Determining the Effects of Species Richness on Community Stability: An Assembly Model Approach

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The stability-diversity debate in ecology has been polarized by the often contradictory results of empirical and theoretical studies. Here we present a novel way to model community assembly based on eigenvalue analysis and consider the stability of assembled communities. In concordance with previous work, we find that communities with weaker mean interaction strength support a larger number of species. However, as communities increase in average size, resistance, measured as the coefficient of variation of community size and resilience, measured as the average return time to mean community size, both increase. Our results suggest that further study of the temporal variation in community properties may be an important tool in resolving the stability-diversity debate.

I. INTRODUCTION

Understanding the relationship between community stability and species diversity has been a major focus in ecology for the latter half of this century. As such, several components of community stability have been studied in the literature [1]. Among these are resistance – the ability of a community to resist change in the face of a potentially perturbing force [1,2], resilience – the ability of a community to recover to normal levels of function after disturbance [3] and invasibility – the ease with which newcomers become established members of a community [4].

While field studies have generally shown that diversity enhances stability [5–7], modeling efforts have tended to support the opposite conclusion [8–11]. Efforts to reconcile these results have begun to elucidate the mechanisms by which diversity may serve to promote or diminish stability. For example, theoretical models have shown that weak interactions between species tend to promote stability [12,13]. Recently, Doak et al [14] have shown that statistical averaging alone, in the absence of species interactions, may lead to positive correlations between species diversity and aggregate community properties such as total biomass (but see Ref. [15]). By building simple models that reflect our intuition gleaned from empirical work, we may converge on an understanding of how the disparate processes involved lead to the patterns observed.

Much of the theoretical work on the subject was stimulated by Robert May's seminal work showing that randomly constructed interaction matrices decrease in stability as they increase in complexity [9]. Subsequent authors have examined the effects of hierarchical organization [16,17], feasibility criteria and Lotka-Volterra dynamics [10] on interaction matrices with results similar to May. Recently however, McCann et al [13] analyzed realistic consumer-resource configurations in simple communities (4 species) and showed that weak to intermedi-

ate links between species dampened oscillations between consumers and resources. While this work clearly points to a mechanism promoting stability, it is unclear how this result scales to communities with more than four species. Though the theoretical work of May has been criticized as an over simplification of nature, it has been instructive as a null model where dynamics are influenced by diversity alone [18]. The challenge to ecologists is to determine how processes co-varying with complexity affect stability.

An alternative approach to modeling communities is to assemble them one species at a time, thereby relaxing the conventional assumption, held in many theoretical studies, that communities are created spontaneously. Models of this kind typically draw species from a limited pool of resources and consumers until a final community state is reached [19–21]. 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 examining the resilience and resistance of communities using such an approach.

Here we present the results of a simple community assembly model. Like Ref. [9], we use interaction matrices as our descriptor of community interaction, but rather than generating these spontaneously, we assemble them one species at a time. This results in a dynamic view of community structure that differs substantially from May's and, in so doing, provides us with new intuition about the possible ecological mechanisms that may affect stability.

II. METHODS

The following model is presented within an ecological framework of interacting populations. Much like previous work in this area, however, the problem is a general one with potential application to economic, social, informational and other such networked systems. While our approach is inspired by ecological intuition, our results may have broader application. 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 $C = E(p)$) of our ecological network approximates the values reported in empirical food web studies. We compare scenarios $C = 0.05$, 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$(0, \sigma^2)$ 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 population 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 the 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,

$$\frac{dx}{dt} = Ax, \qquad (1)$$

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 [9], 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 [22] 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 stability properties of the system. This is done 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 [9]. 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 stability properties of the system and repeat the process. The model is allowed to run for $5 \times 10^5 - 10^6$ iterations, which is more than sufficient to assess the steady state properties of the system.

