Biodiversity of plankton
by species oscillations and chaos

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Biodiversity has both fascinated and puzzled biologists1. In aquatic ecosystems, the biodiversity puzzle is particularly troublesome, and known as the ‘paradox of the plankton’2. Competition theory predicts that, at equilibrium, the number of coexisting species cannot exceed the number of limiting resources3–6. For phytoplankton, only a few resources are potentially limiting: nitrogen, phosphorus, silicon, iron, light, inorganic carbon, and sometimes a few trace metals or vitamins. However, in natural waters dozens of phytoplankton species coexist2. Here we offer a solution to the plankton paradox. First, we show that resource competition models6–10 can generate oscillations and chaos when species compete for three or more resources. Second, we show that these oscillations and chaotic fluctuations in species abundances allow the coexistence of many species on a handful of resources. This model of planktonic biodiversity may be broadly applicable to the biodiversity of many ecosystems.
\[
\frac{dN_i}{dt} = N_i(\mu_i(R_1, \ldots, R_k) - m_i) \quad i = 1, \ldots, n
\]  
\[
\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^{n} c_{ji} \mu_i(R_1, \ldots, R_k)N_i \quad j = 1, \ldots, k
\]  
\[
\mu_i(R_1, \ldots, R_k) = \min \left( \frac{r_i R_1}{K_{1i} + R_1}, \ldots, \frac{r_i R_k}{K_{ki} + R_k} \right)
\]  
\[
K = \begin{pmatrix}
1.00 & 0.90 & 0.30 & 1.04 & 0.34 & 0.77 \\
0.30 & 1.00 & 0.90 & 0.71 & 1.02 & 0.76 \\
0.90 & 0.30 & 1.00 & 0.46 & 0.34 & 1.07
\end{pmatrix}
\]
\[
r_i = 1 \text{ d}^{-1} \text{ and } m_i = D = 0.25 \text{ d}^{-1}
\]
\[
C = \begin{pmatrix}
0.04 & 0.07 & 0.04 & 0.10 & 0.03 & 0.02 \\
0.08 & 0.08 & 0.10 & 0.10 & 0.05 & 0.17 \\
0.14 & 0.10 & 0.10 & 0.16 & 0.06 & 0.14
\end{pmatrix}
\]
Figure 1 Oscillations on three resources. a, Time course of the abundances of three species competing for three resources. b, The corresponding limit cycle. c, Small-amplitude oscillations of six species on three resources. d, Large-amplitude oscillations of nine species on three resources.
Natural phytoplankton communities, however, are frequently limited by more than two resources. For certain species combinations, three-species competition generates sustained oscillations (Fig. 1a, b). This occurs if the species that are better competitors for resource 1 but become limited by resource 2. The surplus of species should be competitively excluded. Here we develop a solution for the plankton paradox that does not invoke external factors. We consider a constant and homogeneous environment, and derive an explanation for biodiversity based on the corresponding chaotic attractor. The trajectory is plotted for the period from $t = 1,000$ to $t = 2,000$ days.

Figure 1
- **a**: Time course of the abundances of three species competing for three resources. The corresponding limit cycle.
- **b**: Time course of total community biomass.
- **c**: Time course of total community biomass.

Figure 2
- **a**: Time course of the abundances of five species competing for five resources. The corresponding chaotic attractor.
- **b**: Chaos on five resources.
- **c**: Time course of total community biomass.
species than limiting resources generate oscillations. These oscillations allow the coexistence of many species on four resources (J.H. and F.J.W., unpublished results). Yet even these small-amplitude oscillations (Fig. 1d) depend on the precise parameter settings.

With five resources, many simulations show irregular species fluctuations (Fig. 2a). The pattern of species replacement never shows the local minima and maxima of species 1, plotted during the period from $t = 2,000$ to $t = 4,000$ days, as a function of the half-saturation constant $K_{41}$. Part of a is magnified in b.

