Methods and Metaphors in Community Ecology: The Problem of Defining Stability

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Scientists must sometimes choose between competing definitions of key terms. The degree to which different definitions facilitate important discoveries should ultimately guide decisions about which terms to accept. In the short run, rules of thumb can help. One such rule is to regard with suspicion any definition that turns a seemingly important empirical matter into an a priori exercise. Several prominent definitions of ecological "stability" are suspect, according to this rule. After evaluating alternatives, I suggest that the faulty definitions resulted from an overemphasis on population dynamics in community ecology. Machine metaphors of nature may have given rise to a related problem of experimental design.

Introduction

As E. Nagel pointed out over a half-century ago (1945), progress in science often involves increasing precision and uniformity in the use of key terms. Precision and uniformity, however, have little or no value in themselves. They are useful only to the extent that they enable scientists to clarify or, indeed, to discover important relations among the referents of those and/or other terms. Until that happens, alternative

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definitions of the same terms may legitimately vie for acceptance.[1] Criteria for choosing between competing definitions include, for instance, the degree to which they promote interplay between theoretical and empirical results. No doubt there are many other useful rules of thumb for choosing the "right" definition(s) and thus the best-defined object(s) of study.

Ecology, especially, needs good definitions, since the science has so many implications for the understanding and solution of environmental problems. One major environmental problem is the spasm of extinctions currently afflicting our planet. Notions of ecological stability have played a role in attempts to solve this problem by helping to motivate passage of the Endangered Species Act in the United States (Shrader-Frechette and McCoy 1993). It is ironic that in the same year the Act was passed, May (1973) claimed to refute the very hypothesis that had helped to justify it—the "diversity-stability hypothesis."[2]

According to the diversity-stability hypothesis, increasing the diversity of (number of species in) an ecological community increases its stability. A number of authors, dating perhaps as far back as Spencer (1897; also see van Emden and Williams 1974) had written on the diversity-stability hypothesis by the time May presented his surprising result. His clarification (and refutation) of the hypothesis, however, was of singular value in stimulating further research. This heuristic value has extended beyond the confines of the diversity-stability question by dovetailing with work stemming from Paine (1966) and Cohen (1978) to foment research programs on numerous aspects of food-web structure and behavior. Ecological studies since 1973, then, have testified to the merit of providing a precise definition for a scientific term like stability and placing it into a rigorous theoretical framework.

However, some precise definitions, in some contexts, are misleading. In this article, I will point out a problem shared by several precise definitions of ecological stability in the context of the diversity-stability question. This problem is separate from and independent of considerations raised in earlier critiques (e.g., those reviewed by DeAngelis et al. [1983]). Because the problem has gone unnoticed, it still threatens to distort ideas about diversity-stability relations.

The problem is of philosophical interest because it illustrates a rule

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[1] At least one philosopher of science has even embraced the equivocation that such alternative definitions make possible, as "a powerful method of conceptual improvement" (Hull 1988, p. 7). In this article, I will not take a stand on whether equivocation does on balance more harm or good in science.

[2] Callicott (1996) aptly discussed the implications of this development and other aspects of "deconstructive ecology" for environmental ethics and policy.

of thumb for scientific definitions and because it may be tied to reductionism and machine metaphors of nature. The rule of thumb is: Do not employ a definition that turns what was originally thought to be an important empirical matter into a generic a priori exercise. I contend that three influential definitions of stability create a severe a priori bias in favor of the conclusion that diversity decreases stability—in other words, a bias against the diversity-stability hypothesis. The bias is a priori in the sense that it exists before any empirical data is gathered and even before any particular theoretical models are applied. Because of this, statements about diversity and stability, so defined, do not say much about the particular structure of reality or even our models of it. After thus critiquing certain definitions, I evaluate alternatives. Finally, I explore possible connections between definitions of stability, experimental design, reductionistic research strategies, and machine metaphors of nature.

The Problem with Certain Prominent Definitions of Community Stability

The stability of an ecological community can be defined in a bewildering number of more or less precise ways (Pimm 1984). Often, but not always, it is defined in terms of the community's capacity to respond in a certain way to perturbation from an equilibrium state. Different definitions of stability diverge with respect to (i) the type of perturbation assumed (if any), (ii) the form of response evaluated, and (iii) the kind of variable involved. A fourth consideration, the method of combining information about component species into an overall stability value for the community, turns out to be crucial to the argument below.

