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Examining the effects of species richness on community stability: an assembly model approach

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We build dynamic models of community assembly by starting with one species in our model ecosystem and adding colonists. We find that the number of species present first increases, then fluctuates about some level. We ask: how large are these fluctuations and how can we characterize them statistically? As in Robert May's work, communities with weaker interspecific interactions permit a greater number of species to coexist on average. We find that as this average increases, however, the relative variation in the number of species and return times to mean community levels decreases. In addition, the relative frequency of large extinction events to small extinction events decreases as mean community size increases. While the model reproduces several of May's results, it also provides theoretical support for Charles Elton's idea that diverse communities such as those found in the tropics should be less variable than depauperate communities such as those found in arctic or agricultural settings.

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Theoretical studies have generally supported the notion that as community complexity increases, stability decreases (Gardner and Ashby 1970, May 1972, Gilpin 1975, Pimm and Lawton 1978, Hogg et al. 1989). Authors of such work typically analyze the local or species-deletion stability of randomly organized interaction matrices and/or Lotka-Volterra systems. With few exceptions (e.g. in donor-controlled communities) theoretical research has shown a negative relationship between stability and complexity (Pimm 1982). Conversely, empirical work generally shows that as communities increase in species richness they also increase in stability (McNaughton 1978, Tilman and Downing 1994, Tilman et al. 1996, Naeem and Li 1997). Studies conducted in controlled microcosms demonstrate a positive relationship between species richness and aggregate measures of community stability such as total biomass (Tilman et al. 1996, Naeem and Li 1997). Though this disconnect between theory and experiment is partially due to varying definitions of stability, it has nevertheless led to what has become the 'diversity-stability debate' in ecology (McCann 2000).

An alternative approach to modeling communities as randomly constructed entities is to assemble them one species at a time. Models of this kind typically draw species from a limited pool of resources and consumers until a final community state is reached (Post and Pimm 1983, Drake 1990, Law and Morton 1996). A clear advantage to this approach is the realism embodied in the methodology. As such, models of this kind have closely corroborated experimental manipulations in microcosm experiments. While much effort has been focused on analyzing the invasibility of these models, there has been little work analyzing their statistical properties.

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Here we construct dynamic models of community assembly starting with one species and then adding colonists to our hypothetical ecosystem. As with previous studies, we find that the number of species initially increases, then fluctuates about some level. We ask: how large are these fluctuations and how can we characterize them statistically? We present the results through an ecological lens, though much like previous work in this area, the model may have broader application to other networked systems such as those found in economics, sociology and computing.

Methods

We begin with one species in our model ecosystem and add colonists to the network one at a time. New colonists interact with resident species with probability p, where p is chosen such that the resultant connectance C (where $E(C) = p$), of our ecological network approximates the values reported in empirical food web studies. We compare scenarios $p = 0.05$, 0.10 and 0.15. Once a link has been established between two species, interaction strengths are then assigned from a specified distribution. We focus our analysis on normal (0, σ) distributed interactions, where σ is a joint measure of the population of a species and average interaction strength between species. For the remainder of the paper we refer to σ simply as interaction strength, though it can be (as in equations containing nonlinear terms) a weighted measure of interaction strength and populations size depending on the specific form of the underlying equations. We focus on normally distributed interactions because weak interactions are thought to be more common in nature than strong ones but we also test uniform (− a, a) and beta (r, s) distributions where beta parameters r and s are chosen such that the distribution of interaction strengths is basin shaped thus emphasizing strong interactions. Species interactions in our community are represented by a matrix A with elements a_{ij} such that perturbations of species from a community equilibrium satisfy the equation,

$$\frac{dx}{dt} = Ax, \tag{1}$$

where A is the Jacobian matrix resulting from a Taylor expansion of a set of nonlinear first-order differential equations around one of their equilibrium points, retaining only the linear terms. The variable x indicates deviation from the equilibrium. As in May (1972), we do not specify the form of these equations, so that our model remains simple and general. This also means that we do not need to consider feasibility issues (Roberts 1974) since such considerations are only relevant when explicit dynamics (e.g. Lotka-Volterra) are specified. Diagonal terms a_{ii} are set to -1 so that populations are self regulated and normalized with respect to their intrinsic growth rates. We then analyze the local stability of the system by calculating the eigenvalues of the community matrix A. We use the condition that if the real part of the dominant eigenvalue is greater than zero, then the equilibrium point at which the community exists is unstable (May 1972). If it is unstable, we remove a species at random. Conversely, if it is stable, we add another species with a binomial (n, p) distributed number of links, where n is the number of species, and randomly chosen interaction strengths as described above. We then analyze the local stability of the system and repeat the process. The model is then allowed to run for $5 \times 10^5 – 10^6$ iterations, which is more than sufficient to assess the statistical properties of the system.

