

Self-organized similarity, the evolutionary emergence of groups of similar species

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Ecologists have long been puzzled by the fact that there are so many similar species in nature. Here we show that self-organized clusters of look-a-likes may emerge spontaneously from coevolution of competitors. The explanation is that there are two alternative ways to survive together: being sufficiently different or being sufficiently similar. Using a model based on classical competition theory, we demonstrate a tendency for evolutionary emergence of regularly spaced lumps of similar species along a niche axis. Indeed, such lumpy patterns are commonly observed in size distributions of organisms ranging from algae, zooplankton, and beetles to birds and mammals, and could not be well explained by earlier theory. Our results suggest that these patterns may represent self-constructed niches emerging from competitive interactions. A corollary of our findings is that, whereas in species-poor communities sympatric speciation and invasion of open niches is possible, species-saturated communities may be characterized by convergent evolution and invasion by look-a-likes.

biodiversity | coexistence | competition | evolution | niche construction

One of the classical puzzles in biology is the question how so many species can coexist in nature (1). Niche differentiation is obviously an important aspect. However, it is clear that other mechanisms must be involved, as similarity in coexisting species is often striking. For instance, in planktonic communities, impressive numbers of species coexist in a seemingly homogeneous habitat with little scope for niche differentiation (2), and in tropical rainforests numerous similar tree species coexist (3). An explanation that is close to the intuition of many naturalists is that the niches of all of these seemingly similar species really differ in aspects that are not easily detected. Another, slightly less intuitive class of explanations for the coexistence of so many species in nature is that various mechanisms may help to prevent competitive exclusion. Examples are predation (4, 5), chaotic population dynamics (6, 7), environmental variability (2, 8, 9), and incidental disturbances (10, 11). The interaction of such mechanisms at multiple scales of space and time may maintain much of the biodiversity observed in nature (12, 13). A rather different aspect is stressed in the neutral theory of biodiversity (3, 14) that sparked some controversy over the past years (15). The essential assumption is that species are equivalent, so that no species can out-compete another. Although it may be argued that species sharing an ecological niche and facing the same fundamental tradeoffs will coevolve to have roughly the same competitive power (16), real neutrality is of course a limit case (17), and the results have been shown to be quite fragile to relaxation of the assumption (18, 19). Nonetheless, one may ask whether strong similarity might in some way still help to facilitate coexistence.

To explore how we might bring the seemingly disparate worlds of niche and neutral theory together, we use a classical Lotka–Volterra competition model

$$\frac{dN_i}{dt} = rN_i \left(K_i - \sum_j \alpha_{i,j} N_j \right) / K_i \quad i = 1, 2, \dots, n; \quad \alpha_{i,j} = 1,$$

[1]

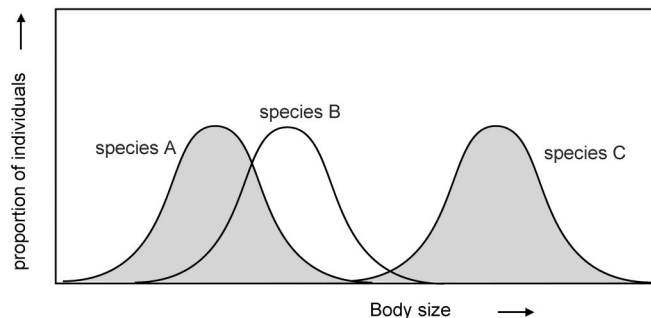


Fig. 1. To study competition, we place species randomly along a hypothetical niche axis. To facilitate an intuitive interpretation, one may think of the niche axis as a gradient that is related to the size of organisms. If we assume that individuals of the same size compete strongest, niche overlap and resulting competition coefficients can be computed (45) for sets of species of given size distributions (see *Methods*).

where N_i is the density of the species i , r is the maximum per capita growth rate, K_i is the carrying capacity of species i , and $\alpha_{i,j}$ is the competition coefficient scaling the effect of species j on species i . We chose the competition coefficients in such a way (see *Methods*) that the model mimics competition between species along a niche gradient (Fig. 1).

Pattern Formation in Communities of Competing Species

As a first approach to analyze how competition along a niche axis would structure a community, we place a large number of species at random positions on an infinite niche axis (mimicked by making it circular, see *Methods*) and compute the resulting competition coefficients. We then run the competition model to see to which state it converges. Although one would intuitively expect that the survivors of this competition game would be species that are equally spread out over the niche axis, the surprising result is that simulations converge to a very long transient pattern of self-organized lumps that contain multiple coexisting species of similar size (Fig. 2a). Numerical experiments (not shown) revealed that the distance between species lumps on the niche axis depends on the niche width of the species in the sense that the lumps are spread further apart if the standard deviations of the species size distributions (the niches) are broader. Thus, coexistence of different lumps is a straightforward effect of avoidance of competition. However, species that are similar enough apparently escape this rule of limiting similarity and may coexist within the lumps.

Although this pattern of lumpy coexistence is transient, it can exist for thousands of generations (defined as $1/r$). Eventually one species in each hump survives, giving rise to the intuitively expected pattern of equally spaced single species. However, it has been argued that long transients may be much more important than

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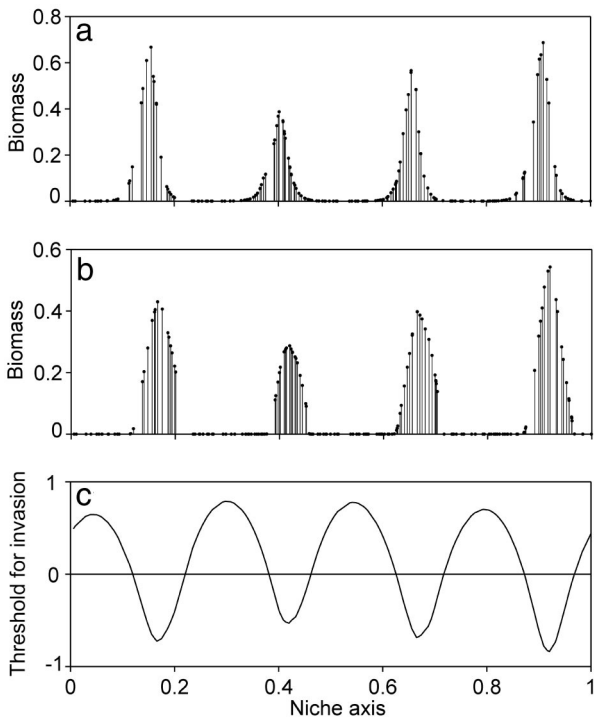


Fig. 2. Self-organized lumpy patterns in the abundance of competing species along a niche axis. (a) A transient state after a simulation run of 1,000 generation times. (b) A stable pattern of species abundance reached after 5,000 generation times in the presence of mild density-dependent losses ($g = 0.02$, $H = 0.1$, Eq. 2). (c) The competitive threshold for invasion of a new species expressed as percentage deviation of its carrying capacity (K) relative to that of the resident species is lowest in the species lumps, showing that these represent relative windows of opportunity for invasion, and attractors in the fitness landscape. Note that the relatively low predation loss at low densities allows starting invaders to enter with a competitive power (K) slightly below that of residents.

previously recognized (20, 21), and the rather persistent pattern of lumpy species distributions in our simulations may be an example in case. In fact, the extreme slowness of competitive exclusion among similar species is in line with what can be observed in simple two-species Lotka–Volterra models where the time to displacement tends to infinity as species become equivalent and their zero-growth isoclines coincide (17).