One major motivation for defining stability is to make the following "diversity-stability hypothesis" precise: communities with more species tend to be more stable than those with fewer species. Here, diversity is defined simply as the number of species. May (1973) employed one precise definition of stability and challenged the hypothesis by showing that community models based on Lotka-Volterra equations predict the opposite—more diverse communities tend to be less stable. Let us call the type of stability that May explored "neighborhood stability," defined as follows: the probability that the population size of every species in a community would return to equilibrium if there were an arbitrarily small perturbation in the population size(s) of one or more of the species.[3]

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[3] Strictly speaking, neighborhood stability is an all-or-nothing property: a community is neighborhood stable if the population size of every species in a community would return to equilibrium after an arbitrarily small perturbation in the population size(s) of

In order to improve upon the dubious relevance of arbitrarily small perturbations, Pimm (1979, 1980) offered a different definition of stability based on the capacity of species to persist in the face of a rather large perturbation: the complete and permanent removal of one of their fellow species in the community.[4] Pimm called this type of stability "species-deletion stability" and defined it as follows: the probability that removing one species would not lead to any further local extinctions.[5] This definition, along with some computer simulations, led Pimm to agree with May's conclusion that theoretically, at least, diversity decreases stability.

Two different definitions of stability, then, were employed in two different theoretical contexts. In both contexts, researchers obtained results inimical to the diversity-stability hypothesis. These influential results have significantly undermined ecologists' confidence in that hypothesis. Many consider it to have been decisively refuted (Shrader-Frechette and McCoy 1993). This opinion is unwarranted, however, since both analyses rest on flawed definitions of stability, as do the many other analyses that have employed the same or similar definitions. I do not purport to know whether stability, properly defined, increases or decreases with diversity. A good deal more research is required to answer that question. Neither is the critique presented here meant to establish any single definition of community stability for all times and all places. The goal is, rather, only to rule out certain definitions. Thus, certain kinds of stability—properly defined—may very

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one or more of the species; it is unstable if any of the populations would not reequilibrate. However, May presented his results in terms of the *probability* that a community, randomly selected from a certain hypothetical population of communities, is neighborhood stable in this strict sense. For the sake of simplicity, then, and for ease of comparison with other quantitative definitions of stability, I have simply equated neighborhood stability with this probability.

[4] Pimm's definition represents an improvement with respect to the other rule of thumb mentioned in the introduction—that a definition should "promote interplay between theoretical and empirical results." It is obvious that the loss of an entire species is both more empirically important and more empirically detectable than an "arbitrarily small perturbation" to a species' population size.

[5] "The precise definition of species deletion stability is an index, S, on the interval 0,1:

$$S \equiv \sum_{i=1}^{n} r_i p_i,$$

where n is the number of species in the community; r_i is a weighting term, the probability that, if a species is lost from the community, it will be the ith species (hence the r_i sum to 1.0); the p_i are the probabilities that if the ith species is lost there will be no more losses from the community ($p_i \leq 1$)" (Pimm 1979, p. 353).

well increase, while others decrease with diversity (as suggested by Tilman [1996]).

The problem with neighborhood and species-deletion stability stems from the way in which they both combine information about component species into an overall stability value for the community. Both kinds of stability involve the chances that, if there were a perturbation, *all* of the component species would respond in a certain way. Neighborhood stability is the probability that all of the species would bounce back to their preperturbation population sizes. Species-deletion stability is the chance that they would all avoid extinction or, in other words, persist.

At first glance, these all-or-nothing criteria might seem reasonable. There is, however, a problem: the criteria get more and more strict as the number of species increases. Requiring that every single species in a fifty-species community have a given property—*any* property—is a much stricter criterion than requiring that every species in a ten-species community have the same property. This means that as the number of species increases, the probability that the criteria are met almost certainly decreases. This leads to a *default* expectation that stability will decline with increasing diversity. This expectation has nothing to do with any particular features of ecological communities or of the Lotka-Volterra equations used to model them. Normally, the more components there are in a system—*any* system—the less the chance that every single one of them will have a given property, such as the capacity to persist or to reequilibrate after a perturbation.