Figure 3 Bifurcation diagram, for five species competing for five resources. The graphs show the local minima and maxima of species 1, plotted during the period from $t = 2,000$ to $t = 4,000$ days, as a function of the half-saturation constant $K_{41}$. Part of a is magnified in b.
We note that the oscillations are not generated by fluctuating resources but rather by the competition process itself. The amplitude of the oscillations (Fig. 2a) is magnified in the bifurcation diagram for five species competing for five resources. The pattern of species replacement never repeats itself. Each time one species tries to become dominant, there are several other species that invade. The species invade at different rates, and the amplitudes of the oscillations in Fig. 1c are so small that trajectories that start with almost identical species abundances slowly diverge, and gradually become completely uncorrelated. The competitive chaos occurs in a weak competitor for resource 4 (a), competition leads to sustained oscillations of any real-world data set. Yet even these small-amplitude oscillations are apparently sufficient for the coexistence of six species on three resources. Similar results were obtained with large-amplitude oscillations (Fig. 1d): in the end, a total of nine species coexist on three resources. The bifurcation diagram in Fig. 3 illustrates how the model predictions depend on the parameter regime. Resource 4 is the resource that most limits the growth rate of species 1. If species 1 is a weak competitor for resource 4, the abundances of species 7–12 are magnified, and trajectories that start with almost identical species abundances while at the same time it may stabilize global ecosystem properties like total community biomass. For certain species combinations, competition for four resources generates oscillations. These oscillations allow the coexistence of many species on four resources (J.H. and F.J.W., unpublished results).}

**Figure 4.** Competitive chaos and the coexistence of 12 species on five resources. a, The abundances of species 1–6; b, the abundances of species 7–12.
The possibility that competition models may generate oscillations and chaos was already recognized in the mid 1970s. Also, it is well established that non-equilibrium conditions may favour species coexistence. What is new here is that we found both phenomena in a single competition model. Moreover, our findings do not stem from an artificially constructed model, but are based on one of the standard models of phytoplankton competition. We
Early-warning signals for critical transitions

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Complex dynamical systems, ranging from ecosystems to financial markets and the climate, can have tipping points at which a sudden shift to a contrasting dynamical regime may occur. Although predicting such critical points before they are reached is extremely difficult, work in different scientific fields is now suggesting the existence of generic early-warning signals that may indicate for a wide class of systems if a critical threshold is approaching.
Box 1 | Critical transitions in the fold catastrophe model
Figure 1 | Some characteristic changes in non-equilibrium dynamics as a system approaches a catastrophic bifurcation (such as $F_1$ or $F_2$, Box 1).
Box 2 | Critical slowing down: an example

To see why the rate of recovery rate after a small perturbation will be reduced, and will approach zero when a system moves towards a catastrophic bifurcation point, consider the following simple dynamical system, where $\gamma$ is a positive scaling factor and $a$ and $b$ are parameters:

$$\frac{dx}{dt} = \gamma(x - a)(x - b) \tag{1}$$

It can easily be seen that this model has two equilibria, $x_1 = a$ and $x_2 = b$, of which one is stable and the other is unstable. If the value of parameter $a$ equals that of $b$, the equilibria collide and exchange stability (in a transcritical bifurcation). Assuming that $x_1$ is the stable equilibrium, we can now study what happens if the state of the equilibrium is perturbed slightly ($x = x_1 + \varepsilon$):

$$\frac{d(x_1 + \varepsilon)}{dt} = f(x_1 + \varepsilon)$$

Here $f(x)$ is the right hand side of equation (1). Linearizing this equation using a first-order Taylor expansion yields

$$\frac{d(x_1 + \varepsilon)}{dt} = f(x_1 + \varepsilon) \approx f(x_1) + \frac{\partial f}{\partial x}(x_1) \varepsilon$$

which simplifies to

$$f(x_1) + \frac{d\varepsilon}{dt} = f(x_1) + \frac{\partial f}{\partial x}(x_1) \varepsilon \Rightarrow \frac{d\varepsilon}{dt} = \lambda_1 \varepsilon$$