The apparently weak forces of competitive displacement in our lumps of species suggest that it might be relatively easy for the numerous processes known to reduce the risk of competitive exclusion to stabilize the coexistence in our species lumps. As an example of such a mechanism, we take top-down control because there is increasing evidence that natural enemies including pathogens are responsible for preventing most species from becoming very abundant (22, 23). We explored the effect of such a regulation assuming losses to increase (up to a maximum g) when population density exceeds a threshold (H)

$$\frac{dN_i}{dt} = rN_i \left(K_i - \sum_j \alpha_{i,j} N_j \right) \left/ K_i - g \frac{N_i^2}{N_i^2 + H^2} \right. \quad [2]$$

Indeed, this leads to permanent coexistence of similar species in lumps while leaving the gaps empty (Fig. 2b). The result is robust against change of the niche axis from circular (“infinite periodic”) to finite linear. The only change here is that there is an edge effect in that the lumps become somewhat narrower and species more abundant toward the ends of the niche axis (Fig. 6a, which is published as supporting information on the PNAS web site).

Note that, in view of earlier findings (4, 5), it is not surprising that predation stabilizes coexistence. Indeed, other processes known to facilitate coexistence (2, 4–11) would likely do the same job. What is new here is not the coexistence *per se*, but rather the self-organized pattern in which stable coexistence is found only for sufficiently similar and sufficiently dissimilar species and not for species of intermediate dissimilarity. In other words, not the lumps but the gaps are the surprising thing.

Invasion Resistance

It seems counterintuitive that coexistence can become easier if two species are more similar. After all, their competition becomes more intense. This apparent paradox can be explained by a rather universal mechanism. In situations where species are far apart in niche space, intermediate positions between these species are open niches (and obviously the best places for new invaders). However, it follows from classical niche theory that as niches of resident species become more closely packed, the positions between the species turn into the worst places in the “fitness landscape” (24). As more species interact, it becomes increasingly difficult to grasp the net effect in an intuitive way, as we end up with an intricate balance between direct and indirect competition effects. For instance, one can imagine that two competitors in a lump will facilitate each other indirectly by suppressing a common competitor that takes an intermediate position on the niche axis between them.

The counterintuitive phenomenon that competition in species lumps may be less severe than in the empty gaps can be revealed in our self-organized communities by looking at the critical conditions for new species to invade successfully at different points at the niche axis (Fig. 2c). The spaces between the species lumps can only be invaded by more competitive species, whereas the lumps are relative windows of opportunity in which a new species can invade even if it is a relatively weak competitor. Although the hills and valleys in the fitness landscape look convincing, they are in fact quite subtle. As a result, their effect can be easily disturbed by difference in competitive power between species. If the carrying capacity of the species is drawn randomly, the pattern becomes much less regular (Fig. 6b) due the effect of randomly occurring strong competitors. Thus, although on an ecological time scale the self-organized patterns of lumpy coexistence may be stabilized by processes such as density dependent predation, they are easily overwhelmed by intrinsic differences in overall competitive power between species.

Evolution

To explore how evolution would shape our model communities, we allowed the species to evolve slowly in the direction on the niche axis where they experience less competition (see *Methods*). Starting with species of randomly chosen sizes, the simulated evolution leads to convergence toward stable lumps of similar coexisting species (Fig. 3). In contrast to the patterns generated on an ecological time scale, these evolutionary results are remarkably robust. For instance, although variation in competitive power easily prevents a regular pattern to arise on an ecological time scale (Fig. 6b), evolutionary reshuffling of the species positions in the niche space enabled self-organization into regular smooth patterns (e.g., Fig. 3b) despite considerable random variation in competitive capacity used in these simulations. Obviously, as the relative importance of variation in other selection pressures (captured in our random factor) increases, the evolutionary process obviously becomes less directional and the lumpy pattern becomes more blurred (Fig. 3c and d). In summary, the numerical experiments suggest that on an evolutionary time scale self-organization may be a strong directional force creating stable lumps of similar species even in the face of stochasticity in competitive power and evolutionary dynamics.

Self-Organized Versus Preexisting Niches

An important simplifying assumption in our model so far is that initially (when all of the competing species are at negligible density),

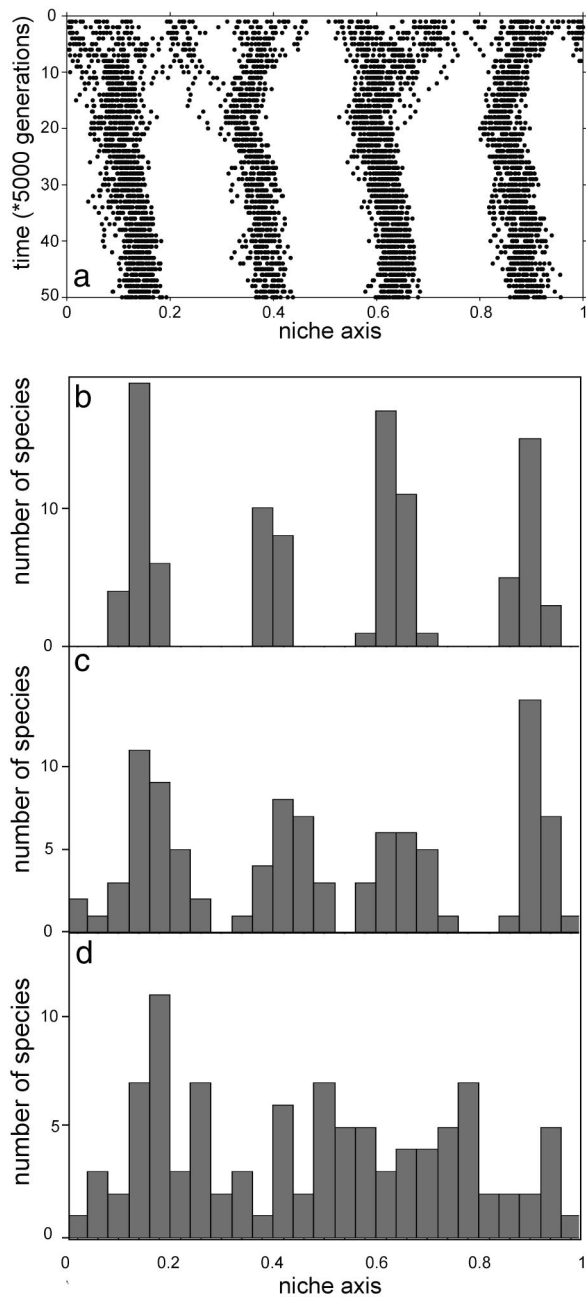


Fig. 3. Simulated evolution of 100 species (dots in *a*) that are initially randomly distributed over the niche axis results in convergence toward self-organized lumps of similar species in the presence of density-dependent losses. The carrying capacity of the species is randomly drawn between 9 and 10. (*b–d*) Resulting frequency distributions of species sizes for increasing values of the parameter representing random variation in other factors that affect evolutionary pressure ($w = 0.025, 0.04, \text{ and } 0.05$, respectively). $g = 0.5, H = 5$, Eq. 2.

each place on the niche axis is equally good. In practice, this will of course rarely be the case. For instance, some body sizes will usually be better than others, as some types of food items, predators, or refugia are more abundant than others. As different species adapt to such preexisting niches, they will converge evolutionary. Indeed, all textbook examples of classical convergent evolution are of this type. An important question therefore is whether convergence to self-organized niches (the species lumps) might still be expected in a world which also has externally determined niches. We explored this by adding a function ($f(L)$) to the model that affects the net

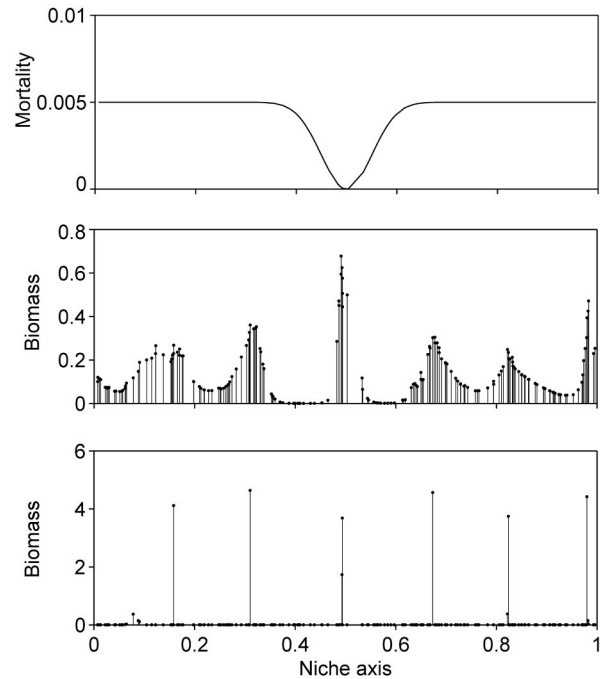


Fig. 4. A slight preexisting niche, simulated by a tiny dip in the background mortality rate around the value 0.5 on the niche axis [*Top*; the function used to generate this particular example is $f(L) = m_A - a(1/2 + 1/2\cos((L + 0.5)2\pi))^2$, $m_A = 0.005 \text{ d}^{-1}$; $a = 0.005 \text{ d}^{-1}$], is enough to function as a “condensation point” that anchors the self-organized pattern of species lumps to a fixed position [*Middle*, after 5,000 time steps; *Bottom*, after 20,000 time steps].

