Analysis of Dynamical Complex Network of Ecological Stability Diversity and Persistence

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Abstract

Explorations of ecological networks have led a long line of scientists to debate the influence of diversity (number of nodes) in terms of species richness and complexity in terms of the number and structure of interactions. This research on how vast numbers of interacting species manage to coexist in nature reveals a deep disparity between the ubiquity of complex ecosystems in nature and their mathematical improbability in theory. In this paper ecological networks are assumed to be complex dynamical network. Population dynamics is simulated over ecological complex network and species migration and changing food habits are found to be two keystones to species persistence on the earth. Also a comparative study on stability, complexity and persistence over complex dynamical network is shown. Here, we show how integrating models of food-web structure and nonlinear bioenergetic dynamics bridges this disparity and helps elucidate the mechanics of ecological complexity. Structural constraints of these networks including the trophic hierarchy, contiguity, and looping formalized by the "niche model" are shown to greatly increase persistence in complex model ecosystems. We explore the interplay of structure and nonlinear dynamics by systematically varying diversity, complexity, and function in order to "elucidate the devious strategies which make for stability in enduring natural systems." ([19]). Our exploration expands on previously proposed strategies and shows how recently discovered structural and functional properties of ecological networks appear to promote stability and persistence in large complex ecosystems.

Keywords: Dynamical complex Network, Ecological Network Structure, Food web, Stability, Diversity, Persistence, Species Migration, Changing Food Habit.

Bioenergetic Model of Nonlinear Food-Web Dynamics

All models of network structure require the number of species in the system (S) and the density of trophic links (L) in terms of directed connectance. $C = L/S^2$) as input parameters, but vary in the degree to which they constrain network organization In the random (model ([1], [2]), any possible link among S species occurs with the same probability equal to C of the empirical web. This creates webs as free as possible from biological structuring while maintaining the fundamental observed network properties of S and C. The modified ([3]) cascade model ([1]) creates a hierarchical structure by assigning each species a random value drawn uniformly from the interval [0,1] and giving each species a probability $p = 2CS/(S-1)$ of consuming only species with values less than its own. The niche model ([3]) similarly assigns each species a randomly drawn "niche value." The species are constrained to consume all species within one beta-distributed range of values whose mean $= C$ and whose uniformly and randomly chosen center is less than the consumer's niche value.

The dynamic model closely follows previous work ([4],[5],[6],[7]) but is generalized to n species and arbitrary functional responses. Extending the earlier notation ([4]) to n-species systems, the variation of Bi, the biomass of species i, over time t, is given by n

$$B'_i(t) = G_i(B) - x_i B_i(t) + \sum \left(x_i y_{ij} \alpha_{ij} F_{ij}(B) B_i(t) - x_j y_{ji} \alpha_{ji} F_{ji}(B) B_j(t) / e_{ij} \right) \quad (1)$$

The first term $G_i(B) = r_i B_i(t)(1 - B_i(t)/K_i)$ is the gross primary production rate of species i where r_i is the intrinsic growth rate that is non-zero only for basal species, and K_i is the carrying capacity; the second term is metabolic loss where x_i is the mass-specific metabolic rate; the third and fourth terms are gains from resources and losses to consumers respectively, where y_{ij} is the maximum rate at which species i assimilates species j per unit metabolic rate of species i; α_{ij} is the relative preference of species i for species j compared to the other prey of species i. α_{ij} is normalized so that the sum of α_{ij} ($0 \leq \alpha_{ij} \leq 1$) across all j is 1 for consumer species and 0 for basal species; $F_{ij}(B)$, a non-dimensional functional response that may depend on resource and consumer species' biomasses, gives the fraction of the maximum ingestion rate of predator species i consuming prey species j; e_{ij} is the conversion efficiency with which the biomass of species j lost due to consumption by species i is converted into the biomass of species i. Dividing the last term by e_{ij} converts the biomass assimilated by consumer j into biomass lost by resource i. Non-zero α_{ij}'s are assigned according to the topology specified by the structural models. The many parameters in these equations have been estimated from empirical measurements ([4]) and there are wide ranges of biologically plausible values.