III. RESULTS

Communities in our model initially grow monotonically and then settle into a pattern of growth spurts and collapses [Fig. 1]. This process of community growth and decline ultimately defines a stationary stochastic process in the sense that a limiting distribution of states is approached assymptotically. In other words, the driven stochastic system attains a non-equilibrium steady state. Fourier transformation of the resulting time series shows that the spectra can be modeled by a power law of the form,

$$P = \gamma f^{\alpha}, \qquad (2)$$

where P is the power spectral density of the time series, f is the frequency and γ and α are constants. An exponent of $\alpha = -3$ indicates that the process of community growth and collapse is more correlated than a random walk which has exponent -2 [23].

Previous studies, both empirical and theoretical, have shown that as communities grow, they settle into a climax state thus becoming less invasible [19,24,25,20,21]. 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. 2 we illustrate the size distribution of the communities for the values 0.3, 0.4 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 [12,13]. 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. Resistance in our model system may be thought of as the amount by which community size changes in relation to the mean. A cursory glance at the variance of community distribution [Fig. 2] indicates that it gets larger as community size increases. This would seem to indicate that larger communities are more unstable. We do not believe, however, that variance is an accurate descriptor of resistance here, so instead we investigate the resistance 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 the relative loss, i.e., how many species these communities lose on a percentage basis, that we are concerned with.

Our results [Fig. 3(a)] show that increasing mean community size leads to decreasing values of CV, indicating that more diverse communities are more resistant. 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. This distinction addresses the question of what exactly we mean by stability in nature, a point which we will return to later.

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 increasing stability with increasing diversity. What appears to be driving the reduction in CV is the assembly process itself. Fig. 3(a) also reveals that as connectance C increases for a given community size, CV decreases, indicating that more highly connected communities are more resistant.

Another way to investigate the resistance of our communities is to look at the size distribution of the species extinction cascades. Communities with more large cascades relative to small ones would be less resistant 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. 4). Specifically,

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

where S is the cascade size, $N(S)$ is the number of such cascades and κ and β are constants.

The value of β increases with increasing mean community size where $a, b > 0$. 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 increase in resistance as they get larger.

In order to investigate the resilience of our communities, we looked at average 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 at a maximum or minimum distance away from the mean. The length of each of these interval periods was stored in a vector. Resilience was then taken to be the mean of this vector divided 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 with different means. Here, we compare means drawn from distributions with different variance. The qualitative results of both resilience measures were the same. Namely, as seen in Fig. 3(b), resilience increases with increasing mean community size and decreasing connectance.

IV. DISCUSSION

May's results and subsequent work indicate that, in general, large randomly assembled ecosystems tend to be less dynamically stable as their diversity increases (measured by degree of connectivity, system size and distribution of interaction strength). High diversity networks are possible however, though they will become more and more rare with increasing diversity. The assembly of ecosystems, constrained by stability condition, is a process by which one can obtain large ecosystems through a procedure akin to a selective search process in the space of all possible ecosystems. The goal of the process is to come up with the most diverse ecosystem that is yet dynamically stable. Our method, therefore, is a compromise between the often contradictory approaches of ecological field study and mathematical modeling of ecosystems. Real ecosystems are clearly not randomly constructed, but rather gradually assembled through a long series of invasions and extinctions. This is a non-equilibrium situation where the system is constantly changing over time, driven by external factors such as weather, invasion by species from the outside or some other kind of disturbance. The assembly model tries to simulate this process of gradual formation and thereby tries to build up a realistic ecosystem.

While at first glance our results appear to contradict [9], the situation is more complex. May's general result was that if either the number of species n, the connectance C, or the interaction strength σ exceeds a critical value, the system becomes unstable. Specifically if $nC\sigma^2 > 1$ then the system will almost surely be unstable. Our model shows the same directional relationship between the variables σ, n and C on community size that May demonstrated on community stability. However, because our

method of constructing communities progresses according to a specified algorithm that reflects the community building process, our systems are not subject to the same stability criterion as in [9]. Building larger communities in our model does require tuning down mean interaction strength or connectance, but once a community is established, more diverse communities are more resistant and resilient than less diverse ones.

