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Beyond neutral science

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Biodiversity science is unusual in that an emerging paradigm is not based on a specific process, but rather depends largely on stochastic elements, perceived as neutral forces. Here I suggest that these forces, which have been justified, in part, by the concepts of symmetry and equalizing mechanisms, have application to the understanding of stochastic models but do not constitute forces that operate in nature. Another process now regularly classified as a neutral force, limited dispersal, represents a fundamental demographic process that is not neutral with respect to species differences, but rather differs among species in important ways. Finally, I suggest that the dramatic shift in ecological research to focus on neutrality could have a cost in terms of scientific understanding and relevance to real biodiversity threats.

The new explanation for biodiversity

Within the last decade, the unified neutral theory [1] (see Box 1) has become a dominant part of biodiversity science, emerging as one of the concepts most often tested with field data and evaluated with models (Figure 1a). A 2007 National Science Foundation funding program on *Advancing Theory in Biology* lists neutral theory along with evolution by natural selection as one of four examples "with far-reaching implications for understanding key biological processes and their fundamental consequences across different levels of biological organization" (http://www.nsf.gov/pubs/2008/nsf08513/nsf08513.htm). Articles regularly appear in *Science* and *Nature*. The many tests of this theory that do not support it [2–12] have not diminished its popularity as a null model from which much can be learned, if for no other reason by rejecting it (e.g. [13]).

Not only advocates and opponents but also those favoring an intermediate position to unify niche and neutral theory (reviewed in Ref. [14]) can overlook the more fundamental lack of theoretical or empirical evidence for neutral forces in nature [15]. Proponents, contrarians and unifiers alike have debated the relative importance of different stochastic forces (e.g. 'demographic stochasticity' versus 'environmental fluctuations'), lack of model fit to specific data sets, or phenomena that it cannot explain (e.g. relative abundances of species) [13]. Although I agree with many of the problems pointed out by others, I do not repeat them here. Instead, I consider a more questionable interpretation of stochasticity as an actual 'force,' a notion that permeates both theoretical and empirical arguments on both sides (and the middle). A previous paper [15] used technical illustrations to make these points. In light of how

confusing stochasticity can be, there might be merit in a nontechnical discussion of these issues.

I start by discussing why stochasticity can be confusing and why it can be misinterpreted to suggest neutral forces. I then address concepts that have increasingly been part of neutral discussions, including 'equalizing mechanisms,' 'symmetry' and limited dispersal (Box 1). I address at least three ways in which confusion can arise. First is the idea that there might be a theoretical basis for the notion that increased diversity comes from species being more similar in terms of functional overlap. Some recent efforts to integrate niche and neutral theory use the idea of equalizing mechanisms as a unifying rationale. The idea here is that niche and neutral processes combine to generate coexistence as a balance between stabilizing forces and equalizing mechanisms, the latter referring to equivalent fitness. From a different perspective, I point out that although the concept of equalizing mechanisms has utility, the concept does not mean that being 'more equal' in any functional sense makes coexistence more likely. A second point of confusion is the idea that symmetry in models (one definition of neutrality [16]) might be used to infer symmetry (thus, neutrality) in nature. Because of the way parameters are defined, the concept of 'symmetry' has particular relevance for the Lotka-Volterra competition model. However, as with neutrality, we cannot use inference to conclude symmetry in nature. A third source of potential confusion could come from classifying dispersal limitation as a neutral process, that is, one that can be equated with functional or demographic equivalence. I suggest that 'limited dispersal' is not obviously relevant to the question of whether or not species are functionally equivalent (it differs importantly among species, it is subject to natural selection and so forth).

Second, I provide a perspective different from the view that science is enriched by reversion to a process-free theory of nature. I use the term 'process-free' in the sense

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Glossary

Equalizing mechanisms: a term applied to some models, describing the degree to which a term interpreted as the density-independent growth rate of a species differs from that of competitors.
Limited dispersal: one of the factors determining the scale at which species interact.
Limiting similarity: the concept that the more similar two species are, the less likely they are to coexist, although definitions can vary [20].
Neutrality: equivalence among species in a demographic sense, a functional sense, or both.
Niche differences: responses to and effects on the environment; includes the concept of limiting similarity.
Species abundance distributions: a frequency distribution, where species are binned according to abundance.
Symmetry: the species identity of an individual does not matter.