While a wide variety of functional responses have been proposed in the literature ([9]-[14]), our model uses two different families of functional responses that have both mechanistic and empirical justifications ([11]). The first F_H, ([18]) is based on a parameterized form ([12],[13]) of Holling's ([14],[9]) type II and III responses and generalizes earlier multiple species type II responses ([7], [8]). F_H of predator I consuming prey j is

$$F_{Hij}(B) = \frac{B_i(t)^{1+q_{ij}}}{\sum_{k=1}^{n} \alpha_{ik} B_k(t)^{1+q_{ij}} + B_{0ji}^{1+q_{ij}}} \tag{2}$$

Where B_{0ji} is the half saturation density of species j when consumed by species i and q_{ij} controls the form of F_H. The functional response decelerates and accelerates feeding on relatively rare and abundant resources as q increases and decreases, respectively (Fig. 1). The range $0 < q_{ij} \leq 1$ generalizes F_H so that it can smoothly vary from standard type II responses ($qij = 0$) used in many earlier studies ([4],[5],[6],[7],[14],[8]) to the standard type III response ($q_{ij} = 1$) ([2],[13],[4]) that stabilizes two-species systems.

Topology and Dynamics

We analyzed the behavior of our dynamic network models with respect to the combined variation of several key parameters. The models' high dimensionality prevents full examination of all the combinations of parameter values that were analyzed. Instead, we present a sequence of results that describes the effects of varying a few parameters and then fix these parameters and analyze effects of varying other parameters. Fixing the parameters at different values quantitatively changes the results. Therefore, we focus on overall behaviors that resist qualitative changes due to alternative choices. Each simulation begins by building an initial random, cascade, or niche model web of a certain size (S_0) and connectance (C_0). The integrated structure-dynamic model then computes which species persist with positive biomass greater than an extinction threshold of 10-15 after 4000 time steps. Following any extinctions, a "persistent web" with SP species and connectance CP remains. As the structural models are stochastic, this procedure is repeated a large number of times so that statistical properties of the integrated structure-dynamic model is ascertained. Both the functional response control parameters and a predator's preferences among prey are varied to study effects of food web dynamics on persistence and food-web structure. For each model iteration, we define absolute persistence $PA = SP$ and relative persistence as $PR = SP/S_0$. Overall persistence P is the mean value of PR across a set of iterations. Topological properties of the persistent webs were compared to different versions of niche webs. Here, we focus on the distribution of trophic levels and connectivity among species by examining the fractions of top, intermediate, basal, omnivorous, and herbivorous species, mean trophic level, and the standard deviation of the connectivity of each species.

Effect of Dynamics and Structure on each other

Our results generally illuminate how the structure of ecological networks may influence their function by examining the effects of diversity and complexity on ecosystem dynamics. One early and remarkably durable theory based on linear stability analyses of random networks ([19]) proposed that S and C have hyperbolically negative effects on stability. Qualitatively similar effects occur in our nonlinear analyses of more ecologically realistic networks, but the effects are linear rather than hyperbolic ([19]), perhaps due to the differences between linear stability and nonlinear persistence. C affects persistence much more strongly than does S. This is illustrated by the regressions in which variance in C explains over twice as much variance of PR as does variance in S. This Greater importance of C than S to persistence had been previously noted but the negative effects of C observed here are opposite the previously noted positive effects ([22],[8],[20]). The contiguous niches and looping ([23]) in the niche model appears confer even more persistence on food-web networks. The hierarchical ordering of the cascade and niche models is easily interpreted as a mechanistic formalization of energy flowing from plants to upper trophic levels. Models that ignore such distinctions between plants and animals by making all species capable of growing without consuming other species ([20]) fail to detect the significance of non-random and hierarchical network structure ([24]). Niche space as formalized by the niche model is much less easily interpreted and deserves more study to understand which evolutionary, ecological, and mathematical factors underlie the improved the model's improved empirical fit and persistence. These effects of network structure on dynamics closely mirror the degree to which model networks mimic the structure of ecological networks. This suggests that scientists should be somewhat sceptical of models that mimic very few network properties.

Our work illuminates how the functioning of ecological networks influences their structure by examining the effects of nonlinear dynamics on the topology of complex food webs. Within network science, such analyses and influences

may be only generalizable to networks such as food webs and pollination webs ([24]) whose nodes critically depend on interactions for their continued existence. Within ecology, our results show for the first time that the stabilizing effects of both predator interference and respective decelerated and accelerated feeding on rare and abundant resources found in small modules of two species also apply to much larger networks with 50 or more species. This enables large complex food webs to sustain many more species than networks governed by standard type II responses. We also show that small and perhaps empirically undetectable changes in functional responses foster greatly increased persistence in model ecosystems ([21]). This suggests that tiny amounts of prey switching behaviour of consumers ([14], [20]) or refuge seeking behaviour of resources ([13], [25]) has large effects on the structure and dynamics of complex ecological networks. This suggestion complements recent empirical findings ([25]), suggesting these functions as some of nature's more prevalent and important stabilizing strategies. More strikingly, persistent webs have higher fractions of basal species and consumers with lower mean trophic levels than do niche webs. This is consistent with the niche model's systematic overestimation of empirically observed food-chain lengths ([3]) assuming that empirical webs have more persistent topologies than do niche webs.