To illustrate this default expectation, consider a sequence of coin tosses. The coin does not have to be unbiased, nor must the different tosses be independent of each other. For the moment, however, let us assume that they are independent. Let the probability of heads be .75, and let us define the "stability*" of a sequence in a manner analogous to the definitions of stability given above for ecological communities: the probability that every toss in a sequence of coin tosses comes up heads. It is obvious that the probability of stability* declines monotonically with the number of tosses. In a one-toss sequence it is .75, in a two-toss sequence $.75^2$ or .56, in a three-toss sequence $.75^3$ or .42, and so on. It might be objected that a sequence of coin tosses is a much different kind of "system" than an ecological community. Furthermore, a coin's tendency to land heads-up is a quite different kind of property than a species' propensity to reequilibrate or persist after a perturbation. However, the point of the example depends only on the relationship between the separate probabilities of several individual events and the probability of their conjunction. In this case, the separate probabilities (of heads at a single toss) are all .75, and the probability of their conjunction (the probability of all heads in a sequence) is $.75^n$, where n is the number of tosses. In the appendix I show that a similar result holds when the independence assumption is relaxed.

Throughout the history of ecology, most of its practitioners have considered the relationship between diversity and stability to be an important empirical matter. The definitions of neighborhood and species-deletion stability, in contrast, turn this relationship into an artifact of probability theory. This suggests that not only do the definitions of neighborhood and species-deletion stability miss something about the "original, vague notion" of stability, but they also fail to capture and might even obscure other equally precise properties that would more reasonably go under the name of "community stability." So, if the two definitions discussed above are unsound, how should stability be defined? Do the definitions employed in other studies suffer from the same problem as that diagnosed above? Finally, what might have given rise to the faulty definitions? Below, I address the first two questions together before turning to the third.

Alternative Definitions[6]

One strategy that avoids the problem described above is to define stability in terms of some functional property of the overall community. McNaughton (1977), Tilman (1996), and others have taken this tack in conducting empirical studies of biomass stability. Community biomass—the total mass of living organisms in a community—is related to the community's abilities to store carbon, produce oxygen, hold soil, and so forth. Tilman used the following value as an inverse measure of biomass stability: "biomass variability" is the variation, normalized for the amount present, of community biomass over time.[7] This definition escapes the problem, described above, afflicting the definitions of neighborhood stability and species-deletion stability. In that sense, biomass variability is a more appropriate measure of community (in)-stability.[8]

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[6] As noted before, definitions of community stability are strikingly abundant. Here, I will focus on only a few. For others, not discussed herein, see Holling (1973) and Van Voris et al. (1980).

[7] Specifically, biomass variability is the standard deviation, divided by the mean, of community biomass over time.

[8] After this manuscript was accepted, Doak et al. (1998) suggested that Tilman's definition actually creates a bias in the opposite direction from the one discussed herein. In other words, they claimed a bias in favor of, instead of against, the diversity-stability

But community function is not the only legitimate basis for a definition of community stability. An ecologist might, in another context, want to define stability so as to more directly reflect the suitability of a community for the species in it. The desire to conserve species could easily motivate a definition such as the following: "average extinction resistance" is the average, over all the species in a community, of the species' probabilities of persisting, that is, not becoming extinct, within a given period of time.[9] This would reflect one important aspect of the "quality of life," or lack thereof, in a community. Communities with a high average extinction resistance would be considered more stable because they are more hospitable for their component species than are communities with a low average extinction resistance.

Hairston et al. (1968) defined stability in terms of extinction resistance but did not average the measure over all the species in a community. Instead, their measure involves the same kind of all-or-nothing criterion as neighborhood and species-deletion stability: "total extinction resistance" is the probability that all of the species in a community will persist, that is, not become extinct, within a given period of time.[10] It is important to recognize the distinction between average and total extinction resistance. Total extinction resistance is the *joint* probability that species 1 will persist, and species 2 will persist, and . . . and species *S* will persist, where *S* is the total number of species in a community. Average extinction resistance, on the other hand, is the *average* of the probabilit*ies* that species 1 will persist, that species 2 will persist, . . . and that species *S* will persist. Average extinction resistance

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hypothesis. However, Tilman et al. (1998) seem to have effectively countered this criticism.