Box 1. Definitions related to neutral theory

Terms used in the context of neutral theory can be viewed as applying to different levels of complexity, from responses to and effects on the environment and shared resources (level 1 in Figure I) through to demographic rates (level 2), population growth and fitness (level 3) and patterns of abundance, including biodiversity (level 4).

Niche differences

For stable coexistence in competition models, species must differ in terms of how they respond to and/or affect the environment, including resources, they share with other species. The niche is determined by resources and by all other factors that potentially influence population growth and fitness (recent reviews include Ref. [50]). Functional equivalence could imply that each species has the same responses to, and effects on, the variables that define its own niche and those of others. Absence of niche or functional differences (level 1 in Figure I) has been examined in several studies (e.g. [18,51,52]).

Neutrality

Neutrality has been defined as the 'per capita ecological equivalence among all individuals of every species in a given trophically defined community' ([1], p. 28). As in Figure I, species could occupy different niches at the level of resource and environmental requirements, but still be classified as 'neutral' at level 2, as implied by this definition. This concept of neutrality can be viewed as a decoupling of niche and demographic rates.

Symmetry and neutrality

'Symmetry' is defined as follows: 'the species identity of an individual does not matter: it has no effect on individual's predicted fate or the fates of its offspring, nor does it have any influence on the fates of others' [16]. It is suggested that a neutral model should be defined as one that is symmetric at the individual level. Suppose an individual were to suddenly change its species identity. Its competitive environment could change depending on whether or not it found itself surrounded by others of the same species or of a different species. If this identity change did not affect its competitive environment, the species are defined to be symmetric. This definition makes an important distinction in the case where a model assigns to different species the same parameter values without implying that the species are the same. This is the case for the Lotka-Volterra model:

$$\frac{1}{n_i}\frac{dn_i}{dt} = r_i(1 - \alpha_{ii}n_i - \alpha_{ij}n_j). \qquad [1]$$

For two species *i* and *j*, if $\alpha_{ii} > \alpha_{ji}$ and $\alpha_{jj} > \alpha_{ij}$, the two species coexist, despite the fact that the following could be true: $\alpha_{ii} = \alpha_{jj}$, $\alpha_{ij} = \alpha_{ji}$. This equivalence of values describing the effect of each species on its own growth rate versus on the growth rate of the other species does not imply equivalence of species. Ref. [16] emphasizes that the identity of an individual matters to the extent that it determines the amount of competition coming from its own species relative to that of the other species, if for no other reason than they will not have precisely the same abundance. If one failed to recognize the definitions of parameters in the Lotka-Volterra model, one could misinterpret the implications of having equivalent parameter values. For example,

there could be tradeoffs that stabilize coexistence and go unrecognized in models like this, if one failed to see that such tradeoffs can contribute to the parameter relationship, such as $a_{jj} > a_{ij}$. Thus, it is important to recognize the underlying assumptions of a model.

Ref. [15] made a different point, that it is not informative to test the hypothesis of sameness in a low-dimensional model, regardless of whether or not sameness is defined in this symmetry sense.