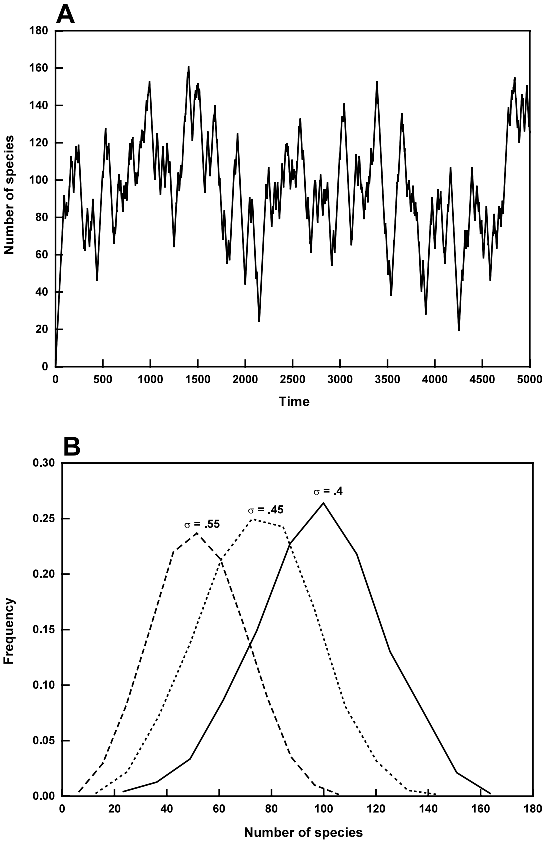

Fig. 1. (A) The number of species in the model ecosystem is plotted over time for a connectance = 0.05 and interaction strength σ = 0.4 from a normal distribution. (B) The corresponding distribution of species diversity of such communities is plotted for three different mean interaction strength levels σ.

Results

Communities in our model initially grow monotonically and then settle into a pattern of growth spurts and collapse (Fig. 1A). This process of community growth and decline ultimately defines a stationary stochastic process in the sense that a limiting distribution of states is approached asymptotically. A Fourier transform of the resulting time series can be modeled by a power law of the form,

$$P = \gamma f^{\alpha}, \tag{2}$$

where P is the power spectral density of the time series, f is the frequency and γ and α are constants. An exponent of $\alpha \approx -3$ indicates that the process of community growth and collapse is more correlated than a random walk, which has exponent $\alpha \approx -2$ (Feller 1966).

Previous studies, both empirical and theoretical, have shown that as communities grow, they settle into a climax state thus becoming less invasible (Post and Pimm 1983, Dickerson and Robinson 1986, Robinson and Edgemon 1988, Drake 1990, Law and Morton 1996). Studies of this kind focus on a limited set of species interacting over a narrow time horizon. The pattern we observe is similar to other community assembly models in its initial growth, but it differs markedly in that a final climax state is never reached. Our model may be thought of as acting on a longer time scale such that a balance of colonization and extinction is maintained.

In Fig. 1B we illustrate the size distribution of the communities for the values 0.4, 0.45 and 0.55 of average interaction strength σ from a normal distribution. The mean of the distribution shifts to higher values as σ decreases. This indicates that communities with overall weaker interactions can support a larger number of species, which agrees, in principle, with the general theoretical result that weak links are more stabilizing (May 1974, McCann et al. 1998). Communities with strong links in our system cannot sustain as many species as those with weaker links because the probability of becoming unstable, as species are added to communities with strong interactions, increases more rapidly than in communities with weaker interactions.

Due to the stationarity of this stochastic process, it is appropriate to analyze the stability of the system in terms of variation in community size. Communities that vary widely around the mean are less stable than communities that stick more closely to the mean. A cursory glance at the variance of community distribution (Fig. 1B) indicates that it gets larger as community size increases. We do not believe, however, that variance is an accurate descriptor of stability here, so instead we investigate the variability of our communities by calculating the coefficient of variation (CV), which standardizes the measure of fluctuation in community size for different means. Large communities are more likely to lose more species than small communities because they have more to lose. It is how many species these communities lose on a percentage basis that we are concerned with.