growth in a way that depends on its position (L) on the niche axis, modifying Eq. 1 to

$$\frac{dN_i}{dt} = rN_i \left(K_i - \sum_j \alpha_{i,j} N_j \right) / \left(K_i - N_i f(L) \right)$$

$$i = 1, 2, \dots, n; \alpha_{i,i} = 1. \quad [3]$$

As a first step to see the effect of predetermined niches, we created a single niche in the middle of our niche axis by making mortality rates slightly lower there (Fig. 4). It appears that even if such predetermined niche opportunities are only providing a slight advantage (a dip of 0.005 d^{-1} in a background mortality rate), they may serve as a condensation point that anchors the self-organized pattern (Fig. 4). In the simulations with equally strong competitors in a homogeneous niche space (Fig. 2), coincidental clumps in the random initial species distributions serve as random condensation points to trigger the pattern formation, but apparently this effect is easily overwhelmed by the slightest heterogeneity in predetermined niche opportunity.

To explore a more natural situation, we created niche opportunities that vary randomly over the niche axis. We used a red-noise function on 200 points of the niche axis (25) to create a realistic autocorrelation of opportunity along the axis rather than white noise. Not surprisingly, the resulting preexisting niches do affect the pattern of species distribution along the niche axis if they are strong enough. However, despite substantial external niche forcing (variation of $\pm 0.1 \text{ d}^{-1}$ in net growth rates), regular patterns of species distribution arise that reflect the mechanism of self-organization (Fig. 7, which is published as supporting information on the PNAS web site). In summary, our model suggests that patterns in nature may often reflect a mix of the self-organized patterns and preexisting niche opportunities.

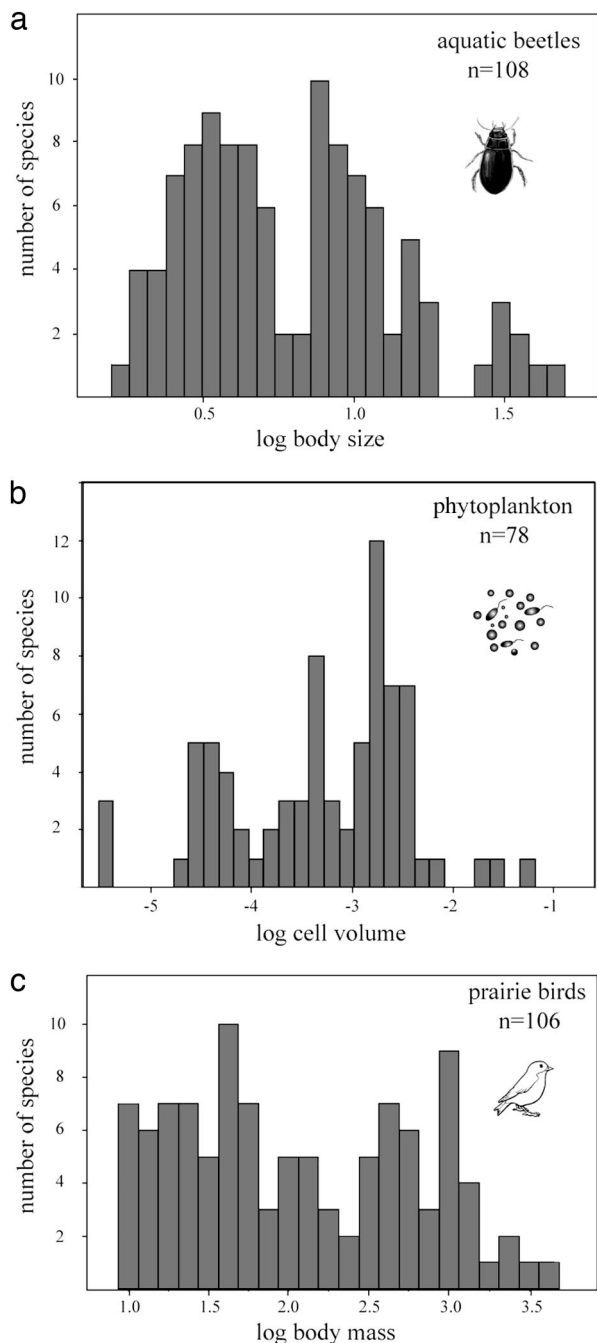


Fig. 5. Size distributions of species in nature often show a lumpy pattern, illustrated here for European aquatic beetles (*a*, data compiled by Drost *et al.*; ref. 46), phytoplankton species of the Dutch Border Lakes (*b*, unpublished data from the RIZA Institute), and American prairie birds (*c*, data compiled by Holling; ref. 38).

between many species in nature, the striking regularity of many of the patterns observed suggests that the mechanism of self-organization we propose may play an important role in many systems too.

Finally, it is worth noting a remarkable link to Hotelling's theory (41) in social sciences suggesting that competition of companies or political parties will often lead to convergence rather than differentiation. In this field of research, the focus is on the problem that such convergence is not in the interest of the public. For instance, having more of the same kind of TV channels is not better (42). By

contrast, the seeming redundancy of similar species in nature may be essential to ensure ecosystem functioning in the face of adverse impacts (43, 44).

Methods

As a starting point to compute competition coefficients that allow us to mimic competition of species for resources along a niche axis (Fig. 1 and Eq. 1) we characterize the width of the niche by normal distributions on the niche axis (L)

$$P_i(L) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(L-\mu_i)^2/(2\sigma^2)}. \quad [4]$$

We assume that competition intensity between species i and species j is related to niche overlap, and thus to the probability P that individuals of the two species are at the same position on the niche axis, which is the product of both probabilities

$$\int_{-\infty}^{\infty} P_i(L)P_j(L)dL. \quad [5]$$

We calculate competition coefficients as the ratio of the probability of matching an individual of competing species j and the probability of matching a conspecific (45), which can be solved as follows (cf. 24)

$$\alpha_{i,j} = \frac{\int_{-\infty}^{\infty} P_i(L)P_j(L)dL}{\int_{-\infty}^{\infty} P_i(L)^2dL} = e^{-\frac{\mu_j^2 - \mu_i^2 - 2\mu_j\mu_i}{4\sigma^2}}. \quad [6]$$

To avoid edge effects, the niche axis is defined circular ("periodic") so that each species has equal numbers of competitors on both sides. Alternatively we checked the effect of having a finite linear niche axis of length L_{\max} . In this case, niche overlap is calculated as

$$\int_0^{L_{\max}} P_i(L)P_j(L)dL, \quad [7]$$

and the competition coefficients are computed as

$$\begin{aligned} \alpha_{i,j} &= \frac{\int_0^{L_{\max}} P_i(L)P_j(L)dL}{\int_0^{L_{\max}} P_i(L)^2dL} \\ &= e^{-\frac{(\mu_j - \mu_i)^2}{4\sigma^2}} \frac{\operatorname{erf}\left(\frac{2L_{\max} - \mu_i - \mu_j}{2\sigma}\right) + \operatorname{erf}\left(\frac{\mu_i + \mu_j}{2\sigma}\right)}{\operatorname{erf}\left(\frac{L_{\max} - \mu_i}{\sigma}\right) + \operatorname{erf}\left(\frac{\mu_i}{\sigma}\right)}. \end{aligned} \quad [8]$$

Time in the model is scaled in units of r (so $r = 1$) and the carrying capacity K is set default to 10. We used a fourth order Runge–Kutta solver as implemented in MATLAB. For the default simulations, 200 species were assigned randomly (following a uniform distribution) to a certain position (μ_i) on the niche axis, each with the same niche width (standard deviation $\sigma = 0.15$).