Equalizing mechanisms

Equalizing mechanisms have been defined as 'those reducing the magnitude of the fitness difference' between species ([17], p. 347). In this context, the term 'fitness difference' does not refer to per capita growth rate, but rather comes from a term in an equation of population growth rate. This term comes about by decomposing the equation into two additive terms, one that includes interspecific competition and one that does not. Based on this isolation of the equalizing and stabilizing terms, Ref. [17] refers to the situation where there is no 'fitness difference' (both species have the same value for the equalizing term) as 'symmetric.' One way of thinking about this term is as an indication of similarity of rates. For example, if two species have similar mortality rates, the value of this term could be similar. Although equalizing mechanisms have been described as a neutral force that operates together with niche differences to explain diversity [18], it does not relate to functional equivalence.
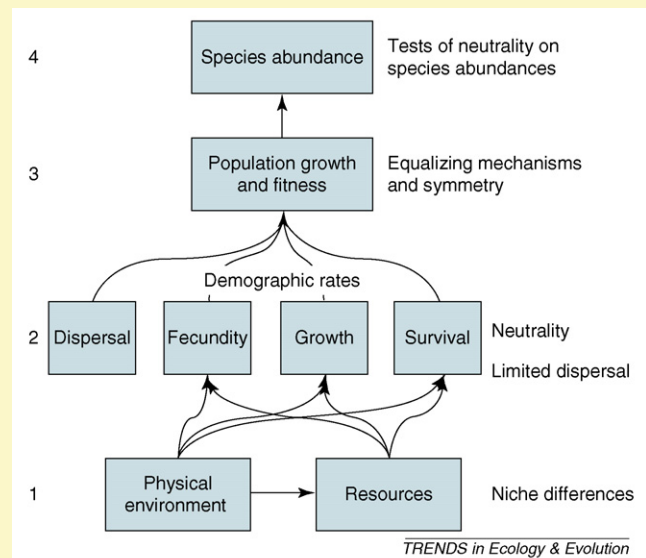
Figure I. One way of organizing terms used in the neutral debate, by level of organization. Niche differences (level 1) influence demographic rates (level 2), but similar demographic rates do not imply similar niches. Tests of neutrality on species abundance patterns (level 4) are far removed from niche differences and demographic rates.

that a neutral interpretation of models can miss the fact that stochastic elements themselves generate the dynamics of interest. Like the sources of confusion mentioned above, this problem with neutral theory has not been part of the debate, both sides arguing the relative importance of stochastic forces in nature instead of recognizing them as existing only in models. Productive application of models requires recognition that stochastic elements stand in for unknown processes. In ecological models, stochasticity is typically implemented in ways that assure species differences, whether or not those differences qualitatively change dynamics. Because the neutral view of biodiversity maintenance is without expli-

