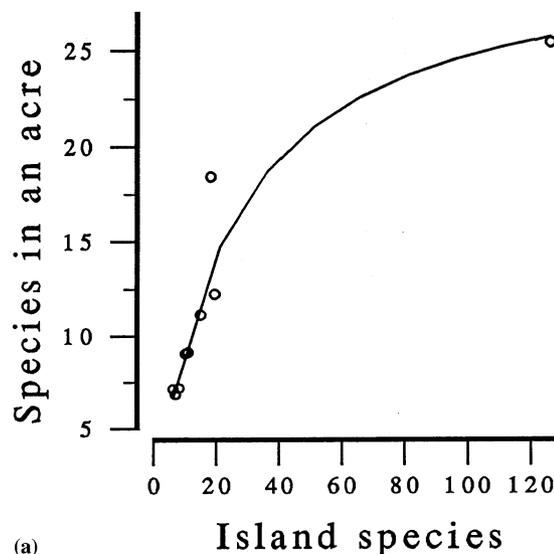


Fig. 5. E. O. Wilson's ant data (Wilson 1961) exhibits a tendency toward an asymptotic Echo a) and z -values that increase as island diversity rises b).

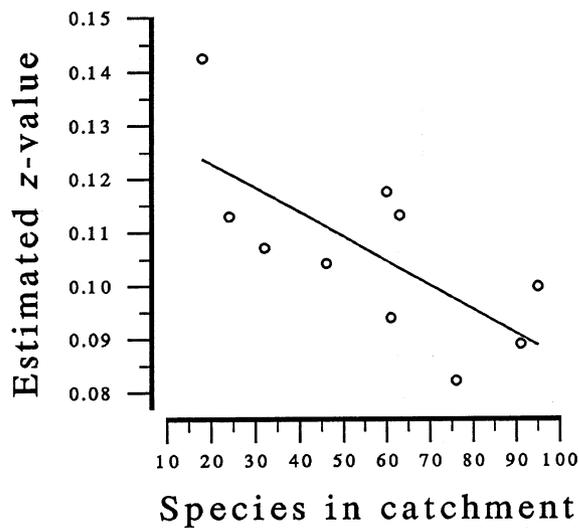


Fig. 6. The Ivorian fish data (Hugueny and Paugy 1995) has a linear Echo and exhibits z-values that decline with increasing regional pool diversity.

work on SPTIs exists (Rosenzweig 1998, McKinney and Frederick 1999), they remain a gold mine of opportunity for pattern discovery. And we aver that the third piece of the puzzle, α -diversity, the piece that reflects resource subdivision, has never once been successfully measured! Its measurement requires carefully collected, carefully analyzed data over enough space and time to estimate the diversity at a point, i.e., at the imaginary limit where space and time vanish (Rosenzweig 1999).

Although we do not yet have the patterns in hand, we do have some fascinating hints that they will matter. Preston (1960) hypothesized that SPARs and SPTIs would share slopes, and he may have been correct (Rosenzweig 1998, McKinney and Frederick 1999). If they do share slopes, it would mean that coevolution somehow balances spatial and temporal niche differentiation. What are the mechanisms that control whether natural selection will set species on the path to temporal or spatial or resource differences?

There is another sort of difference in the manner in which species coexist in regions. It deals with the pattern of subdivision of a niche axis. MacArthurian subdivision imagines a set of complementary specializations, and that is sometimes taken to be the end of theory on the subject. But it is not. Some species coexist by differing in their tolerance for sub-optimal conditions despite the fact that they are best at the same position on a niche axis (Rosenzweig 1991). Can we find patterns in the proportion of these alternative mechanisms of subdivision? Can we learn to predict them? Can we determine rules for their deployment in communities and regions?

We base all the former questions on investigation of niche coevolution. Yet, there is a more traditional

question. It assumes the existence of an already coevolved regional set of species and seeks rules for the assembly of subsets of species into communities. We believe the study of assembly rules also has a promising future, and that it may be aided by expanding its analyses to include such topics as coevolution has suggested.

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