To mimic evolution, each species iterates its position on the niche axis each 5,000 time steps to increase its fitness. The fitness of the species is defined as the inverse of the carrying capacity that an invader would need to invade successfully, which can be computed from the condition for positive growth at low initial density (24)

$$K_i > \sum_j \alpha_{i,j} N_j.$$

The evolutionary step-size is set to 0.01 niche units, and the species move on the niche axis in the direction where their fitness increases. We also explored the effect of a variable evolutionary speed, by making the step size dependent on the steepness of the gradient in competition pressure along the niche axis. Because this gave basically the same result, we stuck to the simple version for the simulations presented in the manuscript. To capture variation in conditions that would also affect selection pressure we add a random factor to the

evolutionary movement drawn randomly and uniformly between $-w$ and w .

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Supplementary figures

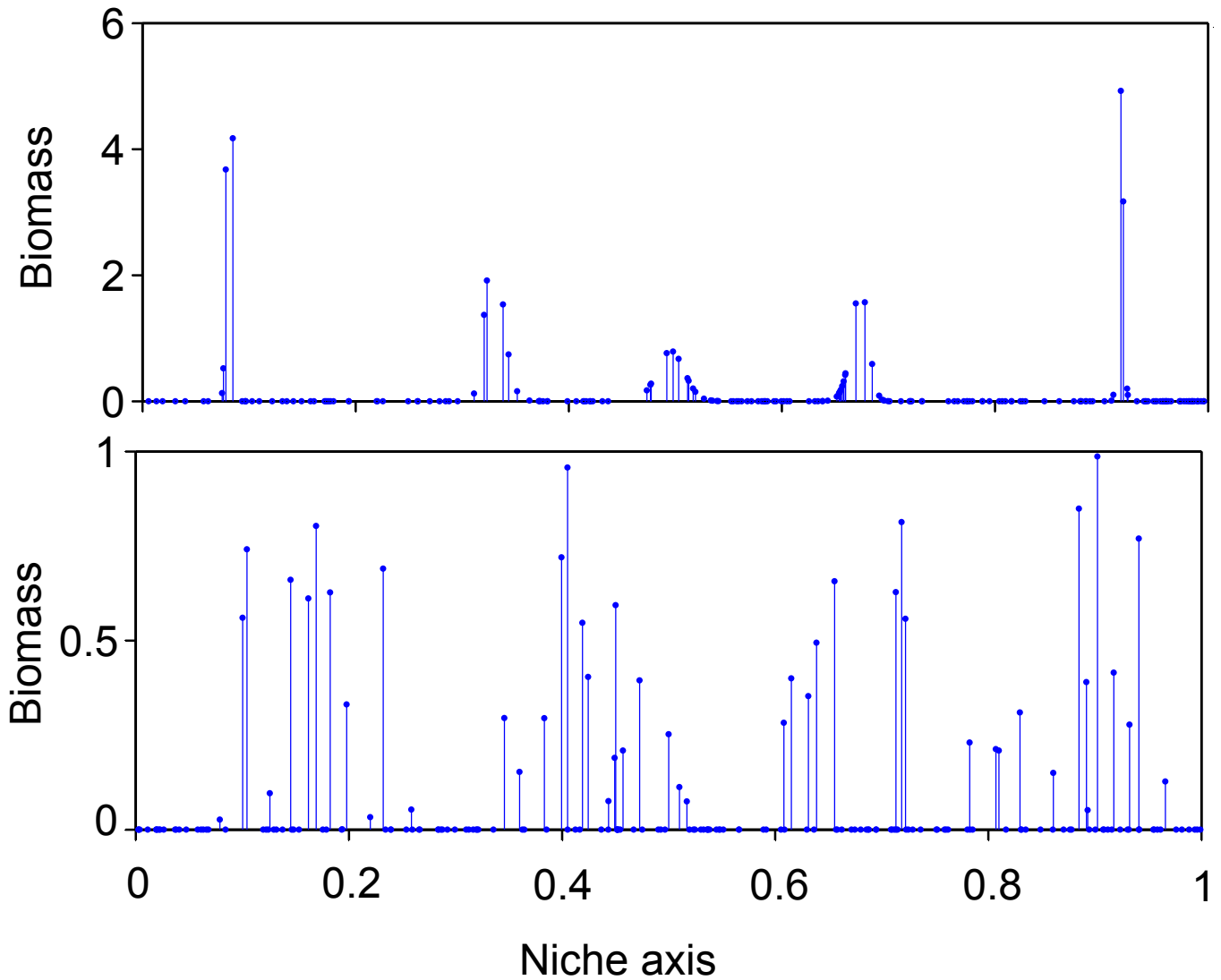


Fig. 6. Effects of finite niche axis (a) and randomness in competitive strength (b) on the patterns. (a) Biomass distribution after 10,000 generation times ($1/r$) in a simulation on a finite linear niche axis of length 1 (parameters as in simulations shown in Fig. 2). (b) Biomass distribution of species after 5,000 generation times ($1/r$) in a simulation in which the K of the species is randomly drawn between 9.5 and 10.5. Other parameters as in simulations shown in Fig. 2.