cit process (rather than acknowledge species differences, it relies on models having stochastic elements that make species differences implicit), it is hard to relate to real-world problems. At a time when ecologists have shifted so much attention to the neutral explanation for biodiversity, a journal such as *Conservation Biology* has essentially ignored it (Figure 1b), apparently finding little that could apply to real organisms faced with actual extinction threats. The rise of neutral theory as the dominant conceptual framework might have a cost. I suggest that ecologists can fail to appreciate this cost, and I mention some of the alternative research directions that hold more promise.
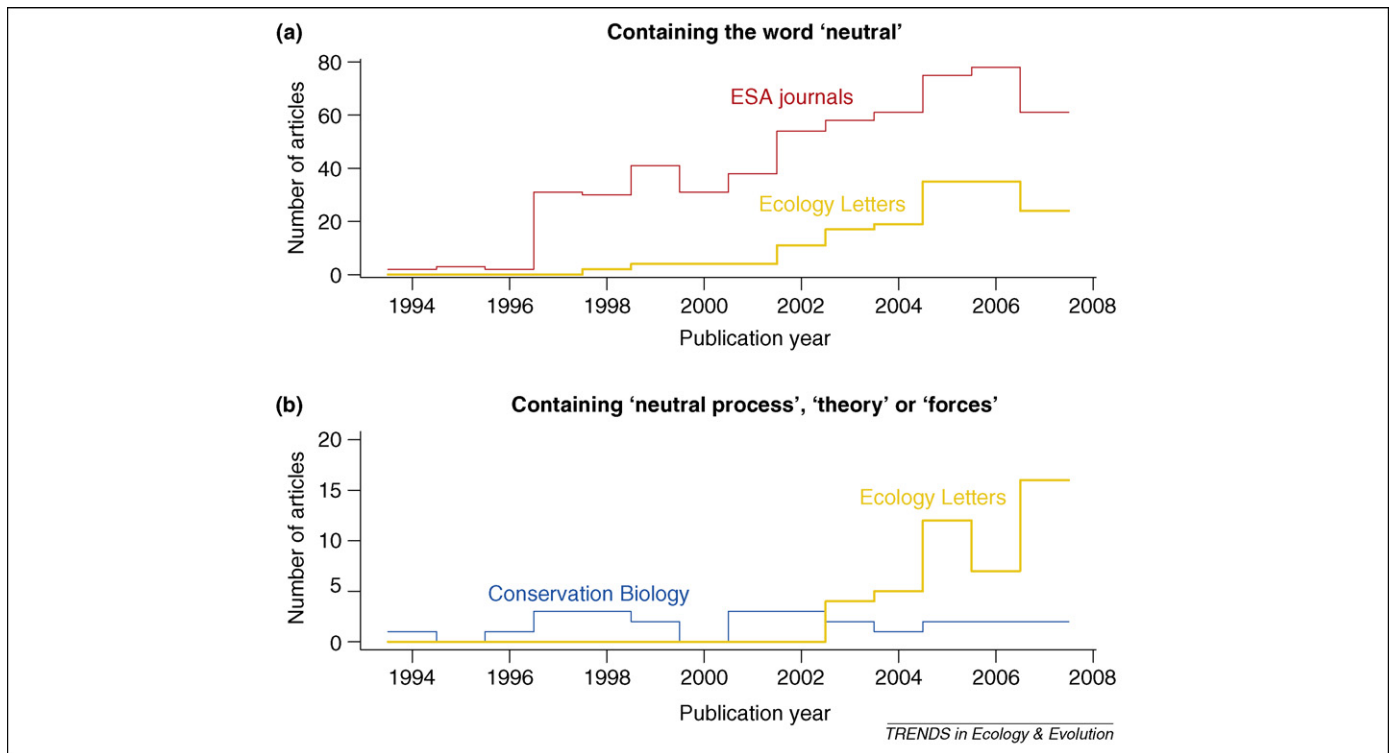
Figure 1. The number of articles since 1994 containing **(a)** the word 'neutral' or **(b)** any of the terms 'neutral process,' 'neutral theory' or 'neutral forces.' Totals extend through October 2007. Because the term 'neutral' is applied in molecular evolution and in policy, I have used terms more closely linked to the neutral theory of biodiversity for the analysis of articles in *Conservation Biology* (b), in which the word 'neutral' alone often refers to population genetics and policy (e.g. 'policy neutral'). In *Ecology Letters* (a), the word 'neutral' is overwhelmingly associated with neutral theory.

Stochasticity can be confusing

Models to explain biodiversity necessarily include only a subset of the processes that occur in nature, with stochastic elements needed to stand in for the leftover variation. A small fraction of the many ways in which species differ have been observed, quantified and included in models. A useful attribute of models is simplicity, which motivates researchers to introduce stochasticity to take up leftover variation. This is the case both in forward models (a model that starts with parameter values and predicts data) and in so-called inverse models (a model that starts with data and estimates parameters). What is defined in models as stochastic versus deterministic depends on knowledge and objectives. Models can be stochasticized if we cannot identify important causes, if relationships are more complex than we care to specify deterministically or if we do not know how to specify the interactions. Still, processes perceived as stochastic at one level of abstraction have explanations at another.

To simplify the more technical discussion of Ref. [15], consider a word model like this:

$$\text{response} = \text{f(covariates, parameters)} + \text{error}$$

(the additive structure is not critical to anything I will say about this model). The first term is deterministic and explanatory. It crudely states how processes contribute to the response. The second term is not explanatory. It takes up uncertainty by representing variation we cannot account for in the first term. Both terms are important, because only part of the variation in the response can, by a simple function, be described or attributed through obser-

vable processes to covariates. One way to view progress in science is what occurs when variation moves from the second term (unknown) to the first term (known). As information accumulates, we can incorporate more process in the first term. The neutral literature advocates movement in the opposite direction: strip away known processes and focus on rejecting a model that is predominantly stochastic, one that contains less than what is known. There are many good reasons to build simple models with stochastic terms. With neutral theory, it is not simplicity so much as the interpretation that can be reconsidered.