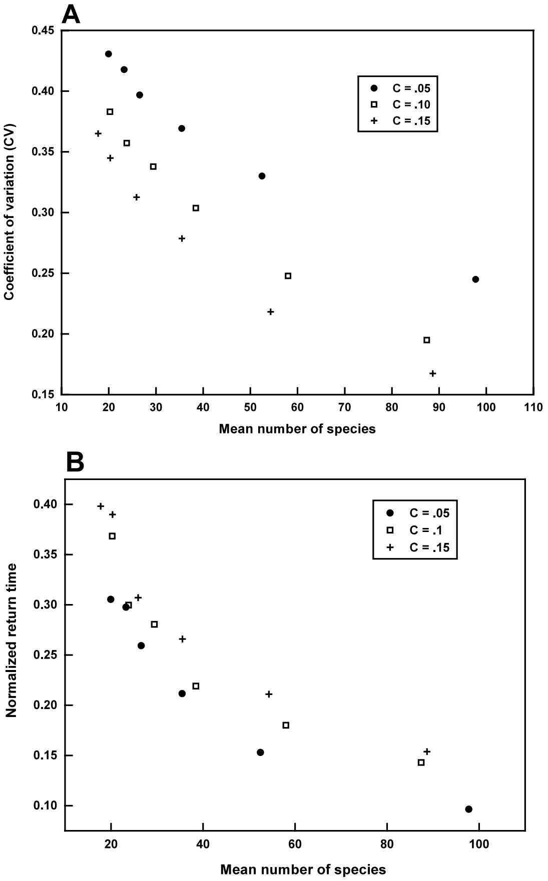

Fig. 2. (A) The coefficients of variation and (B) return times to equilibrium are plotted for communities with different mean number of species for three different connectance levels C.

Our results indicate (Fig. 2A) that increasing mean community size leads to decreasing values of CV indicating that more diverse communities are less variable. To be more specific, diverse communities in absolute terms lose more species than depauperate ones, but as a percentage of their members they lose less.

The distribution from which interaction strengths were drawn did not change our results qualitatively. Communities assembled from uniform and basin shaped beta distributions both showed the same pattern of decreasing CV with increasing diversity. What appears to be driving the reduction in CV is the assembly process itself. Figure 2A also reveals that as connectance C increases for a given community size, CV decreases.

Another way to investigate the variation of our communities is to look at the size distribution of species extinction cascades. Communities with more large cascades relative to small ones may be thought of as more variable than communities with more small cascades relative to large ones. The distribution of these extinction cascades generally showed a power law variation with exponent β (represented as slope on a log-log plot) over one decade followed by an exponential cut-off due to the finite size of our system (Fig. 3). Specifically,

$$N = \alpha S^{-\beta} \qquad (3)$$

where S is the cascade size, N is the number of such cascades and α and β are constants. The value of β increases with increasing mean community size where α and β are greater than zero. The larger the value of the exponent, the more negative the slope of the power law and thus the smaller the frequency of large cascades, corroborating our previous result that communities decrease in variation as they get larger.

In addition to analyzing the variation in community size, we investigated return times to mean community size. We did this using two approaches. In the first, we used the mean of our time-series as a threshold, and evaluated the number of time-steps between each departure and subsequent return to this threshold. In the second, we looked at return times to the mean from points a maximum or minimum distance away from the mean. The length of each of these interval periods was stored in a vector. We then take the mean of this vector and divide by the variance of the time series. Normalizing the mean by the variation is analogous to the normalization procedure we previously used for variance. In that case we compared the variance of distributions drawn from different means. Here, we compare means drawn from distributions of different variance. The qualitative results of both measures of return time were the same. Namely, as seen in Fig. 2B, return times decrease with increasing mean community size and decreasing connectance.

Discussion

Robert May's results and subsequent work indicate that large randomly assembled ecosystems tend to be less dynamically stable as they increase in complexity (May 1972, Gilpin 1975, Pimm 1982, Hogg et al. 1989). Specifically, if $\sigma^2 nC > 1$ then the system will almost surely be unstable. Real ecosystems are not randomly constructed, however, but rather gradually assembled through a long series of invasions and extinctions. This is a non-equilibrium situation where – driven by external factors such as weather, species invasion or some other kind of disturbance – the system is constantly changing over time. Our assembly model simulates this process of gradual formation, and thereby builds a more realistic ecosystem.