With eigenvalues $\lambda_1$ and $\lambda_2$ in this case, we have

$$\lambda_1 = \left. \frac{\partial f}{\partial x} \right|_{x_1} = -\gamma(b - a)$$

and, for the other equilibrium

$$\lambda_2 = \left. \frac{\partial f}{\partial x} \right|_{b} = \gamma(b - a)$$

If $b > a$ then the first equilibrium has a negative eigenvalue, $\lambda_1$, and is thus stable (as the perturbation goes exponentially to zero; see equation (2)). It is easy to see from equations (3) and (4) that at the bifurcation ($b = a$) the recovery rates $\lambda_1$ and $\lambda_2$ are both zero and perturbations will not recover. Farther away from the bifurcation, the recovery rate in this model is linearly dependent on the size of the basin of attraction ($b - a$). For more realistic models, this is not necessarily true but the relation is still monotonic and is often nearly linear\textsuperscript{16}.
Box 3 | The relation between critical slowing down, increased autocorrelation and increased variance

Critical slowing down will tend to lead to an increase in the autocorrelation and variance of the fluctuations in a stochastically forced system approaching a bifurcation at a threshold value of a control parameter. The example described here illustrates why this is so. We assume that there is a repeated disturbance of the state variable after each period Δt (that is, additive noise). Between disturbances, the return to equilibrium is approximately exponential with a certain recovery speed, \( \lambda \). In a simple autoregressive model this can be described as follows:

\[
x_{n+1} - \bar{x} = e^{\lambda \Delta t} (x_n - \bar{x}) + \sigma \epsilon_n
\]

\[
y_{n+1} = e^{\lambda \Delta t} y_n + \sigma \epsilon_n
\]

Here \( y_n \) is the deviation of the state variable \( x \) from the equilibrium, \( \epsilon_n \) is a random number from a standard normal distribution and \( \sigma \) is the standard deviation.

If \( \lambda \) and \( \Delta t \) are independent of \( y_n \), this model can also be written as a first-order autoregressive (AR(1)) process:

\[
y_{n+1} = \alpha y_n + \sigma \epsilon_n
\]

The autocorrelation \( \alpha = e^{\lambda \Delta t} \) is zero for white noise and close to one for red (autocorrelated) noise. The expectation of an AR(1) process

\[
E(y_{n+1}) = E(c) + \alpha E(y_n) + E(\sigma \epsilon_n) \Rightarrow \mu = c + \alpha \mu + 0 \Rightarrow \mu = \frac{c}{1 - \alpha}
\]

For \( c = 0 \), the mean equals zero and the variance is found to be

\[
\text{Var}(y_{n+1}) = E(y_n^2) - \mu^2 = \frac{\sigma^2}{1 - \alpha^2}
\]

Close to the critical point, the return speed to equilibrium decreases, implying that \( \lambda \) approaches zero and the autocorrelation \( \alpha \) tends to one. Thus, the variance tends to infinity. These early-warning signals are the result of critical slowing down near the threshold value of the control parameter.
Figure 2 | Early warning signals for a critical transition in a time series generated by a model of a harvested population\(^{77}\) driven slowly across a bifurcation. a, Biomass time series. b, c, d, Analysis of the filtered time series
Figure 3 | Ecosystems may undergo a predictable sequence of self-organized spatial patterns as they approach a critical transition. We show
Figure 4 | Critical slowing down indicated by an increase in lag-1 autocorrelation in climate dynamics. We show the period preceding the transition from a greenhouse state to an icehouse state on the Earth 34 Myr
Figure 5 | Subtle changes in brain activity before an epileptic seizure may be used as an early warning signal. The epileptic seizure clinically detected at time 0 is announced minutes earlier in an electroencephalography (EEG) record as a rise in variance in the EEG signal. The period preceding the seizure is characterized by reduced dimensionality and a rise in variance that is due to a fast and permanent change in the system.
Catastrophic Collapse Can Occur without Early Warning: Examples of Silent Catastrophes in Structured Ecological Models

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Abstract

Catastrophic and sudden collapses of ecosystems are sometimes preceded by early warning signals that potentially could be used to predict and prevent a forthcoming catastrophe. Universality of these early warning signals has been proposed, but no formal proof has been provided. Here, we show that in relatively simple ecological models the most commonly used early warning signals for a catastrophic collapse can be silent. We underpin the mathematical reason for this phenomenon, which involves the direction of the eigenvectors of the system. Our results demonstrate that claims on the universality of early warning signals are not correct, and that catastrophic collapses can occur without prior warning. In order to correctly predict a collapse and determine whether early warning signals precede the collapse, detailed knowledge of the mathematical structure of the approaching bifurcation is necessary. Unfortunately, such knowledge is often only obtained after the collapse has already occurred.