This may have important real world implications. Not only does it suggest that increased biodiversity leads to greater stability but it suggests possible consequences for the extinction of species from ecosystems. If removing species causes those species that remain to adapt to changing conditions in such a way that there is an overall increase in average interaction strength, adding species in the future may become more difficult. This argument hinges on the time scale of the response of communities to a loss of species. Longer time scales may lead to adaptations or behavioral modifications that would lead to more specialist life history traits, whereas short times scales likely would not. For example, a generalist predator species faced with the extinction of a prey item, may modify its behavior so as to focus its hunting abilities on its remaining prey species. If, in the future, this prey species recolonizes the system, it may no longer be recognized by the predator as food and so lead to possible instabilities in the system through exploitative competition with the other prey species. Species loss may lead to state changes that cause average interaction strength to increase, thus causing depauperate communities to become the status quo.

Our results indicate that the larger the connectance of our community matrix, the more resistant the community becomes. This lends credence to the view traditionally espoused by field ecologists that the more highly connected an ecosystem is, the more stable it should be [26]. Though this idea once 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 [27], May's result ran counter to this argument. In a sense, our model seems to corroborate both views. Stronger interactions and increased connectivity lead to smaller communities, yet given a diverse, highly connected system, it is more likely to be stable than its low diversity, sparsely connected counterpart.

Measures of stability have tended to depend on whether the work was theoretical or empirical. Empirical studies have traditionally focused on dependent variables having to do with aggregate measures such as total community biomass [5,28], respiration and water retention [29]. Modeling studies, on the other hand, have tended to avoid such methodology and focus on the effects of diversity on species richness per se [9,22,10,17,13]. As such, it is not surprising that the results of these efforts have differed so much in the direction of their findings. While this work still differs from empirical studies in its focus on species richness as a dependent variable rather than the more common aggregate community properties that have been the mainstay of empirical studies, it offers a clear mechanism that may be expected to drive diversity-stability relationships in the real world. Furthermore, we suggest that the coefficient of variation may be a more accurate measure of stability than variance when measuring time series with different means. While this is not a new idea [14] it is one that should give us pause. Should we be worried about species loss on an absolute basis or a relative basis? Large communities simply have more species and so we would expect them to lose more species. The fact that we predict that they they will lose less on a percentage basis, however, implies that there is a stabilizing effect of being large.

V. CONCLUSION

Building basic models based on a knowledge of ecological process allows us to explore the underlying mechanisms at work in a system. Our results indicate that the dynamics of the assembly process leads more diverse communities to be more resistant and resilient to perturbation. Furthermore, increasing the connectance of the community leads to higher resistance and lower resilience. By adding community assembly to the modeling framework laid out by May, we gain new insight into the relationship between complexity, diversity and stability. Our results indicate that the larger and more highly connected the ecosystem, the weaker the average interaction strengths will be. Given two communities in the real world, however, the more diverse, more connected system is likely to be the most stable. This work suggests that the assembly process and, more generally, community flux over time, provides a useful framework for investigating the effects of species diversity and other ecological interactions on stability. It also implies that the traditional approach of taking snapshot views of community pattern may be inadequate in efforts to build an understanding of underlying community process.