Confusion over stochasticity

One of the largest contributors to the emergence of neutral theory is the interpretation that the second term represents an explanation or force for maintaining coexistence. Perhaps the most common example concerns 'demographic stochasticity,' the idea that fluctuations in birth and death rates are inherently stochastic and thus can serve as a mechanism for coexistence that does not involve actual species differences. Two points to stress here are (i) there is no science that says demography is inherently stochastic, and (ii) we can neither interpret demographic stochasticity in models as a mechanism nor as being consistent with the assumption of species sameness. Here I summarize the more technical discussion of Ref. [15].

First, there is no evidence for stochasticity in nature at observable scales. Stochasticity is an attribute of models. When an individual gives birth or dies 'at random,' that event results from real processes. Those processes might be

unknown or they could result from processes we choose not to include in a model. Through massive investment and decades of study of our own species, we have identified many sources of mortality and linked them to risk factors. In light of the unusual level of knowledge of our own species, we know that many of those risk factors differ from those of other species, even from species having mortality schedules not too different from our own (recall that neutralists infer sameness from observations of similar demographic rates).

Is there a limit to knowledge of mortality risks? Of course, but lack of information is not to be confused with the existence of a stochastic force. The more we learn about a process, the 'less stochastic' it becomes. For most species, we know little more than the annual mortality rate. Lacking additional information, this annual rate represents an average value that is applied to the species as a whole. As soon as we identify an explanatory variable, be it age, size, resource availability, diet or infection status, the stochasticity is reduced. We now recognize the population as a mixture of individuals subject to different risks. Conditioned on the known covariate, the variance declines (see Ref. [15]). This occurs because we have moved variation from the second term (unexplained) to the first term (explained). By understanding more of the factors affecting mortality, we continue to decrease the stochasticity in the model. The fact that there might be a practical limit to how much we know does not mean that there exists some residual inherent stochasticity. For example, mortality is treated as deterministic in many models of annual plants—beyond a specified age, an individual is dead with probability 1. This deterministic treatment is synonymous with 'complete knowledge,' obviating the need for stochasticity. Like other factors that define niche differences, this example requires knowledge of a covariate, age. Because knowledge is rarely complete, we often need stochasticity in models.

The fact that stochasticity represents a way of simplifying models leads directly to the second point that is missed in the neutral debate. When a stochastic influence is included for each species in a population model, species are by definition different. This is the case regardless of whether or not the stochasticity qualitatively impacts the outcome of competition. In a stochastic model, we cannot interpret species having identical parameter values (e.g. the same birth and death parameters) as being identical— each is affected by a sequence of fluctuations different from the sequence experienced by another. The fact that the differences are described as "random" does not change the fact that they are different. In a lottery model [17] fluctuating recruitment success is important for coexistence. If species always and everywhere have the same recruitment success in a lottery model, there would be no coexistence. Stochasticity in the model allows species to differ. To interpret this mechanism, we need to consider what might cause those fluctuations in nature. Failure to recognize stochasticity as a surrogate for processes that introduce species differences makes it seem that diversity might be enhanced if species are more alike. Rather than address how species differ, neutral theory concerns models where the process is simply unspecified. When we do specify

species differences in models, coexistence is achieved by finding ways to reduce interspecific competition.

Given that only a small part of the variation in nature can be linked to specific regulating factors, and that stochasticity in models has limited capacity to generate diversity, how do we proceed? Before discussing why it could be productive to shift emphasis to process-based studies that move beyond the traditional emphasis on a few limiting resources or to a new emphasis on neutrality, I turn to ideas that have become part of the neutral discussion and discuss why they do not provide evidence for neutral mechanisms in nature.

Some points of confusion
Point 1: equalizing mechanisms explain coexistence of competitors
Since the introduction of neutral theory, there have been efforts to unify niche versus neutrality. Some view it as a 'false dichotomy,' and recommend efforts to determine how niche and neutral processes operate together to generate coexistence through a balance between stabilizing forces (e.g. factors that reduce interspecific competition) and equalizing mechanisms (Box 1), the latter referring to equivalent fitnesses [17]. Several recent papers discuss a connection between neutral theory and equalizing mechanisms [14,18–20]. The notion that there are equalizing mechanisms in nature suggests that being more alike can promote diversity, sameness being defined as having equivalent fitnesses. In any model of stably coexisting species, standard fitness metrics for all species are, on average, $R_0 = 1$ and $1/N \, (dN/dt) = 0$. However, this fitness equality means the populations are not changing in abundance; it does not mean that they are 'equal,' or even similar.