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in its most general form, consists of three ordinary differential equations for, respectively, juvenile ($J$), adult ($A$), and predator density ($P$):

\[
\frac{dJ}{dt} = f(A) - g(J) - \mu_J J; \quad \frac{dA}{dt} = g(J) - h(A, P) - \mu_A A;
\]

\[
\frac{dP}{dt} = h(A, P)c - \mu_P P
\]

Here, $f(A)$ is a function that specifies the reproduction rate of adults, $g(J)$ specifies the maturation rate of juveniles, and $h(A, P)$ is the predation rate on adults. Parameters $\mu_J$, $\mu_A$ and $\mu_P$ are death rates, and $c$ is a conversion factor. We use a realization of this model with $f(A) = bA$, $g(J) = J/(1+J^2)$, and $h(A, P) = AP$. For a
the per capita death rates is giving similar results to directly perturbing population numbers after every time unit. For numerical integration we used the Cash-Karp Runge-Kutta method [14] for solving ordinary differential equations.

Results

In Figures 2A through 2D, we gradually increase the predator death rate towards the catastrophic collapse of the predator density at \( m_P < 0.553 \) (corresponding to point \( T_1 \) in Figure 1), and we monitor the coefficient of variation for all three state variables.

**Figure 1. Bistability and catastrophic collapse in a structured predator-prey system.** Bifurcation diagram as a function of predator death rate \( m_P \). (A) Equilibrium juvenile density \( J \), and (B) Equilibrium predator density \( P \). The equilibrium curves exhibit a so-called catastrophe fold. Between the bifurcation points \( T_1 \) (\( m_P < 0.553 \)) and \( T_2 \) (\( m_P < 0.435 \)) the system is bistable (indicated by solid lines), with an intermediate saddle-node equilibrium (indicated by the dashed line) which is unstable. Model parameters are \( b = 1, c = 1, \mu_J = 0.05, \mu_A = 0.1 \).

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**Figure 2. Early warning signals in coefficient of variation.** For each value of \( m_P \), starting with \( m_P = 0.4 \), the model is simulated for 60,000 time units, of which the last 50,000 time units are used to compute population averages and variances. Hereafter, \( m_P \) is incremented with \( Dm_P = 0.001 \), towards the catastrophic collapse at \( m_P < 0.553 \). Death rates are perturbed every time unit using white noise with standard deviation \( s = 0.005 \). (A) Noise added to the juvenile population (B) Noise added to the adult population (C) Independent noise added to all three populations. (D) Identical, fully correlated, noise added to all three populations. Colors are blue for juveniles, green for adults, and red for the predators. For other model parameters see Figure 1.

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Notably, no early warning signal is observed for the variation in adult and predator density, regardless of the way in which environmental noise is added to the system. This is striking, because the predator is the species that will collapse at the catastrophe, and yet, it is not displaying any warning signal. There can be an early warning sign in the juvenile density, but only if noise is applied to the juvenile population (Figure 2A), or if noise is added independently to all three populations (Figure 2C). Most surprisingly, the catastrophic collapse happens without any prior warning if environmental noise is applied to the adult population (Figure 2B) or to all three populations in a correlated manner (Figure 2D). The latter procedure corresponds to a situation where changing environmental conditions affect all three populations equally. In Figures 3A through 3D it is shown that also autocorrelation does not provide reliable early warning signals for this system. In case of noise on the adult population (Figure 3B)
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**Figure 4. Effect of the direction of perturbation on early warning signals.** Predator death rate is fixed at $\mu_p = 0.55$ (close to the catastrophe), and the death rate of either the juveniles or the adults is perturbed using white noise with standard deviation $\sigma = 0.005$. System trajectories are plotted in blue for 60 time units. The dominant eigenvector is indicated by the red arrow, and the second and third eigenvector are indicated by the black arrows. (A) When the juvenile death rate is perturbed, the system responds only in the direction of the dominant eigenvector, resulting in an early warning signal that is only apparent in juvenile population fluctuations. (B) When the adult death rate is perturbed, the system responds in the direction of the surface spanned by the second and third eigenvector (indicated in grey), resulting in damped oscillations and absence of early warning. For other model parameters see Figure 1. For an animated rotation of these 3D figures, and for direction and scaling of axis see Movie S1 and S2.