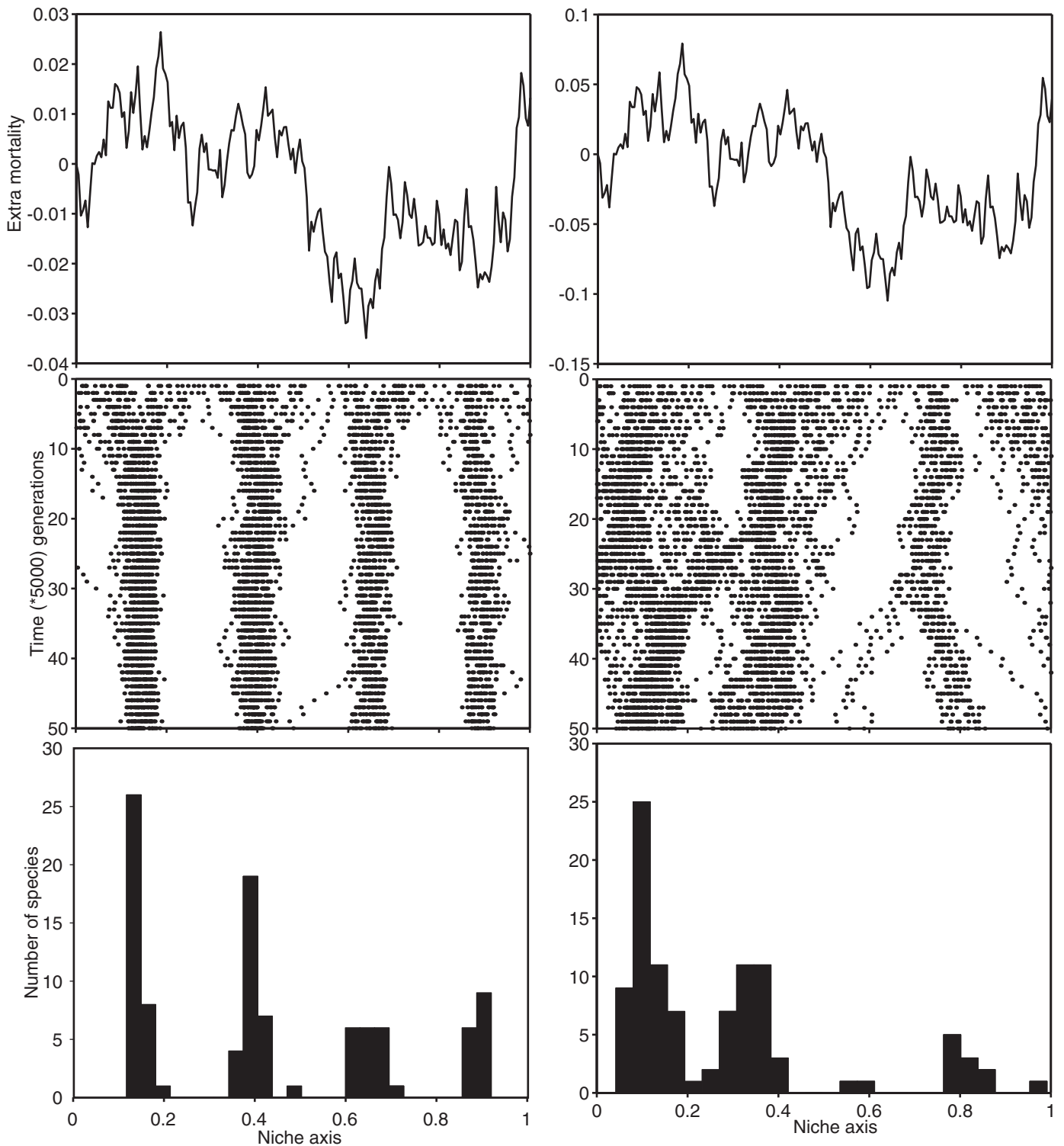


Fig. 7. The implications of interaction between the mechanism of self-organization and the existence of preexisting niches represented by preset variation in background mortality along the niche axis (Top). Simulations of evolution (Middle): in such externally imposed niche landscapes result in remarkably persistent regular spacing of species characteristic of self-organization (Bottom), even though the pattern becomes more distorted as the amplitude of the background mortality differences along the niche axis is larger (Right).

Discontinuities in ecological data

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Historically, ecology has focused on continuous distributions and smooth transitions. Only recently have discontinuities and thresholds become an explicit focus in some areas of ecology, especially in the realm of complex systems. The study of animal body mass distributions has been recognized for its potential to provide insight into the underlying processes shaping animal communities. Hutchinson (1) formalized the understanding of species niches and the potential for competition to shape body mass distributions. However, despite a long history of theoretical and empirical pursuit, the mechanisms driving patterns in body mass distributions remain poorly understood. The work of Scheffer and van Nes (2) in this issue of PNAS demonstrates that community interactions alone can create discontinuous, lumpy distributions of simulated species along a niche axis. Their contribution comes at a time of heightened interest in understanding the mechanisms that may lead to discontinuities in body mass or biomass distributions.

Much of the renewed interest in body mass distributions has followed the publication of a provocative ecological monograph that suggested animal body mass distributions are entrained by landscape structure (3). Holling's paper (3) initially spawned skepticism that body mass distributions are characterized by what Holling termed "lumps" and "gaps." Currently, many ecologists accept that body size distributions are discontinuous, but there remains disagreement regarding the mechanisms responsible. One mechanism proposed focuses on interactions among species living in the same habitat. The strongest and clearest species interaction, other than predation, is competition. However, facilitative interactions are also increasingly recognized for their potential to shape community structure. Scheffer and van Nes (2) demonstrate that species interactions may result in both repulsion and attraction along a niche axis. Attraction occurs when species are similar enough to avoid competition and results in aggregations (lumps) of species, and competition also repulses and disallows species of moderate similarity, resulting in species distributions that are both discontinuous and aggregated. Roughgarden (4) also recognized that species interactions have a strong effect on the distribution of

species and that competitive interactions can lead to both aggregation and discontinuity along a niche axis.

Interestingly, similar patterns have been demonstrated for social-economic systems. Discontinuities have been found in international economic data (5), where the variable of interest was gross domestic product per capita. A discontinuous distribution was found to persist over time, and the overall structure seemed to bound the growth trajectories of individual countries. Explaining the mechanisms behind discontinuities in economic processes is difficult. Barro (6), for example, has hypothesized the existence of a limited number of "convergence clubs" in gross domestic product

Species interactions may result in repulsion and attraction along a niche axis.

data, that is, aggregations of countries whose similar attributes "entrain" their economic performance, a finding that may have parallels in the results of Scheffer and van Nes (2). Further tests of the convergence and convergence club hypotheses have been performed using economic data from other scales, including states (7, 8) and counties in the U.S. Cross-country growth exhibits behavior that is best characterized by means of convergence clubs, in which the economy of the country is autocorrelated with other countries with similar growth, resulting in multiple steady states (9).

City and firm size distributions are also discontinuous (10, 11), suggesting that discontinuities may be a general property of complex systems. Garmestani *et al.* (10) demonstrated that the hierarchical structure of urban systems is discontinuous despite variability in the growth dynamics of individual cities. Growth rates differ by city size (A. S. Garmestani, personal communication), and cities in the southeastern region of the U.S. cluster into size classes, in contrast to the expectation if Gibrat's Law held for these data. Garmestani (personal communication) found that growth is correlated to size, with smaller

cities exhibiting faster growth rates. It is possible that the interaction between endogenous comparative advantages and exogenous trade and transportation patterns triggers discontinuities in city growth rates, which manifest in cities clustering into distinct size classes. A similar mechanism may be responsible for the clustering of firms into size classes within industrial sectors (11). Growth within cities may be viewed as a competitive process leading to convergence and discontinuity, as demonstrated by Scheffer and van Nes (2).

For animal communities, various hypotheses have been proposed to explain the patterns observed in body mass distributions. Energetic, phylogenetic, biogeographical, textural-discontinuity, and community-interaction hypotheses have been advanced to explain observed patterns (12). Energetic and textural-discontinuity hypotheses focus on the scaling of resource acquisition. Biogeographical and phylogenetic hypotheses focus on the role of either geographic or evolutionary constraints on the organization of communities. The community-interaction hypothesis focuses on biotic interactions within species communities, arguing that these interactions shape community structure. Much of the disagreement regarding the mechanisms responsible for discontinuities is due to the scale of the analyses and to the search for single simple, rather than complex interacting, sources of causation.

An explicit embrace of the problem and complexity imposed by scale is often absent from analyses seeking to understand community assembly and structure. The mechanistic hypotheses forwarded to explain discontinuities or other patterns in body mass distributions each applies over a limited domain of scale (Fig. 1; ref. 12), and each partly explains the observed patterns. Community-interaction hypotheses apply to spatially and temporally proximate interactions among species residing within local landscapes. Textural discontinuity and biogeographical hypotheses apply over regional spatial and paleoecological temporal scales, and phylogenetic and energetic hypotheses apply most appropriately over temporally slow and spatially

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See companion article on page 6230.

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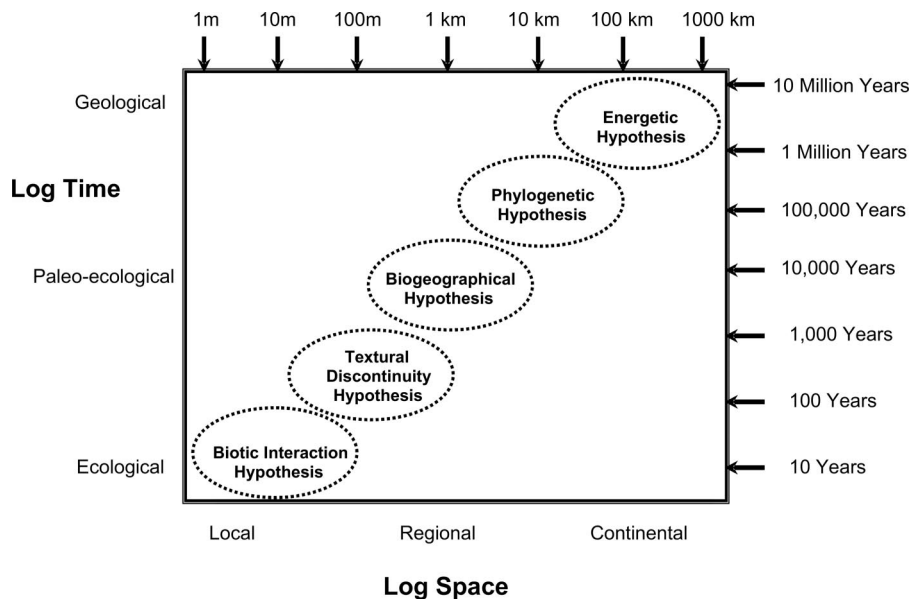


Fig. 1. The scales at which the mechanistic hypotheses explaining discontinuity or multimodality in animal body mass patterns are likely to apply. No overlap among hypotheses is shown, but both the spatial and temporal dimensions of adjacent domains probably interact. Mechanisms acting at larger and slower scales provide nonrandom species pools on which faster and smaller mechanisms work. [Reprinted with permission from ref. 12 (Copyright 2006, Blackwell Publishing).]

broad domains. The scale of appropriate application, relevance, and interpretation varies among the hypotheses.

