

Comment on “Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability”

A central issue in the diversity–stability debate during the last several decades of community ecology and biodiversity research has been the theory that increases in community complexity decrease ecological stability (1, 2). Notwithstanding positive complexity–stability relationships under specific model conditions (3), population persistence in large and complex natural food webs remains a long-standing dilemma in ecology. Certain distributions of fixed interaction strengths in model networks (4) and empirical food webs (5) appear to reduce but not invert the negative effect of complexity on network stability. More recently, Kondoh (6) examined the consequences of variable interaction strengths by modeling consumer species adaptively switching food sources. These models inverted the negative complexity–stability relationship and generated extremely complex yet surprisingly stable networks. These results, if generally applicable to ecological systems, would mark a profound paradigm shift within the diversity–stability debate and environmental biology.

In light of the Kondoh result’s importance, we reexamined the possible inversion of the negative complexity–stability relationship, focusing on three aspects of the original analysis (6). One aspect concerned the use of the random and cascade models but not the recently developed niche model, which reproduces some important structural characteristics of natural food webs more accurately than the former models (7). Another aspect was the use of a linear nonsaturating “type I” functional response of consumption to resource density that has largely been rejected in favor of nonlinear saturating “type II” responses, which capture the fact that organisms generally have maximum consumption rates that are not increased despite further increases in resource density (3, 4). The third aspect concerns the intrinsic growth terms that

cause consumers to grow without consuming resources, presumably because of immigration—though no emigration was allowed in the model (6). Although intrinsic growth terms are usual for organisms, such as plants, that receive energy from outside the ecological community, the persistence of trophic consumers generally depends on whether they can eat and assimilate more energy than

uses a nonlinear saturating type II functional response of consumers to their resource densities (4, 9, 10). We included the innovative foraging model of the original analysis (6) that allows consumers to adapt their consumption preferences towards resources that provide above-average energy gains per unit feeding effort.

We analyzed food web stability among 10-species networks across connectance (C) values from 0.10 to 0.45, where $C = L/S^2$, L denotes the number of trophic links, and S denotes species richness (Fig. 1). It should be noted that the cascade model constraints prevent networks from exceeding $C = 0.45$ when $S = 10$. The large majority of our networks did not persist without extinctions. This difference from the original results (6) most likely resulted from our model’s exclusion of intrinsic growth rates for consumers, who therefore more easily go extinct when they have too few resources. Consequently, we quantified food web stability differently from the measure of community persistence favored by Kondoh (6): the fraction of food webs that experience no extinctions. Instead, we quantified food web stability in a closely analogous manner as “community robustness,” the fraction of species within a network that persist. In contrast to some previous approaches that studied the return of populations to an equilibrium point after a perturbation (1, 5), our stability analysis is concerned with species persistence under equilibrium as well as nonequilibrium conditions and does not include any external population disturbances.

Without adaptive foragers, robustness decreased with increasing connectance (Fig. 1, A and C) as complexity–stability theory has long predicted (1). As the

fraction of adaptive foragers in cascade model food webs increases, community robustness increases and becomes positively correlated with connectance, as noted by Kondoh (6), when the fraction of adaptive foragers exceeds 0.5 (Fig. 1A). In contrast to Kondoh’s analysis, however, we found that this inversion is restricted to networks with initial $C > 0.2$ and adaptation rates of 0.025 and higher (Fig. 1B) for the cascade model.

In our niche-model networks, we obtained qualitatively different results. Although robustness increases with an increasing fraction and strength of adaptive foragers, adaptive

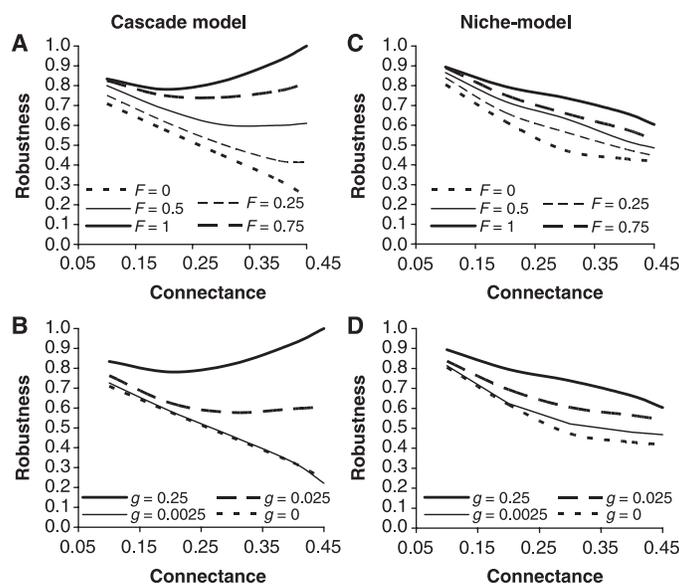


Fig. 1. Relationship between food web connectance and robustness in (A and B) cascade-model and (C and D) niche-model food webs, with different fractions of adaptive foragers, F (A and C), or different adaptation rates, g (B and D). $g = 0.25$ in (A) and (C); $F = 1$ in (B) and (D).

they lose to metabolism and predators (3, 4, 9).