A simulation of bird migration dynamics in wetland ecosystem on complex network

We form a complex network of this type of ecological patches of wetland ecosystem contains aquatic flora-fauna, grass, herbivorous and bird, coupled them by the migration of bird species, that is we consider the only interaction between spatially separated patches be bird migration and other species is considered non-migratory. Thus we form a complete complex network of ecological patches with random weight. Some particular solution of this network showed extinction of non-migratory predator species but migratory one sustained all the time, however not in a stable trajectory. So we tried to address the question whether migration of predator has some impact on sustainability of an ecosystem.

Let there be n distinct patches. We construct a cost matrix that is a normalized (row sum and column sum is one, the matrix is symmetric) n×n matrix with diagonals zero is the cost to go from one patch to another, a migration function and a flag. We assume migration takes place if the catch ability function goes down to certain critical value let the n×1 parameter me cch. Flag is zero if cch less than migration function mg otherwise migration starts and flag goes to 1. So using the same notation for variables the system becomes as follows

$$X(i) = d(i)\frac{x(i)^2 z(i)}{\{x(i)^2 + D_1(i)\}}, \quad \begin{array}{l} flag = 1 \ \ if \ \ cch(i) > X(i) \\ = 0 \ \ otherwise \end{array}$$

Now the migration takes place exponentially from 0 at $X(i) = cch(i)$ and $X(i)$ at $X(i) = 0$.

$$Mg(i) = flag.\left[\frac{\exp(cch(i) - X(i)) - 1}{\exp(cch(i)) - 1}\right]^2$$

$$\begin{cases} \dfrac{dx_i}{dt} = a_i x_i - b_i x_i^2 - c_i x_i y_i - d_i \dfrac{x_i^2 z_i}{(x_i^2 + D_{1i})} \\[2mm] \dfrac{dy_i}{dt} = e_i y_i - f_i y_i^2 - g_i x_i y_i - h_i \dfrac{y_i^2 u_i}{(y_i^2 + D_{2i})} \\[2mm] \dfrac{dz_i}{dt} = -\theta_i z_i + \phi_i \dfrac{x_i^2 z_i}{(x_i^2 + D_{3i})} + \sum_{j=1}^{n} cst_{i,j}.Mg_j.z_j \\[2mm] \dfrac{du}{dt} = -\omega_i u_i + \psi_i \dfrac{y_i^2 u_i}{(y_i^2 + D_{4i})} \end{cases} \quad \forall i = 1,2,\ldots n \qquad (3)$$

Where $x(i), y(i), z(i), u(i)$ are the population of aquatic flora and fauna grass bird and herbivores species respectively. $cch(i)$ is the critical catch ability parameter for each patch. Where a_i is the 'non reproductive growth rate' of the 'aquatic flora and fauna biomass' (x_i), b_i measures the 'severity of the intra species competition' among individual 'aquatic flora and fauna', d_i is the 'maximum rate' at which bird population (z_i) consumes the 'aquatic flora and fauna'; D_{1i} is the measure of the 'half saturation constant'. Similarly e_i represents the 'non reproductive growth rate' of the 'grass' (y_i) and f denotes the inverse of per capita water availability for y_i. c_i and g_i measure the intensity of

competition between 'aquatic flora and fauna' and 'grass'. h_i is the 'maximum rate' at which herbivorous population(z_i) consumes the 'grass'. θ_i, φ_i and ω_i, ψ_i are mortality rates and conversion coefficient for the bird species and herbivorous species respectively. D_{2i}, D_{3i}, D_{4i} are the half saturation constants appearing in the numerical response of grass, bird and herbivorous respectively.

We have found the same trend for stability persistence data simulating two species prey-predator system in similar complex network. Now we try to approach modeling a closed patch multi species prey-predator system in this way. We consider one predator and n prey in the system. We argue migration is not only spatial migration but also changing behavioral or resource utilization habits of a species could effect on the ecological sustainability. Here we consider the predator has some migratory behavior of its food habit that is if a particular prey becomes scarce the predator changes their food habit preference over other species. Now we divide the ecology in n patches of two species prey predator system with one prey and the fraction of the biomass of the predator equal to the fraction of that prey in all preys. We are arguing that n fractions of prey are migrating (that is changing their food habit) randomly between the patches. Again this changing of food habit is governed by the availability of prey and we define the migration function and coupling similarly. Hence we reach the same migration model with one predator and a prey. As we got the same trend for stability and persistence we could argue that the changing of food habit or migration in larger sense is increasing predator's sustainability with increasing diversity up to some limit.

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