The idea that species sameness helps to explain high diversity seems to contrast with 'limiting similarity,' the idea that being more similar makes it harder for species to coexist [21,22]. In the original terminology, stabilizing mechanisms were defined as classical niche differences [17] (Box 1). Equalizing mechanisms are not actual mechanisms, but rather a statement about similarity in terms of some parameter values that do not have a simple biological interpretation (some confusion comes from equating a density-independent contribution to population growth with 'fitness differences,' which is not what this term actually represents; see Box 1). The concept of equalizing mechanisms does not represent a new 'process' or 'force' for coexistence. It can be viewed as a tool for understanding model behavior [17].

As an example of the effect of making parameter values 'more equal,' consider small fluctuations added to a model that make a small contribution to model behavior. Coexistence depends on structure and parameter values contained in the deterministic relationships. This deterministic component might say that the two species occupy similar niches and compete strongly, in which case they will probably not coexist in the model. The stochastic element might involve distributional assumptions that tend to promote coexistence, say, if they allow opportunities for one species to do well when the other does poorly, and vice versa. But if the magnitude of the stochastic

contribution is small, this tendency to promote coexistence has little effect on dynamics. Making some parameter values more similar might magnify the relative contribution of stochastic elements. To properly interpret this effect requires clarity about how the models go about 'making species more similar,' and what stochasticity represents. If species are made more similar by making them compete more, in the sense of niche overlap, it will be harder to obtain coexistence, despite stochastic terms. However, if species are made more similar by assigning them similar parameter values (e.g. a density-independent growth parameter), there is much greater tendency for stochasticity to have impact as parameter values for the two species tend to converge. As demographic rates are made similar, dynamics are increasingly influenced by stochastic elements, because these elements now account for most of the difference between the two species. However, the stochastic elements are specified only in distributional terms, not as distinct processes—it would be helpful to allow that something is determining the advantages and disadvantages for each species. The model does not contain a 'neutral force'; it is only 'neutral' of information. The fact that this shifting advantage occurs at 'random' does not change the fact that the species are different in the model.

It remains the case that models of competing species find coexistence by reducing interspecific competition. Models do not predict that competitors are more likely to coexist if they are more similar in any functional sense (Box 1). Instead, if species do not compete as strongly and as consistently as most models assume, then diversity is much easier to explain. This diminished role for competition implies species differences or ways to limit competition (e.g. spatio-temporal separation), not sameness.

Using similar demographic rates or fitness as a metric for species sameness can cause more confusion than illumination. Demographic rates and fitness reflect overall population health (level 2 in Figure I in Box 1). They are influenced by competition (level 1 in Figure I in Box 1), but similarity of demographic rates does not imply equivalence in any functional sense. Whereas competition necessarily influences demographic rates, the converse is not true: similarity of growth and mortality rates provides no insight for functional equivalence or the level of competition. There is no need to explain coexistence of species simply because they have similar demographic rates. The concept of equalizing mechanisms does not mean that sameness in any functional sense makes communities diverse.

Point 2: symmetry can make a model neutral

Symmetry is a second concept that can be valuable for assessing model behavior, but it has not yet been shown to support the existence of neutral forces in nature. Species are viewed as 'symmetric' if we could exchange their parameter values without changing model behavior [16]. If swapping parameter values between species or individuals of a species has no effect on model behavior, then one might conclude that species are functionally equivalent [23]. The symmetry concept has utility as a model sensitivity tool. For example, one study [24] swapped submodels for different species in the Sortie

model to help identify aspects of life-history differences that affect model predictions.