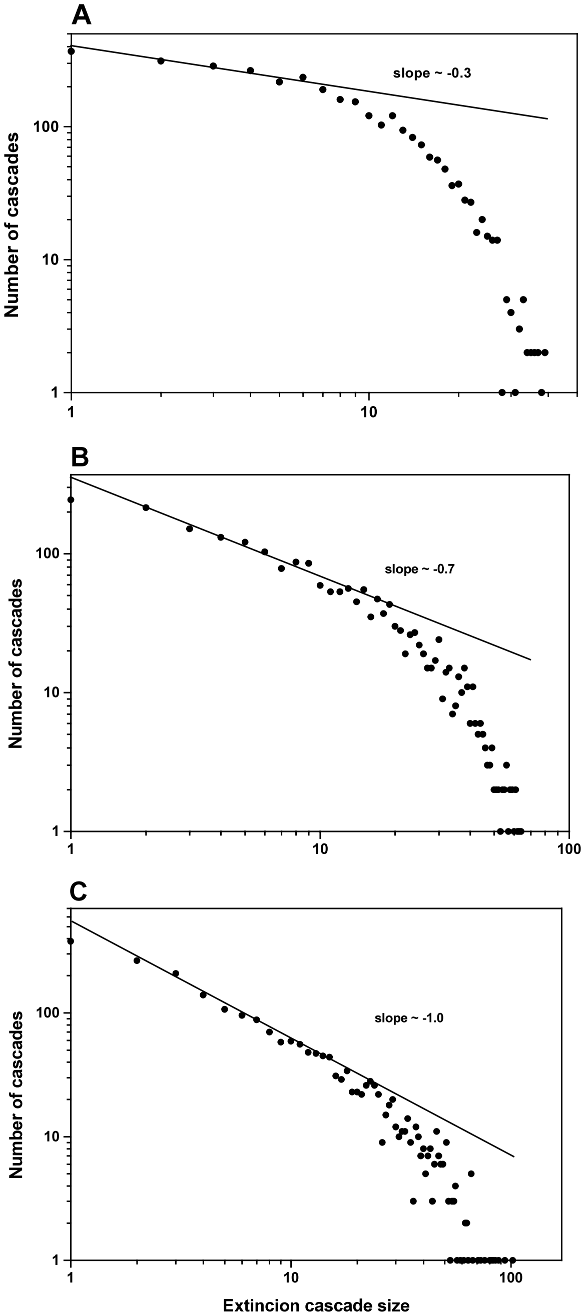

Fig. 3. The distributions of extinction cascades is plotted for communities with a mean of (A) 20 species (B) 52 species and (C) 98 species. Cascade distributions are power law with exponential tails due to the finite size of the system. As community size increases the slope of this power law decreases indicating that the smaller a community gets, the more likely it is to experience large extinctions on a relative basis.

Our model shows the same directional relationship between the variables σ, n and C on community size that May demonstrated on community stability. Because our method of constructing communities progresses according to a specified algorithm that reflects the community assembly process, however, our systems are not subject to the same stability criterion as May. In order to build larger and larger communities, we must decrease mean interaction strength or connectance, but once a community is established, species-rich communities are less variable and return more quickly to mean levels than do less diverse ones.

Our results lend theoretical support to the view, espoused by Charles Elton, that more diverse ecosystems such as those found in the tropics are less prone to large oscillations in species abundance, and hence more stable, than less diverse ecosystems such as those found in the arctic or horticultural fields (Elton 1958). This idea originally received theoretical justification based on the assumption that a multiplicity of predator-prey associations in a community frees it from dramatic changes in abundance when one of the prey or predator species declines in density (MacArthur 1955). May's result, however, ran counter to this argument. Our model corroborates both views. Stronger interactions and increased connectivity lead to smaller communities, yet when the system is diverse and highly connected, it is likely to be less variable than its sparsely connected and less diverse counterpart.

Our focus on CV should give conservation biologists pause. Are we worried about species loss on an absolute basis or on a relative basis? Because large communities have more species, we should expect them to lose more species. The fact that we predict that they will lose less on a percentage basis, however, implies that being large is stabilizing.

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