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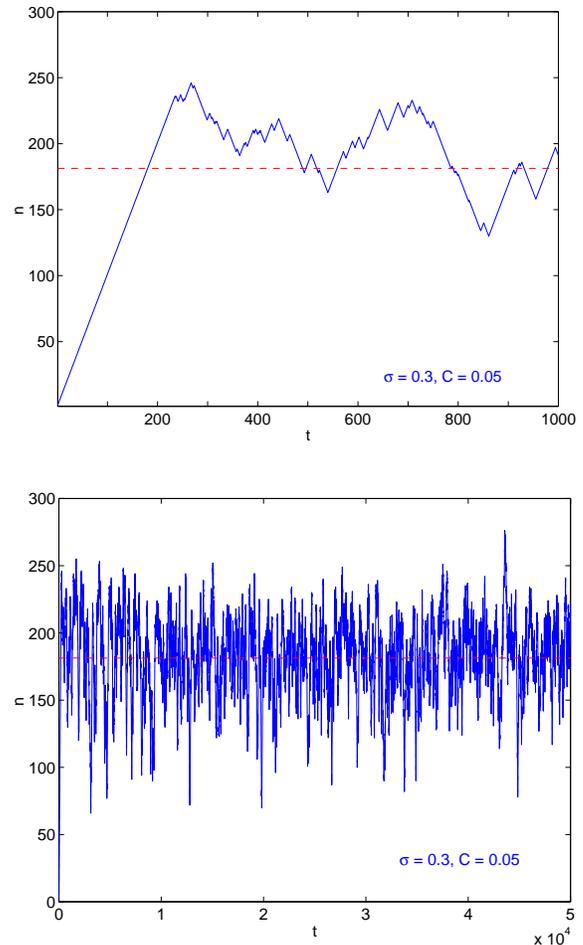
FIG. 1. The number of species n in a model ecosystem is plotted over time for connectance $C = 0.05$ and average interaction strength $\sigma = 0.3$. The top figure shows the first 1000 timesteps of the bottom figure. The dashed line indicates the mean number of species in the community.
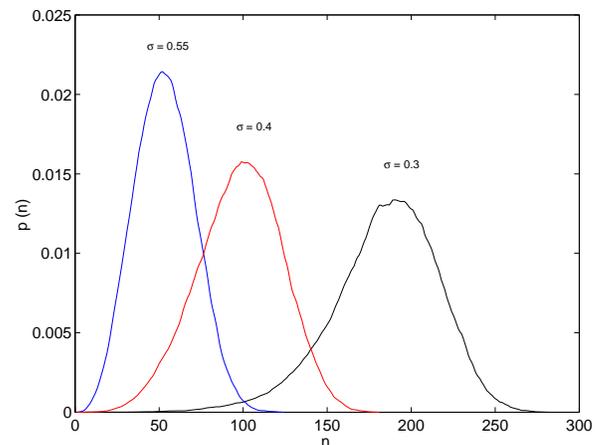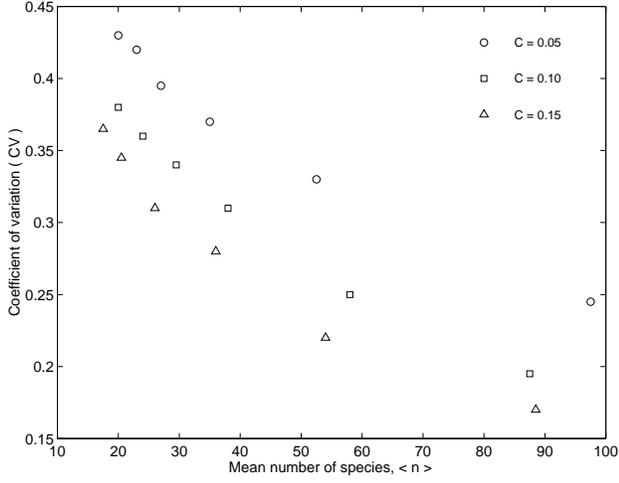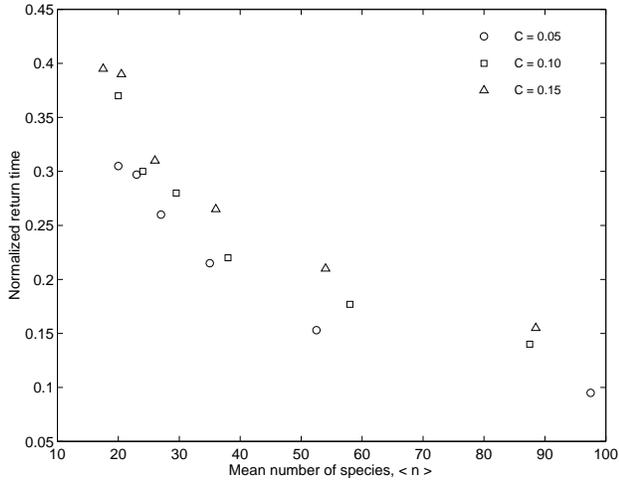