[9] Average extinction resistance can be calculated in either of two ways: the arithmetic mean,

$$\frac{\sum_{i=1}^{S} p[P(c_i)]}{S};$$

or the geometric mean,

$$\sqrt[S]{\prod_{i=1}^{S} p[P(c_i)]};$$

where S is the number of species and $p[P(c_i)]$ is the probability (p) that the ith species (c_i) persists (P; i.e., does not become extinct).

[10] Hairston et al. actually recorded the *frequency* of communities in which any extinctions took place, relative to the total number of communities. In the definition given, I interpreted this frequency as an estimate of the probability that any extinctions would take place in a given community.

"corrects" for the number of species (S) in the sense that, depending on whether one takes the arithmetic or the geometric mean, one either divides by S or takes the Sth root, respectively, of the sum or product, respectively, of the individual species' probabilities.

In general, if community stability is to be defined in terms of species properties, like susceptibility to extinction, then it should be averaged over species. Otherwise it induces the a priori bias against the diversity-stability hypothesis described in the previous section. This bias can, in turn, obscure potentially important discoveries.

We can use total and average extinction resistance to illustrate this point. Imagine a five-species community with a total extinction resistance of 50% and an average extinction resistance of 87%. (The former can never be greater than the latter.) Now imagine a fifteen-species community with 40% total extinction resistance but an average extinction resistance of 94%. These numbers are not arbitrary. For the sake of illustration, I made the simplifying assumption that each species' probability of persistence is independent of the others', and I interpreted average extinction resistance as the *geometric* mean of these probabilities. Total extinction resistance is thus equal to average extinction resistance raised to the power of the number of species.[11] (As mentioned before, in the appendix I develop a similar probabilistic argument that does not depend on the simplifying assumption of independence.)

Total extinction resistance is thus lower in the fifteen-species community than in the five-species community. In other words, the chance that at least one of the species becomes extinct is greater when there are fifteen of them than when there are five. This obscures the fact that species are generally better off in the larger community. Individual species have, on average, a 94% chance of surviving in the fifteen-

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[11] Symbolically,

$$X = s\sqrt{\prod_{i=1}^{S} p[P(c_i)]},$$

where X is average extinction resistance, S is the number of species, and $p[P(c_i)]$ is the probability (p) that species i (c_i) will persist (P). Since the species' probabilities of persistence are independent of each other,

$$Y = \prod_{i=1}^{S} p[P(c_i)],$$

where Y is total extinction resistance. Hence

$$Y = \left(s\sqrt{\prod_{i=1}^{S} p[P(c_i)]}\right)^{s} = X^{S}.$$

species community, as opposed to only an 87% chance in the five-species community.

Two ecologists who addressed the diversity-stability hypothesis and who employed definitions of stability that were averaged over species are MacArthur (1955) and Lawler (1993). MacArthur suggested not just one but a number of definitions. Stability, he said, is the property that "a community in which one species is abnormally common [or uncommon, has] . . . a small effect upon the rest of the community." "A difficulty arises," he admitted, "in making this definition quantitative . . . the concept 'effect upon the other species of the community' required in the definition can be interpreted in many different ways. It could be the average (over all species) maximum change in abundance, or the relative changes, or mean square changes, or different species could be weighted differently, etc." (1955, p. 534). Now, the first of these—the average maximum change in abundance per species—clearly averages stability over species. In this context, the third—"mean square changes"—appears to as well. It is unclear what the second definition, namely "relative changes," means. But the fourth suggestion of weighting different species differently would affect only the method of averaging, presupposing a positive answer to the question of whether to average at all.

Lawler (1993), too, employed properly averaged measures of (in)stability. In her experimental communities, she calculated the following two measures: "average population variability" is the average (over species) of the variabilities (over time) in population size, and "proportional extinction" is the number of species going extinct divided by the total number of species that were present in the community before the extinctions.[12] Proportional extinction is closely related to average extinction resistance. Indeed, one minus the proportional extinction could serve as an estimate of average extinction resistance.

It is unfortunate that an aspect of Lawler's experimental design severely biased her results against the diversity-stability hypothesis. Each of her laboratory "microcosms"—beakers of water, in this case—contained two, four, or eight species of protozoa. But all of the two-species communities had been preselected for stability!