Despite the utility of the concept for discussing model behavior, symmetry tests do not demonstrate equivalence of species in nature. As a simple example, consider two species: call them 'red oak' and 'red maple.' We estimate several parameters for each species, as few as two to perhaps as many as ten (the number of parameters is not the issue), we enter them in a model and analyze the behavior of the model. Some parameter values will be similar for the two species, and others might differ, depending on sample sizes, the sites from which we collected data, the times when the samples were obtained and the many variables that are unmeasured. Upon swapping the parameter values between individuals of different species, we find that the model predictions do not change much (e.g. the species still coexist, or not). What does this experiment demonstrate? It shows that the behavior of this specific model is insensitive to these parameter values. However, it does not tell us that red oak is the same as red maple. The few parameters we are able to estimate (typical ones include growth rate, survival rate and light response for a leaf) are a small subset of the ways in which red oak and red maple differ. Few, if any, of these parameters have overwhelming impact on trophic interactions. Additionally, parameter estimates can be similar despite large differences in the factors controlling them. For example, growth rates and survival rates for species limited by different resources are indistinguishable at times and differ at other times [15]. Most of the processes that affect demography (e.g. disease) are not in the model. Even such well-known hypotheses as Janzen-Connell, where species-specific pathogens might influence mortality rates, have not been adequately measured and are not included in biodiversity models [25,26]. Showing that parameter values fitted to observations have symmetry in models does not tell us that the species from which they derive are equivalent in nature.

Point 3: limited dispersal as functional or demographic equivalence

The recent reclassification of limited dispersal as a 'neutral force' could be viewed as one of the ways in which confusion can arise when specific processes are replaced with a process-free view of coexistence (Box 1). I do not know how limited dispersal came to be viewed as a neutral force. It has long been known that limited dispersal affects dynamics of competing species by increasing interaction with conspecifics or by allowing competition to play out locally as opposed to globally. Short-distance dispersal introduces a scale of interaction, with effects that depend on scales of competition and disturbance and on the intensity of competition (reviewed in Ref. [27]). Short-distance dispersal does not have much impact in simple models when competition between species is weak, because species coexist anyway. When competition is intense, a 'colonization–competition' tradeoff provides an advantage to a competitively inferior species by allowing it to arrive at and rapidly exploit sites not yet reached by a dominant species with a lower colonization capacity [28,29]. Short-distance dispersal can slow competitive exclusion in simple models,

because offspring tend to compete more with conspecifics, at least in the short term [30]. Thus, dispersal clearly has relevance to all spatial models, regardless of whether or not they are viewed as being neutral. It is a real process that differs among species and evolves by natural selection. The new explanation of the role of dispersal in community ecology could be viewed as a harmless semantic shift. On the other hand, there could be a cost associated with redefining processes like dispersal in terms of a process-free theory of nature (see below).

Back to process

Many models of species interactions reflect an increasing recognition of the need to better represent underlying processes [31]. The limitations of low-dimensional models of biodiversity are becoming increasingly apparent. With a small number of parameters, we cannot predict diverse assemblages of competing species. However, it remains hard to see how progress would come from viewing species as interchangeable or from rejecting the hypothesis that they are not. Neutral theory highlights limitations of traditional theory, but does not help resolve them. Instead, neutral theory substitutes for the real mechanisms that are already known models with less process and more stochasticity. Instead of models that make the actual processes explicit, this low-dimensional alternative embraces models that are stripped of process, and instead relies on random elements to provide the species differences that contribute the important dynamics. It suggests scientific progress from rejecting a model already known to be false. A proliferation of explanations based on stochastic regulation and neutral forces is promoting a view of nature as inherently stochastic, explainable without process. Concepts such as 'equalizing mechanisms' and 'symmetry' can be confusing, but regardless of what authors intend by them, it is important to recognize that they do not make neutral theory any more useful.

A different reaction to limitations of traditional models is to explicitly investigate the processes that are misrepresented or simply left out. This approach aims for less stochasticity, not more. Rather than continuing to emphasize traditional, overly simplistic models of 'interaction strength,' which contain parameters that are only crudely related to species interactions, further progress might require explicit treatment of the actual processes involved, as is being done with succession [31–33], species interactions [34], dispersal and migration [35–37], disease [38,39] and responses to global change [40,41], to name a few. Rather than strip away what is known, models can be used to synthesize knowledge [42–44]. Stochasticity still plays a critical role in such models. Unless models make accommodation for the unknown sources of variation in realistic ways, data suggest apparent species differences but not the ones that could cause models to predict high diversity [45,46].