FIG. 2. The frequency distribution of species diversity in an assembled community is plotted for three different average interaction strengths σ.
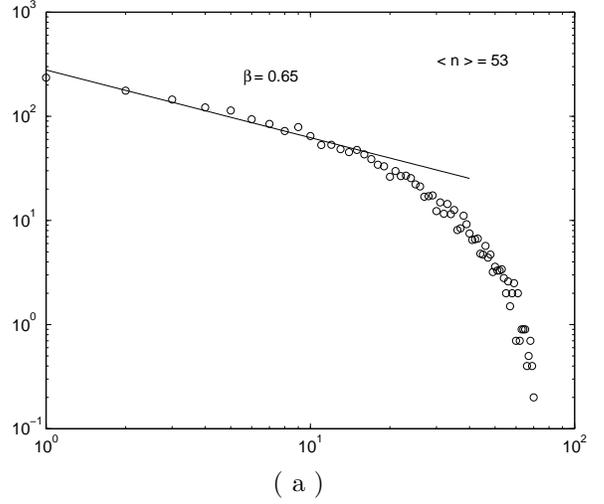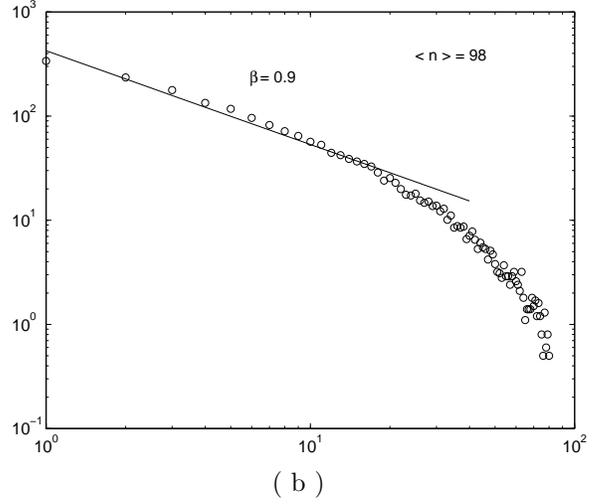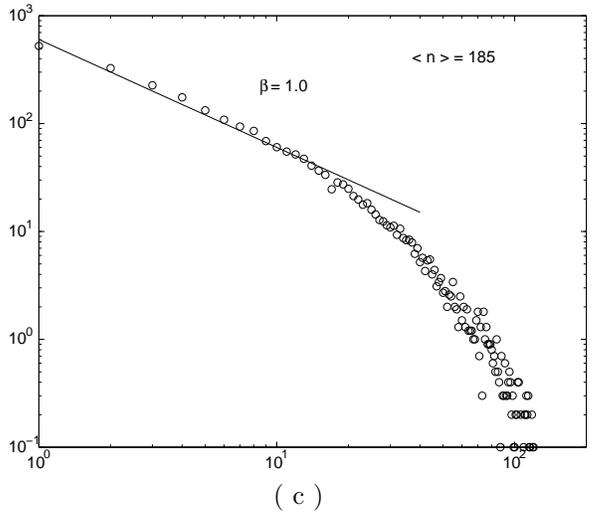
(a)

(a)

(b)

FIG. 3. (a) The coefficient of variation and (b) the normalized return time to equilibrium is plotted for communities with different mean number of species for three different connectance values C.

(b)

(c)

FIG. 4. The frequency distribution of extinction cascade sizes is plotted for communities with a mean size of (a) 53 species (b) 98 species and (c) 185 species.