Lawler constructed all of her communities from a pool of four pred-

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[12] More precisely, "average population variability" is the (arithmetic) mean, over species, of the standard deviation, over time, of $\log_{10}$ (population size $+1$). Taking the logarithm of population size is one way to "eliminate any positive correlation between the mean and the standard deviation" of population size (Lawler 1993, p. 714).

ator species and four prey species with all of the smallest (two-species) communities consisting of one predator and one prey. Given these constraints, sixteen two-species combinations are possible. However, Lawler included only four in her analysis: precisely those four pairs that had previously been shown to persist without either species becoming extinct. All of the smallest (two-species) communities analyzed in the experiment were thus maximally stable in terms of proportional extinction. (Their proportional extinction rate was zero.) But this was only because they had been preselected on that basis.

Lawler then combined these preselected species pairs in various ways to form several different four-species communities and a single eight-species community. Since these larger communities were *not* preselected for stability, it was only to be expected that some of them would have proportionally more extinctions and hence be judged less stable in that sense than the smaller, two-species communities. Lawler did, in fact, find a negative correlation between diversity (number of species) and stability in her experiment, but as we can see now, it was only an artifact. A completely different conclusion might very well have been drawn had a more complete, or at least more representative, set of two-species communities been examined. In the next section, I explore how this problem of experimental design may be connected to the problem of definition discussed above.

Possible Roots of the Problem

Preselecting species pairs for stability, then putting the pairs together to make four- and eight-species communities, presupposes something that I will call the "assembly principle." The assembly principle can be defined as follows: stable larger combinations of species, if they exist, must be composed of stable smaller combinations. In addition to producing a bias against the diversity-stability hypothesis that is similar to the definitionally induced bias discussed above, the assembly principle contradicts a prominent claim made by Diamond (1975). "Some pairs of species," he said, "that form an unstable combination by themselves may form part of a stable larger combination" (1975, p. 423). Even earlier, Paine (1966) showed that a predator species could permit the coexistence of several prey species, one of which would otherwise outcompete all of the others. In other words, a species combination that is larger, in that it includes the predator, is more stable than a smaller species combination lacking the predator.

Despite the bias induced by and the evidence against the assembly principle, the theoretical models of May (1973), like the experimental models of Lawler (1993), presuppose it. The theoretical models give each species a "density-dependent or otherwise stabilized form, so that if disturbed from equilibrium it would return with some characteristic damping time" (May 1973, p. 63). By thus making the smallest—that is, one-species—communities 100% neighborhood-stable, the models guarantee that larger communities, if they differ at all in their stability, are relatively less stable.

Why have some ecologists implicitly incorporated the assembly principle into their models, despite its problems? Wimsatt suggested that notions like the assembly principle arise out of the "mechanical engineering paradigm of making artifacts by stringing together parts" (1976, p. 246). Several other authors have written about the influence of mechanical or machine metaphors on the science of ecology (Taylor 1988; Botkin 1990; Hagen 1992). I will not argue here, as some have suggested, that machine metaphors are altogether unhelpful. Considering that such metaphors have proven amazingly fruitful in other sciences for the past several hundred years, it is unlikely that ecologists' adaptations of them are completely bankrupt. However, like any heuristic device, machine metaphors can mislead as well as inspire. The misguided assembly principle discussed above is a case in point.[13]

I suggest here that another tendency associated with machine metaphors may also have contributed to the problem with definitions of stability: reductionism. I mean specifically microreductionism (Oppenheim and Putnam 1958), the belief that the properties of whole systems can and should be explained primarily in terms of the properties of their parts. Again, I do not suggest that (micro-)reductionism is always wrong, but only that it has pitfalls that should be avoided. Explaining wholes in terms of their parts is a fertile scientific method, but it can sometimes lead scientists to focus too closely on the properties of the parts and thus overlook crucial aspects of the whole.

Wimsatt (1980) argued that an excessive focus on the individual organism as a target of natural selection led evolutionary biologists to overlook serious flaws in mathematical models of selection at a higher level, that of the group (see also Wade 1978). In a similar manner I suggest that an excessive focus on population dynamics led ecologists to overlook flaws in definitions of stability at the higher level of the community. The main difference between Wimsatt's point and my own, besides the different subject matter, is that he discussed problematic assumptions while I have criticized problematic definitions.

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[13] It appears that at least one of the problematic definitions of stability discussed above, that of neighborhood stability, also resulted from viewing ecological communities as vast machines. May acknowledged that his "usage of the terms ("stable" and "unstable") follows that in mechanical systems" (1973, p. 15).