There is a pressing need for an integration of theory relevant to discontinuities. Peterson *et al.* (13) provided a model that suggests scale has an important role in compartmentalizing species interactions, because species interacting with their environment at the same range of scale are most likely to compete. They suggested that this model would lead to a diversity of functions within a scale range and a redundancy of function across scales. That is to say, there would be aggregations of species

along a size axis, and within body mass aggregations there would be a diversity of used niche space, whereas across aggregations (across scales) there would be apparent redundancy of used niche space. The model of Scheffer and van Nes (2) suggests a mechanism that could generate some of the patterns in the distribution of function within and across aggregations that have been theoretically proposed.

How might the model of Scheffer and van Nes (2) relate to the empirical results of Holling (3) and the numerous studies that suggest a relationship between landscape structure and body

mass patterns (12)? Is it possible to reconcile results that suggest that structure in animal body mass distributions is imposed by the landscape with results that suggest structure emerges from interspecific interactions? Does the landscape provide a discontinuous distribution of structure that is the theater on which species interact? To consider species interactions without context can provide insight but will only partially mimic reality and may fail to capture the unexpected emergence of properties and structures that arise within complex systems such as ecosystems. Szabo and Meszina (14) provide some clues regarding the landscape template. They modeled species on a landscape characterized by resource distributions that vary with scale and discovered that more species were able to coexist when more scales of resource distribution were available and that successful species exploited their environment at scales matched with the distribution of resources.

Scheffer and van Nes (2) provide an elegant example of how species interactions can lead to discontinuous patterns of species distributions. Introducing the complexity of scale into niche interaction models and incorporating potentially self-organizing interactions between the environment and organisms within ranges of scale are the next critical steps toward understanding the structure and assembly of animal communities and the ecosystems on which they reside.

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large number of species along the axis and then evolves the system according to standard equations that govern competition between species. The clumps they observe are transient, and each will ultimately be thinned out to a single species. But 'ultimately' can be a very long time indeed: we now know that transient phenomena can be very long-lasting and, hence, important in ecology⁵, and such phenomena can be studied effectively only by simulation. There is also good experimental evidence for long-lasting coexistence between similar species³.

Why clumps, as opposed, for example, to a slowly thinning, uniform cloud of species along the niche axis? Consider Figure 1. In a community consisting of species A and C, where would a third species be most likely to persist successfully? Species B, positioned halfway between A and C, would be competing strongly against two species, whereas if it was in the same location as A or C it would be competing with only one. In the second case, one species would ultimately exclude the other, but — as pointed out above — this will be on a very long timescale. Of course, this argument depends on the width of the utilization distribution curves shown in Figure 1, and the distance between A and C. But this is an aspect of the self-organization of the species: they move into positions such that the void between them is an inhospitable competitive environment.

The emergence of clumps of highly similar species resonates with a proposed solution to another possible problem: the coexistence of large numbers of species in environments that do not seem to allow for much niche differentiation. Plankton and tropical forest plants are the usual examples. These organisms have a simple set of requirements: light, carbon dioxide and a few nutrients. How is it possible to carve out thousands of distinct niches from so few requirements? It has been proposed that such high numbers of species can coexist precisely because their niches are so similar that exclusion takes a very long time, perhaps on the same timescale as speciation^{6–8}.

So much for the theory: what about the data? Scheffer and van Nes present frequency histograms of species' body sizes for three data sets, which they claim show discrete clumps of species along a niche axis. For these data, body size is the niche axis — body size being the single most important variable determining a species' life history. But whereas two of their examples (aquatic beetles and phytoplankton) seem to occur in discrete clumps of species with similar body sizes, a third (American prairie birds) does not: to our eyes, these bird species look smeared out along the axis with little profound clumping. This impression illustrates the difficulty inherent in making objective judgements about clumping based simply on visual inspection of frequency histograms⁹. Statistical techniques have been developed that do, in fact, identify significant clumping among prairie birds as well as other

ECOLOGY

Paradox of the clumps

Sean Nee and Nick Colegrave

A fresh look at an established model in ecology has generated insights into how species coexist with each other. But it has also raised a vexed question: what constitutes the ecological identity of species?

Classical ecology discovered the principle of competitive exclusion — or, more pithily, 'one species, one niche'. In order to coexist, species must have their own individual way to make a living, otherwise the superior competitors would exclude the inferior. Niches might pre-exist: for example, if there are two types of seed in the environment, this provides two niches for specialist seed-eating birds. Or niches might be created by a species evolving into openings in the 'marketplace' of their ecology.

As they report in *Proceedings of the National Academy of Sciences*, Scheffer and van Nes¹ have revisited a well-studied classical model of competing species and discovered something new. Even in the absence of any environmental discontinuities, they find that assemblages of species will self-organize into clumps of species with very similar niches within a clump and a large difference between clumps. So, paradoxically, species both do, and do not, organize themselves into discrete niches.

In the *Origin of Species*, Darwin asked: "Why, if species have descended from other species by fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion, instead of the species being, as we see them, well defined?" This evolutionary question has a closely related ecological counterpart: how similar can species be to one another and still coexist? A well-studied model for this problem is outlined in Figure 1. The question becomes this. With a single, continuous niche axis, how many species can you pack along it? Or, is there a limit to how close the species can be along this axis?

Although some confusion persists about the answer, the canonical result^{2,3} is that there are, indeed, limits to similarity, and coexistence is

possible only for species spaced out along the axis. In other words, we will observe species occupying distinct, spaced niches even in the absence of environmental discontinuities. This has been analytically proven for an even more general class of models than those studied in the classical period⁴. So this aspect of the results of Scheffer and van Nes¹ is not new. Rather, the novelty of their results is as follows.

Previous analytical results produced single species widely spaced along the niche axis. But Scheffer and van Nes find widely spaced clumps of species occupying very similar niches. Why the difference? Analytical work looks at the long-term equilibria of models, whereas a simulation study allows the system to be observed as it moves towards these equilibria. Scheffer and van Nes take the simulation approach, which starts out with a

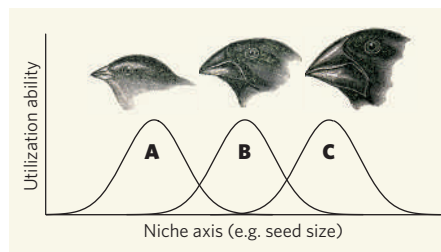


Figure 1 | How similar can species be to one another and still coexist? The question can be tackled by considering seed-eating birds (species A, B and C) in an environment that contains seeds of various sizes. For a given beak size, a bird species can optimally feed on a particular size of seed, and its feeding ability drops off for seeds that depart from this size. More generally, species are characterized by 'utilization functions', which describe the ability to exploit a particular resource as it varies along a niche axis.

MATERIALS SCIENCE

Film review

Free-standing nanofilms are a wonder of membrane technology. Although it's no easy matter to produce them, once made these quasi-two-dimensional objects display fascinating behaviour, combining macroscopic surface area with nanoscopic depth.