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and fully correlated noise (Figure 3D) all autocorrelations are decreasing towards the catastrophe. In case of noise on juveniles (Figure 3A) or independent noise to all variables (Figure 3C), a clear early warning signal again only occurs in the juvenile population.

Apparently, the early warning signals are not generic at all, as a fold catastrophe can occur without prior warning. So, what is flawed in the argument that “critical slowing down” is a generic property of all fold bifurcations? In fact, the statement is completely correct, but the slowing down only occurs in the direction of the dominant eigenvector. In our system, this eigenvector, near the bifurcation, almost exclusively points in the direction of the axis corresponding to the juvenile population. Figure 4A shows that adding noise to the juvenile population will result in the system responding only in the direction of this dominant eigenvector, causing the early warning signal in the juvenile density. In contrast, in Figure 4B, when noise is added to the adult population, perturbations mainly develop in the direction of the second and third eigenvector. The eigenvalues pertaining to these eigenvectors are imaginary, and their real parts become more negative towards the catastrophe, causing increasingly damped oscillations and absence of critical slowing down. As a consequence, the forthcoming collapse is camouflaged. We also examined the linear stability of the system by using the Jacobian matrix (see [7]). Adding noise to the linearized system gives a very similar early warning signature in approaching the bifurcation. In Figure 5A and 5B the linearized system is brought very close to the bifurcation \( \mu_P = 0.5528 \). In Figure 5A, where noise is added to the juvenile population, this population is clearly showing critically slowing down, with very large and slow excursions from the equilibrium, whereas the adult and predator population do not show an early warning signal. In contrast, in Figure 5B, where the same amount of noise is added to the adult population, early warning signals are completely absent from all three populations.

We extensively tested robustness of the silent collapse phenomenon, e.g. by varying the type of noise. In Figure 6A, more natural

**Figure 5. Early warning signals in the linearized system.** The model of Figure 1 is linearized using the Jacobian matrix. Predator death rate is set at \( \mu_P = 0.5528 \) (very close to the bifurcation point T1 in Figure 1). The death rate of either the juveniles or the adults is perturbed using white noise with standard deviation \( \sigma = 0.005 \). (A) When noise is added to the juvenile death rate, the juvenile population (indicated in blue) clearly shows critically slowing down, whereas the adult (green line) and predator (red line) populations do not show early warning signs. (B) When noise is added to the adult death rate, all three populations do not show any sign of early warning. Note that the fluctuations in the juvenile population in Figure 5A are so large, that the full (i.e. not linearized) system would shift to the alternative steady state.

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Figure 6. Early warning signals with correlated noise and discrete noise. Coefficient of variation and autocorrelation are monitored for increasing predator death rate towards the catastrophic collapse at $\mu_P \approx 0.553$. Bifurcation procedure, parameters and colors are identical to Figure 2. (A) Coefficient of variation when pink noise (1/f correlated noise) is added to the death rate of the adult population. (B) Coefficient of variation when discrete white noise is applied directly to the adult population numbers after each time step.