The population is probably better studied than any other level of organization in ecology. This is especially true in theoretical ecology and has led to an overemphasis on population dynamics in models of higher levels of organization, such as the community. Most of the equations considered central in theoretical ecology model population growth: the exponential and logistic growth equations for single species, the Lotka-Volterra competition equations, the Lotka-Volterra predation equations, the Nicholson-Bailey host-parasite equations, and so on. Although some of these same equations can be applied to higher levels, ecologists rarely employ this strategy. One paleontologist (Sepkoski 1978), for example, treated whole species instead of individual organisms as the basic units and used a single logistic equation to describe changes in global diversity. Theoretical ecologists, in contrast, typically cobble together as many equations for population growth as there are species in a community, then implicitly or explicitly track the population trajectories of every single species in order to answer questions about the community as a whole. Since information about species interactions is usually summarized in matrix form, this multiple-equation method is often referred to as the "community matrix" approach.

It is clear that the community matrix approach cannot be very closely tied to empirical work since it would be practically impossible to track the real population trajectories of all the species in any sizable community. Large numbers of population equations make for an exceedingly complex way of looking at communities. These equations were designed to perform well on their own "turf"—single populations and/or pairs or triplets of interacting species. Why should they be expected to provide the most illuminating way to model large communities? Such an expectation seems to rest on the idea that not only are communities ontologically reducible to species populations, in that the former are composed of the latter, but they are epistemologically reducible as well in that the best tools for describing communities are necessarily composed out of the best tools for describing populations.

I would argue to the contrary that the best way to model communities is probably not to conjoin a bunch of equations for individual populations. The success of MacArthur and Wilson's (1967) theory of island biogeography attests to this point. MacArthur and Wilson's model did not track the population sizes of individual species but treated whole species as units and explored how the number of species on an island is affected by the area of that island and its distance from the mainland. The cascade model of food webs by Cohen et al. (1990) is another "less reductionistic" approach to communities that has met with some success.

The point to be made here is that an overemphasis on population dynamics may have caused theoretical ecologists to overlook the problem of bias in their definitions of community stability. As we saw, however, not only theoreticians but some empiricists, as well, fell prey to the same problem of definition. Population-reductionism does not as readily explain why Hairston et al. (1968) used a faulty definition, since they did not track population trajectories in their experiment. Perhaps their usage was an indirect result of prevailing theoretical proclivities. Other experimentalists employed proper definitions (Lawler 1993; Tilman 1996). But Lawler, as well as May (1973), presupposed the problematic assembly principle, thus encountering a pitfall of the machine metaphors often associated with reductionism.

Conclusion

I have thus argued that three prominent definitions of community stability—two theoretical and one experimental—distort the diversity-stability hypothesis by rendering it highly improbable on a priori grounds. I also identified alternative definitions that escape this problem. Finally, I speculated that the faulty definitions resulted from reductionistic research strategies and that the machine metaphors of nature affiliated with these strategies gave rise to a related problem of experimental design.

These arguments do not show that any single definition of community stability will be the best or the only suitable one. As implied in the introduction, that judgment will depend on the degree to which different definitions enable scientists to uncover interesting and useful relations between stability and other variables. The arguments made in this article do, however, indicate that some definitions should be rejected because they threaten to obscure relations between diversity and more important kinds of stability. The arguments illustrate, and thus help to motivate, the rule of thumb for scientific definitions proposed in the introduction: just as we should be skeptical of any definition that leaves one half of a seemingly important dichotomy without any actual instances, we should also treat with suspicion any definition that turns what was originally taken to be an important empirical matter into a generic a priori exercise.

Appendix

For the sake of simplicity, I made a certain assumption in the coin-tossing and extinction resistance examples. To wit, I assumed that the possession of a given property (P) by any given component (c_i) in a system is probabilistically independent of the possession of that same property by any other component (c_j, $i \neq j$). Symbolically,

$$p[P(c_i) \mid P(c_j)] = p[P(c_i)]$$

where i and j range from one to the total number of components.