A remarkable example is reported by Toyoki Kunitake and colleagues in *Nature Materials* (R. Vendamme *et al.* doi:10.1038/nmat1655; 2006). They have prepared an ultrathin film that is barely visible to the naked eye, but is so flexible it can be drawn through a micropipette hole 30,000 times smaller than its width (pictured).

Despite its flimsy appearance, the film can support a liquid body 70,000 times heavier than its own weight, and withstand significant deformation. It is also stable to various environmental and mechanical stresses. Even more impressively, the film breaks records for size in being several centimetres across, yet only around 35 nanometres thick.

This apparently incompatible combination of strength and thinness is a result of the film's hybrid composition. It consists of an organic polymeric network, which makes it pliable and deformable,



interpenetrated by zirconia (zirconium dioxide), which confers strength and stability. To prepare the nanofilm, the two materials are generated simultaneously from their precursors on a spin-coating plate. The chemical processes involved are quite different: the polymer forms by light-induced crosslinking of its

monomers, whereas the zirconium precursor reacts with residual traces of water in the film's polyvinyl alcohol substrate. Nevertheless, the components intertwine to give nanofilms with properties that make them useful as sensors, actuators and separation membranes.

Maria Bellantone

species⁹. This leaves the extent of overlap between statistical and ecological significance as an interesting and open question.

We can go further: on what basis did Darwin make his assertion about the discreteness of species? This question is distinct from debates about the definition of species in nature. Blackberries reproduce asexually, and it is impossible to agree on how many 'species' there are; but, nonetheless, we all know a 'blackberry' when we see one and do not wonder if it is actually a raspberry. Great tits, blue tits and coal tits are all quite distinct when considered as a set, but are surely just more-or-less continuous variants on a tit theme when compared with flamingos. Bacteria that are vastly different genetically are all called *Legionella* because they clump along the single niche axis that matters to us: they all cause Legionnaire's disease.

So what is the correct or meaningful frame of reference when thinking about the ecological nature of species? As well as providing stimulating theoretical results, Scheffer and van Nes¹ have revitalized the fundamental question of how we should look at the ecological identity of species. ■

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STEM CELLS

Good, bad and reformable

Viktor Janzen and David T. Scadden

The ability of stem cells to continuously supply vast numbers of cells is magnificent, but it can be devastating if it runs amok, as in some tumours. So what makes a normal stem cell turn bad, and can it be redeemed?

The stem cell is a bit like the griffin of mythology — half lion, half eagle; grand and powerful, but potentially monstrous in effect. These essentially unspecialized cells can renew their own population while supplying cells that mature (differentiate) into the specialized cells necessary for all tissues. Although this ability to reproduce and self-renew is sublime when functioning properly, its disorder creates masses of dysfunctional replicating cells. Indeed, stem-cell-like cells have been found in a range of human tumours. Not all cancer is due to a stem cell gone bad, but some cancer-initiating cells are probably stem cells, and the rest acquire the stem-cell feature of self-renewal. This raises the troubling spectre that normal stem cells and cancer stem cells might share the molecular features essential to their nature. So attempting to treat cancer by disrupting the functions of the cancer stem cells might also disturb normal stem cells — potentially fatally.

In this issue, however, Yilmaz *et al.* (page 475)¹ and Zhang *et al.* (page 518)² report that there may be key molecular distinctions between the normal and malignant stem cell that might be of use in designing therapies that target malignant stem cells, while sparing normal stem cells.

The investigations centred on a protein called PTEN (for 'phosphatase and tensin homologue'), a known tumour suppressor and

an intracellular modulator of several major cell-signalling pathways. Notably, PTEN inhibits signalling through the AKT pathway that responds to growth factors (Fig. 1a). Growth factors bind to specific receptors on the cell surface and induce a cascade of cellular modifications in which phosphate groups are added to a series of proteins. Essentially, the activation signal is passed along the pathway like a baton in a relay race until it reaches the final 'effector' proteins that carry out the pathway response: for example, changing the expression of particular genes or halting the cell cycle. When the growth factor binds to its receptor, the enzyme PI3K is activated, and it is this step that PTEN inhibits. Activation of PI3K leads to phosphorylation and activation of the AKT protein, which in turn can potentially phosphorylate more than 9,000 proteins. Two key downstream AKT effectors, called mTOR and FOXO, are implicated in cancer development.

Yilmaz *et al.*¹ and Zhang *et al.*² used PTEN-deficient mice to examine how a lack of this protein affects cell proliferation, programmed cell death and cell localization in haematopoietic stem cells (which produce blood and immune cells) (Fig. 1b). Previous work had shown that PTEN deficiency increases the proliferation of stem or progenitor cells (a slightly more differentiated cell type) in the fetal mouse brain. It also increases self-renewal

Emergent neutrality

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Community ecology is in a current state of creative ferment, stimulated by the development of neutral models of community organization. Here, I reflect on recent papers by Scheffer and van Nes, and by Gravel *et al.*, which illuminate how neutrality can emerge from ecological and evolutionary processes, thus suggesting ways to unify neutral and niche perspectives.

Unifying niche and neutral theories

All naturalists know that species differ, and in many exquisite ways. But do such differences matter for determining broad patterns of distribution and abundance in communities? The ongoing debate about neutrality in community ecology [1,2] has focused the attention of ecologists on this fundamental issue. The basic assumption of neutrality is that to understand issues such as the relative abundances of species, species–area relationships, and spatial and temporal turnover in species community composition, one can assume that all species are the same. In neutral theories, relative abundances change by chance, rather than because one species is superior to another.

The provocative core assumption of neutral theory (see Glossary) is that individuals are equivalent with respect to key processes: the stochastic demographic rates of birth, death and dispersal, and the introduction of evolutionary novelty via mutation and speciation. There is an undoubted elegance to minimalist models [2], and neutral models have enjoyed success at explaining patterns such as species abundance and species–area relationships [2,3]. Yet many ecologists [4,5] are uncomfortable with the assumption of ecological equivalence, and close analyses of some systems do reveal non-neutral patterns [5]. Ecologists are now engaged in unifying niche and neutral theories [6]. As I discuss here, recent papers by Scheffer and van Nes [7] and by Gravel *et al.* [8] provide significant insights as to key elements of such a unified theory.

Sources of neutrality in community ecology

There are three reasons why species dynamics might match a neutral perspective.

Speciation creates ecologically equivalent species

First, from the moment that they arise by speciation, species could be equivalent with respect to probabilities of birth, death and dispersal. This justifies a ‘hard’ form of neutrality [9] in which species identity really does not matter in determining patterns such as relative abundances. Allopatric speciation, for instance, can occur

without ecological differences arising between sister species. When species created without ecological differentiation come into contact, their relative numbers should drift by chance [10,11]. Many extant communities are relatively recent products of large-scale Earth processes, such as glaciation cycles. These could generate sets of competitively equivalent species via speciation, and then bring these together in novel assemblages [12] where relative abundances would be governed by ecological drift. One would expect species to be eventually lost by extinction, but the timescale over which such extinctions occur could be quite long.

The world is very noisy

Second, even if species show niche differentiation and tradeoffs in functional traits, the dynamical consequences of such differences might be obscured because of stochastic processes such as climatic variability. In its ‘weak’ form, neutral theory at the very least provides the appropriate null model for evaluating patterns in comparative data sets [9]. There is increasing appreciation of the importance of dispersal limitation in metacommunities over large spatial scales [13]; such limitation tends to increase the role of stochastic and historical processes such as the placement of dispersal barriers in determining local community composition, and so null models might suffice reasonably well in describing community patterns, even if closer scrutiny of species shows that they do differ in niche properties. This is a ‘weak’ version of neutrality.

Ecological and evolutionary processes generate nearly neutral species

Finally, community and evolutionary processes themselves might act on species that are not initially ecologically equivalent but which, for dynamical reasons, converge on states that are, to a reasonable approximation, neutral, at least when examined over certain spatial and temporal scales. In other words, neutrality could be an emergent property of ecological systems. Ecologists have recently shown how neutrality can emerge as a byproduct of ecological and evolutionary processes (e.g. [3,14,15]). Recent papers [7,8] illustrate different but complementary ways in which emergent neutrality can arise.