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Figure 7. Early warning signals in the fully size-structured population model of de Roos and Persson [17]. Independent white noise with $\sigma = 0.002$ is added to the death rates of all juvenile consumers. Bifurcation procedure and colors are identical to Figure 2, with predator mortality staring at $\mu_P = 0.01$ (note that the original article uses parameter $\delta$ instead of $\mu_P$), and incremented with $\Delta \mu_P = 0.0002$ after each 50,000 time units. The fold catastrophe in this model is located at approximately $\mu_P = 0.038$. Coefficient of variation and lag-1 autocorrelation are computed for each value of $\mu_P$ over the last 40,000 time steps. (A) Coefficient of variation, and (B) Autocorrelation. All other parameters have default values as used by de Roos and Persson [17].

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Predicted correspondence between species abundances and dendrograms of niche similarities

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Contributed by Robert M. May, February 24, 2003

We examine a hypothesized relationship between two descriptions of community structure: the niche-overlap dendrogram that describes the ecological similarities of species and the pattern of relative abundances. Specifically, we examine the way in which this relationship follows from the niche hierarchy model, whose fundamental assumption is a direct connection between abundances and underlying hierarchical community organization. We test three important, although correlated, predictions of the niche hierarchy model and show that they are upheld in a set of 11 communities (encompassing fishes, amphibians, lizards, and birds) where both abundances and dendrograms were reported. First, species that are highly nested in the dendrogram are on average less abundant than species from branches less subdivided. Second, and more significantly, more equitable community abundances are associated with more evenly branched dendrogram structures, whereas less equitable abundances are associated with less even dendrograms. This relationship shows that abundance patterns can give insight into less visible aspects of community organization. Third, one can recover the distribution of proportional abundances seen in assemblages containing two species by treating each branch point in the dendrogram as a two-species case. This reconstruction cannot be achieved if abundances and the dendrogram are unrelated and suggests a method for hierarchically decomposing systems. To our knowledge, this is the first test of a species abundance model based on nontrivial predictions as to the origins and causes of abundance patterns, and not simply on the goodness-of-fit of distributions.
Two dendrograms depicting the organization of a hypothetical four species (s_1 to s_4) community. (a) A symmetrical branching structure; (b) an asymmetric one. The sequential splitting process (a physical metaphor for the nested ordering of niche interfaces) is shown in c and d for the dendrograms, with 1 being the root (lowest similarity). The corresponding abundance distributions are given in e and f. Note that the abundances in f that follow from an asymmetric branching structure are less equitable than in e, where the underlying dendrogram was more evenly branched.
partitioning appear to be nearly equivalent processes (21, 23). Weight and energy consumption is only mildly nonlinear (22), energy is potentially problematic (21). It is, however, not a consequence of these biomasses, that is, by density or total abundance times body weight.

i.e., when the underlying resource (niche) space is unconnected and heterogeneous, so that there is no fundamental common root, finding any obvious relationship when the assemblage is excessively heterogeneous. We believe a degree of homogeneity is required insofar as it is typically limited to communities that are taxonomically homogeneous. We found 11 such studies from the literature, involving fishes, amphibians, lizards, and birds communities (Table 1). Note that these studies are essentially limited to communities that are taxonomically homogeneous. However, almost always, many alternative abundance models (20). An additional step in the validation of these models can be produced that yield similar fits. Such tests alone are certainly a valuable initial approach to test a model (19), although the niche hierarchy model can reproduce several nontrivial predictions concerning the link between species abundances and a dendrogram of niche similarity. This is possible here, because the model generates lognormal distributions with a characteristic negative skewness, thereby allowing Nee, Harvey, and May (10) to generate such skewed distributions.

decade later, it was found that for large data sets, the model generates a distribution exponent has a value of \( k \) (18). Nearly any skewness, thereby allowing Nee, Harvey, and May (10) to use that generates such skewed distributions.

In Table 1, we list the 11 data sets that provide both species abundances and a dendrogram of niche similarity. Numbers in parentheses indicate the number of descriptors retained in the studies. Letters \( a \) to \( k \) refer to the graphs in Fig. 3.