If we drop this assumption, the possession of a given property by one component is probabilistically dependent on the possession of that same property by other components:

$$p[P(c_i) \mid P(c_j)] \neq p[P(c_i)]$$

Even in this more general case, it is overwhelmingly likely that the joint probability $p[P(c_1)\ \&\ P(c_2)\ \&\ \ldots\ \&\ P(c_n)]$ will decline as the total number of components (n) increases, unless the average of the individual probabilities, $\overline{p[P(c)]}$, increases with n.[14] In the argument that follows, I assume that all unconditional probabilities are nonzero. This ensures that the conditional probabilities are well defined.

Indeed, if the average probability $\overline{p[P(c)]}$ does not increase with n, the joint probability $p[P(c_1)\ \&\ P(c_2)\ \&\ \ldots\ \&\ P(c_n)]$ cannot increase monotonically with n, and can only remain constant as n increases in one very special and limiting case. Consider a system with a single component, c_1. In this system, the "joint" probability $p[P(c_1)\ \&\ P(c_2)\ \&\ \ldots\ \&\ P(c_n)]$ is the same as the "average" probability $\overline{p[P(c)]}$: both are just $p[P(c_1)]$. Now consider larger systems. We assume that the average probability $\overline{p[P(c)]}$ does not change with n, and ask, "Under what conditions does the joint probability $p[P(c_1)\ \&\ P(c_2)\ \&\ \ldots\ \&\ P(c_n)]$ remain constant as n increases?" The single-component system, together with the assumption and the question, require that for all systems with any number n of components,

$$p[P(c_1)\ \&\ P(c_2)\ \&\ \ldots\ \&\ P(c_n)] = \overline{p[P(c)]}.$$

Let us interpret the average probability as the geometric mean. Symbolically,

$$\overline{p[P(c)]} = \sqrt[n]{\prod_{j=1}^{n} p[P(c_j)]}.$$

From the axioms of probability theory we can derive

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[14] Pimm acknowledged this in the case of species-deletion stability when he wrote that "the chances of at least one plant [for example] becoming extinct would increase with the numbers of plants even if the individual probabilities remained the same" (1980, p. 144). This means that the joint probability that all of the plants persist would decrease as the number of plants increased, even if the probability that any single plant persists (and hence the average probability over all the plants) remained constant.

$$\prod_{j=1}^{n} p[P(c_i) \mid P(c_j)] \geq \frac{\{p[P(c_1) \;\&\; P(c_2) \;\&\; \ldots \;\&\; P(c_n)]\}^n}{\prod_{j=1}^{n} p[P(c_j)]}$$

for all i between one and n.

The preceding inequality and the equation just before it together entail that

$$\prod_{j=1}^{n} p[P(c_i) \mid P(c_j)] \geq \frac{\{p[P(c_1) \;\&\; P(c_2) \;\&\; \ldots \;\&\; P(c_n)]\}^n}{\{\overline{p[P(c)]}\}^n}.$$

But since $p[P(c_1) \;\&\; P(c_2) \;\&\; \ldots \;\&\; P(c_n)] = \overline{p[P(c)]}$,

$$\prod_{j=1}^{n} p[P(c_i) \mid P(c_j)] \geq 1.$$

But then

$$p[P(c_i) \mid P(c_j)] = 1$$

for all i and j between one and n.

This also entails that

$$p[P(c_i) \mid \neg P(c_j)] = 0$$

for all i and j between one and n, and that

$$p[P(c_i)] = p[P(c_j)]$$

for all i and j between one and n.

Thus, if the average probability remains constant as the number of components increases, the only way for the joint probability not to decrease is for a very peculiar one-for-all and all-for-one phenomenon to occur. Either all of the components possess a given property or none of them do.

Although undoubtedly some properties behave in this way, none of those discussed in this article do. For example, in any sizable ecological community, at least some particular species can be lost without every single one of the others becoming extinct. Nor do any interesting analogues that spring to mind display the radical degree of interdependence implied by the above result. In most human communities, for instance, at least some particular person can die without all of the others expiring as well. Not even typical machines or typical organisms behave as required above. An automobile, for instance, can lose certain of its parts, such as a rearview mirror, without all of its other parts necessarily being destroyed. In a similar fashion, we as organisms can lose certain organs, such as our appendixes, without spelling doom for all of our other organs. Thus, neither ecological communities, nor tossed coins, nor any of the systems with which ecological communities are most commonly analogized—organisms, machines, or human communities (Hagen 1992)—display the strong constraint given above.

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