Understanding diversity will require more complexity than traditional models, not only on the process side but also in the attention to how stochasticity is represented. Models do not have to be large—added complexity needs justification. I am making a different point, that making models smaller (less process) emphasizes the stochastic

contribution, which needs to be recognized as such. Stochasticity provides an alternative to deterministic detail, but some structures will be more capable of capturing variation than others. Environment–competition correlations can enter through stochastic terms [47], as can differences among individuals that reflect high-dimensional niches [15,45,46], and lags [47], each in ways that can affect dynamics. These approaches each allow for dependence structures more complex than simple uncorrelated noise. Still, they might not adequately substitute for a more explicit treatment of processes behind the variation and correlations. For instance, episodic drought can affect demographic rates of different species in different ways. If competitors are also affected, there is an environment–competition correlation—during drought, competition can change. A correlation between environment and competition might enter a model through stochastic terms (e.g. a covariance matrix), but it might be better represented by an explicit treatment of different species responses to drought and how those responses affect competition. Ecological models are enriched by judicious use of stochastic elements. The need to keep models simple motivates stochastic treatment, but only as a surrogate for processes.

Beyond neutral science

The unified neutral theory can be seen as a shift to a process-free theory of biodiversity. Aside from the limited value of rejecting a null hypothesis of no difference, a result that does not help us understand a high-dimensional world, there could be more direct costs. A preoccupation with neutral theory could marginalize biodiversity science, competing for resources with process-based studies, while having little to offer conservation and policy. A manager faced with a species at risk knows that species are different and accepts the need to learn more about this particular species to save it. At a time when a large number of process-based observational and experimental studies are informing conservation, the unified neutral theory is having impact only in the basic science journals and not those devoted to conservation of diversity. A divergence of science and application (Figure 1b) might be viewed as a harmless preoccupation of theorists. It is also possible that resources increasingly devoted to a process-free theory of nature can compete with the important task of understanding the processes that control biodiversity.

What is the alternative approach to understanding biodiversity? Neutral theory contributes to the recognition of the limitations of low-dimensional niche models, a problem eloquently described a half-century ago [48]. There remains much to learn about the few resource axes that forest ecologists have long recognized as limiting for plant growth (e.g. annualized light indices, average soil moisture and indices for a small number of nutrients). However, a broader set of factors contributes to biodiversity and collectively can contribute more variation to population success than do the low-dimensional niche differences of traditional theory [45,46]. Analysis of real processes, which can require larger models, is an alternative to the study of sameness, which is now being done with simple models where stochasticity dominates dynamics. Complexity and

uncertainty need not be celebrated or studied for their own sake, but embraced out of desperation, recognizing that the only thing worse than acknowledging complexity is ignoring the fact that it might be overwhelmingly important.

When two sides disagree, it is tempting to look for unity somewhere in the middle, an explanation that blends elements of both. I suggest that there could be more support not for a middle ground between 'niche versus neutral,' but rather one of higher dimensionality [15,46]. Acceptance of the inadequacy of low-dimensional models makes the explanation for high diversity less daunting. Nature demonstrates that the only requirement for staggering levels of diversity is that species now and then do well enough to offset the mortality losses that can dominate much of the time. Demonstration of this reality is not dependent on our capacity to write a model that predicts high diversity. Competition needs to be limited in space and time, a requirement that niche differences can fulfill, provided that they are not low dimensional. We know that a model having species differences along many dimensions could explain diversity (e.g. [49]). We do not yet know what those dimensions are, but we do know what many of them could be, and progress will require that we study the possibilities. The structuring of unexplained variation among individuals is consistent with this view [15]. Clearly, high diversity depends on species differences, and better understanding will require deeper insight as to those differences. It will not come from rejecting the hypothesis of sameness, but from research directed at potential mechanisms.

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