Table 1. Catalogue of the 11 data sets that provide both species abundances and a dendrogram of niche similarity

<table>
<thead>
<tr>
<th>Fig. 3 graph</th>
<th>Taxonomic group and study site</th>
<th>Ecological descriptors</th>
<th>Similarity or distance index</th>
<th>Clustering method</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a )</td>
<td>Fishes, Rio Manso, Brazil</td>
<td>Ecomorphology (15)</td>
<td>Pearson ( r )</td>
<td>Ward</td>
<td>42</td>
</tr>
<tr>
<td>( b )</td>
<td>Amphibians, tropical forests, Mt. Kupe, Cameroon</td>
<td>Morphology (2) and microhabitat use (28)</td>
<td>Gower similarity</td>
<td>UPGMA</td>
<td>43, 44</td>
</tr>
<tr>
<td>( c )</td>
<td>Lizards, tropical forests, Mt. Kupe, Cameroon</td>
<td>Morphology (1) and microhabitat use (18)</td>
<td>Gower similarity</td>
<td>UPGMA</td>
<td>43, 44</td>
</tr>
<tr>
<td>( d-g )</td>
<td>Birds, four types of Ponderosa pine forest, U.S.</td>
<td>Activity, foraging methods and sites (7)</td>
<td>Euclidean distance</td>
<td>UPGMA</td>
<td>45</td>
</tr>
<tr>
<td>( h )</td>
<td>Birds, Hubbard Brook forest, U.S.</td>
<td>Foraging methods (27)</td>
<td>Euclidean distance</td>
<td>Complete link</td>
<td>46, 47</td>
</tr>
<tr>
<td>( i )</td>
<td>Birds, mixed forest, Australia</td>
<td>Foraging methods (25)</td>
<td>Euclidean distance</td>
<td>Complete link</td>
<td>48</td>
</tr>
<tr>
<td>( j )</td>
<td>Warblers, Himalayan slopes, Pakistan</td>
<td>Morphology (6) and foraging methods (4)</td>
<td>Gower similarity</td>
<td>UPGMA</td>
<td>44, 49</td>
</tr>
<tr>
<td>( k )</td>
<td>Waterfowl, Finland</td>
<td>Feeding methods (17)</td>
<td>Percentage similarity</td>
<td>UPGMA</td>
<td>50</td>
</tr>
</tbody>
</table>

Numbers in parentheses indicate the number of descriptors retained in the studies. Letters \( a \) to \( k \) refer to the graphs in Fig. 3.
Fig. 2. Dendrogram of niche similarity for the lizards inhabiting the tropical forests of Mt. Kupe, Cameroon. \( n \), abundance; \( \#b \), number of bifurcations from the root to a terminal node. (a–g) Bifurcations and the corresponding fractional abundance; for bifurcation c, fractional abundance = \( \max (49 + 39, 17) / (49 + 39 + 17) \). See Fig. 3c for the relationship between \( n \) and \( \#b \). (Top to bottom) Species are \( C. \) montium, Chameleo pfefferi, Leptosiaphos sp.A, Cnemaspis koehleri, L. sp.B, L. sp.C, R. spectrum, and Chameleo quadricornis.
A way to test the presumed link between abundances and dendrograms is to gather data from a variety of different communities and perform a simple metaanalysis as follows. Compute the Pearson correlation between abundances and the number of bifurcations for each community in the ensemble. Then compute the binomial probability of obtaining the observed number of negative correlations, under the null hypothesis that negative and positive values are equally likely. Although few of the individual correlations are significant (Fig. 3), as expected, we find a predominance of negative relationships between abundance and number of bifurcations in the niche overlap dendrogram. Only one correlation is positive, which yields a significant binomial probability of 0.012 for the ensemble.

**Test of Evenness–Shape Correlation.** Here we test the predicted positive correspondence between equitability in abundances and symmetry in the shape of the dendrogram. We measure evenness in abundances by the probability of interspecific encounter (29), an unbiased estimator. The symmetry of the dendrogram was measured by the shape statistic derived by Siegel and Sugihara (30):

\[ E = \frac{N_1}{N_1 + N_2}, \]

with \( N_1 \) the number of edges (branches) from terminal node to the nearest common ancestor of terminal nodes (e.g., in Fig. 2, for \( N_1 = 4 \) and \( N_2 = 1 \)). This index was then normalized by the range between the minimum and maximum value of for the given number of species; this standardized index \( E_{\text{st}} \) equals 0 for perfect ordering as in Fig. 1b and 1 for the most symmetric dendrogram as in Fig. 1a.