Emergent neutrality in a closed Lotka–Volterra community

Scheffer and van Nes [7] begin with the classic Lotka–Volterra competition model for a spatially closed community and assume that interspecific competition reflects overlap in niches along a niche axis. If a large number of species are placed at high abundances randomly along

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Glossary

Allopatric speciation: divergence of a single ancestral lineage (identified as a single species) into two or more descendent lineages (also recognized as species), mediated by the disjunct spatial separation of the evolving lineages.

Dispersal kernel: a function that describes the spatial pattern of dispersal. The word 'kernel' arises from the use of these functions in integral equations, which are used frequently in spatial ecology.

Dispersal limitation: limitation of distribution or abundance because of either constraints on dispersal or inadequate production of dispersing individuals. Empirical assessments of dispersal limitation require introductions (e.g. seed additions); distributions are dispersal limited if individuals can successfully be introduced into empty sites; abundances are dispersal limited if introductions boost the population size of an established population.

Ecological drift: by analogy with genetic drift, the relative abundance of species that are ecologically equivalent should change only owing to chance events.

Intraspecific density dependence: influence of changes in density on per capita vital rates, or dispersal rates.

Metacommunity: a set of local communities linked by dispersal of multiple potentially interacting species.

Neutrality: the hypothesis that differences in species traits do not either affect the chances of that species being present or absent in a community, or influence changes in their relative abundances.

Neutral theory: mathematical theories that formalize the assumption of neutrality, enabling quantitative predictions about species relative abundances, species–area relationships, and other aspects of community organization (see [2]).

Species sorting: a theory of community structure that assumes most species in a regional species pool can reach local communities, but that only a subset of species persist, in particular, those species whose traits match local abiotic conditions and persist in the face of interspecific interactions with other community members.

the niche axis with sufficient overlap (so that there is strong competition among most species), an intriguing pattern emerges, in which lumps of multiple species are clustered closely together, with pronounced gaps between them maintained by competition. Although in the long run, only one species in each lump persists, transient coexistence is observed for thousands of generations. This is because if species are similar, the expected time course to competitive exclusion can be long, even if one species is competitively dominant [10]. Because many extant communities might not be close to their deterministic equilibrium [12], we should expect to observe guilds of effectively neutral species for historical reasons.

The authors [7] consider several extensions of their model, such as intraspecific density dependence operating on common species. This can stabilize the 'lumps' so that they persist indefinitely (but also makes the emergent neutrality less evident). The authors mimic evolution by enabling each species to shift in its modal niche position by a small amount in the direction of increasing mean fitness. Such microevolutionary jostling, superimposed on transient competitive dynamics, can lead to sharply separated clusters of species along a niche axis; the pattern in this case is essentially permanent. When considering pairs of competitors, or species-poor assemblages, competitive divergence is expected, but when considering entire, species-rich communities, convergence among subsets of the community can generate sets of nearly competitively equivalent species. Hence, neutrality can emerge from dynamical processes within a community.

Assessing the theoretical results

To evaluate theoretical results such as these, it is helpful to consider a range of alternative model formulations. Bonsall *et al.* [14] previously examined a model for competition with quite different assumptions, which nonetheless

arrives at comparable conclusions. The authors used a discrete generation framework to examine parasitoids competing for a shared host species. Because there can be multiple infections of single host individuals, this system blends asymmetric interference competition (only one parasitoid emerges per parasitized host) with exploitative competition (ability to attack the host in the first place). Assuming a tradeoff between interference and exploitative abilities (or other life-history traits, such as longevity), and taking an adaptive dynamics approach to the introduction of variation in parasitoid traits, Bonsall *et al.* [14] show that distinct clusters of species arise, separated by substantial gaps along the tradeoff axis. Again, community processes lead to sets of species that are roughly competitively equivalent, and so effectively neutral in their dynamics within each set.

The convergence of results between the quite different models considered by Scheffer and van Nes [7] and by Bonsall *et al.* [14] is striking, and suggests that emergent neutrality arises across a wide range of assumptions about interspecific interactions.

Emergent neutrality in an open community with space competition

Gravel *et al.* [8] utilize a quite different competition model and also consider open rather than closed communities, yet end up with similar conclusions. Beginning with Hubbell's [2] model of space competition for space (when an adult dies, the probability a given species recruits into that spot depends upon its relative abundance within either a metacommunity or a neighbourhood defined by a dispersal kernel), they incorporate niche differentiation by assuming the relative survival of each species to depend upon a continuous niche axis. Different species have different optimal conditions for survival. Without immigration from an external source, competition crafts a community structured by niche differentiation. Given immigration, neutrality (as measured by variance among replicate runs) increases, and the effect is more pronounced with increasing immigration rates and high species richness. Several processes contribute to these results. With higher species richness, average abundance per species declines, hence stochasticity and dispersal limitation loom larger. Moreover, it is more likely that species sorting [13] will lead to sets of relatively similar species being present, where some weakly excluded species are maintained by immigration [10].

Conclusion

In the work reported by Scheffer and van Nes [7], Gravel *et al.* [8] and others (e.g. [3,6,14,15]), community structure reflects both niche organization and neutrality. These studies suggest that the emergence of nearly neutral suites of species is more likely in species-rich communities than in those that are species poor. In both cases, the indefinite coexistence of species requires the operation of processes outside those producing neutrality (e.g. direct density dependence in [7], and immigration from a source in [8]). In general, to understand coexistence, one must consider both forces that are stabilizing (so that each species can increase when rare) and equalizing (so that species are relatively similar in response to non-regulatory

environmental factors) [10,16]. Near-neutrality might arise when stabilizing forces are relatively weak, and equalizing forces are strong, and is likely to be more pertinent to some taxa and environmental settings, than to others.

Despite this caveat, these recent papers point to an emerging reconciliation of niche and neutral perspectives in community ecology. Ecologists should now systematically explore these issues across a wide array of community models and, perhaps more importantly, devise critical experimental tests of these ideas. For instance, in microbial communities, ecological and evolutionary dynamics occur on a manageable timescale; the quasi-species that are observed in viral evolution are not dissimilar from the clusters of species that emerge in the models of Scheffer and Nes [7] and Bonsall *et al.* [14], and so these systems might provide empirical tests of these theories. In field systems, if patterns of relative abundance are due to drift, then perturbations that change the initial patterns of relative abundances (without causing extinctions) should tend to persist, rather than rapidly returning to the initial state of the community.

Niche and neutral perspectives have quite different implications for how one should manage natural resources and craft conservation strategies. A unified theory of communities that judiciously blends both perspectives is needed if ecologists are to understand the processes governing biodiversity at a fundamental level and then apply this understanding to the urgent problem of maintaining diversity in our rapidly changing world.

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Letters

Muscling out malaria

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Recent updates in *Trends in Parasitology* [1] and *Trends in Ecology and Evolution* [2] highlighted the back-to-back articles in *Science* [3,4] that demonstrated the potential biocontrol of malaria by targeting mosquitoes with entomopathogenic fungi (*Metarhizium* and *Beauveria* spp.). The wide impact of the original articles and the need to find alternatives to pesticidal control are likely to encourage the incorporation of these fungi into biocontrol programs, although several concerns have been raised [1,2,5]. Here, we detail some of these and advocate an inclusive

approach to malarial biocontrol that proceeds with a full appreciation of the complicated biology of the pathogenic fungi concerned.

There is a long history of using *Metarhizium* and *Beauveria* in insect biocontrol [6] with ‘Green Muscle’, a broad consortium set up to control locusts using *Metarhizium*, as an excellent example (for more information, see <http://www.lubilosa.org>). Green Muscle developed from the initial conception that spores could be suspended in oil to facilitate germination in arid regions [7], which made infecting mosquitoes feasible [4]. However, failures in biocontrol have been more common than successes and are often due to the ‘ephemeral and amateurish activities’

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