Fig. 4 presents the relationship between the shape of the dendrogram and the evenness of the abundance distribution. As predicted, communities with asymmetrical dendrograms have abundance distributions more uneven than those exhibiting symmetrical structure. The observed relationship between the shape of the dendrogram \( E_{\text{st}} \) and evenness (probability of interspecific encounter) yields a correlation coefficient \( r = 0.88, P = 0.001 \). This relationship remains significant after controlling for the effect of species richness \( S \) on evenness (partial \( r = 0.82, P = 0.004 \)). In sum, predictions of the niche hierarchy model due to niche ordering (sequential niche fragmentation) are upheld. Abundances can give insight into less visible aspects of community organization.

**Fig. 3.** Relationship between species abundance and the number of bifurcations in the dendrogram of niche overlap. See Table 1 for summary. Pearson’s correlations are given; * denotes an individual \( P \) value significant at the 0.01 level. All correlations are negative except for \( h \). The binomial null hypothesis for the ensemble is rejected with a probability of 0.012. There is a significant negative correlation between a species’ abundance and how highly nested it is in the dendrogram, suggesting that species with many niche interfaces are generally less abundant than those with fewer.
Fig. 4. Relationship between the shape of the dendrogram and the evenness of the abundance distribution for the 11 studies of Table 1. As predicted by the niche hierarchy model, asymmetric dendrograms have lower evenness than symmetric ones (Pearson correlation $r = 0.88, P < 0.001$). Thus abundances can give insight into less visible aspects of community organization.
As noted by Siegel and Sugihara (30), a triangular distribution of data to 0.75 was found for replicate two-species assemblies. The distribution in Fig. 5 differs significantly from distributions obtained by reshuffling the abundances in the known dendrogram. This exercise shows that the derived breakage distribution was similarly obtained by pooling the simulations for all ensemble observed frequency distributions. The permuted distributions of fractional abundances of all communities to generate the ensemble expected null distribution for a given community. Because the expected breakage distribution was right-skewed triangular with a mode close to 0.66, whereas those governed by multiple unrelated factors will have more equitable distributions (like the lognormal or the broken stick). This prediction is clearly amenable to experimental tests where a single ecological factor dominates and a more even species abundance distribution after a perturbation (32, 33).

Fig. 5. Binary apportionment rule: frequency distribution of pair-wise fractional abundances of all bifurcations of the 11 data sets. Shaded bars, observed distributions; open bars, null distribution obtained by randomly shuffling the observed abundances in the observed dendrograms. Observed distributions differ significantly from their randomized counterpart ($P = 0.005$).
served distributions for verification. A very interesting recent example is the approach by Hubbell (6), which is based on the basic processes of birth, death, migration, and speciation. It generates a class of flexible multinomial distributions whose various free parameters can be tuned to match some characteristics of recent data sets (i.e., lognormal distributions with a negative skew). Gross fits of theoretical distributions to data can be helpful as a first step in model validation; however, they are often not unique (especially when more free parameters are allowed), and nearly all are post hoc. A central aspect of Hubbell’s neutral theory (and indeed of statistical ensemble arguments as a genre) is that all species are regarded as equivalent: all individuals of the community have the same probability of speciating, migrating, and dying. It is a beguilingly simple null hypothesis for the absence of biological uniqueness and structure. Although it can be tuned to fit the negatively skewed lognormal, it does not reproduce the ubiquitous canonical lognormal observed by Preston (9).

between observed and theoretical distributions. Goodness-of-fit tests are certainly a valuable initial approach to test a model (19), but they are far from definitive. Almost always, many alternative models can be produced that yield similar fits. Such tests alone cannot provide any guarantee that the model is correct, or even interesting, and this problem is not new in the field of species abundance models (20). An additional step in the validation of a model is to test its assumptions and further implications (if