Our reexamination tested the effects of adaptive foraging on food web stability using biologically and ecologically realistic structural and dynamic models. The structural models include the cascade (8) and niche models (7). The cascade model only allows higher-ranked species to eat lower-ranked species; the niche-model relaxes this constraint, allowing looping and cannibalism. We also used an empirically corroborated bioenergetic model of the nonlinear dynamics of species’ biomass that assigns an intrinsic growth rate only to primary producers and

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foraging never makes the connectance–robustness relationship positive (Fig. 1, C and D). Note that for niche-model networks without adaptive foragers, increasing C saturates of the negative connectance–robustness relationship, indicating that a minimum persistent web size (S) of 4 or 5 species is reached.

Together, these results indicate that the previously reported inverting effect of adaptive foraging on the negative complexity–stability relationship (6) is restricted to a highly specific model framework. Network persistence was mostly restricted to models including consumption-independent consumer growth. Positive complexity–stability relationships in such donor-controlled systems have been well known for several decades (3). After the removal of this internal consumer growth, positive effects of complexity on community robustness—that is, on species persistence—required simple network structures as provided by the cascade model, relatively high connectance values ($C > 0.2$), and a large fraction of adaptive foragers ($F \geq 0.5$; Fig. 1A) with high adaptation rates ($g \geq 0.025$; Fig. 1B). Although realistic values for the fraction of adaptive foragers and their adaptation rates are subject to speculation, our results clearly demonstrate that positive complexity–stability relationships are not to be expected for more complex network structures such as those given by the niche model, which include empirically common phenomena like looping and cannibalism. Furthermore, even in simple networks, the necessary connectance is higher than the large majority of empirical values (11), which requires that consumers are capable of consuming more than 20 per cent of the coexisting species on average. Irrespective of the primacy of food web models and the reasonableness of connectance values, our

results do not support the previous conclusion (6) that adaptive foraging can invert negative complexity–stability relationships into positive ones, irrespective of the structure of the network.

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10. As a dynamic model, we used a multispecies generalization of a widely used, empirically informed bioenergetic model (9) of the variation in biomass of species i , B_i , in time t depending on resources j in an n -species system:

$$\frac{dB_i}{dt} = r_i B_i(t) \left[1 - \frac{B_i(t)}{K_i} \right] - x_i B_i(t) + \sum_{j=1}^n \left[x_j y_{ij} \alpha_{ij} F_{ij}(\bar{B}) B_j(t) - x_j y_{ji} \alpha_{ji} F_{ji}(\bar{B}) B_j(t) \right] \quad (1)$$

where r_i is the growth rate and is nonzero only for producer species; K_i is the carrying capacity; x_i is the mass-specific metabolic rate; 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 consuming species j , normalized so that its sum equals one for consumer and zero for producer species. We used a multispecies generalization of the Holling (12) type II functional response of species i consuming species j :

$$F_{ij}(\bar{B}) = \frac{B_j(t)}{\sum_{k=1}^n \alpha_{ik} B_k(t) + B_{0ij}} \quad (2)$$

where B_{0ij} is the half saturation density of species j when consumed by species i . Based on previous empirically supported estimates (9), we applied empirical parameter values to the bioenergetic model, $x_i = 0.5$, $y_{ij} = 6$, $K_i = 1$, $B_{0ij} = 1$, that may describe a community dominated by invertebrates. We assigned random initial abundances to the populations, $B_i(0) = 0.05$ to 1, and measured the number of nonextinct species [$B_i(t) > 10^{-30}$] at $t = 4000$.

Following previous work (5), adaptively foraging species evolved their consumption preferences toward resources that provide above-average energy gains per unit feeding effort:

$$\frac{d\alpha_{ij}}{dt} = g_i \alpha_{ij} \left[x_j y_{ij} \alpha_{ij} F_{ij}(\bar{B}) - \sum_{k=1}^n x_j y_{ik} \alpha_{ik} F_{ik}(\bar{B}) \right] \quad (3)$$

where g_i is the adaptation rate of species i .

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13. The study was supported by the German Academy of Naturalists Leopoldina with funds of the German Federal Ministry of Education and Science (BMBF-LPD 9901/8-44) and by the U.S. National Science Foundation programs in Biocomplexity, Biological Databases and Informatics, and Interdisciplinary Graduate Education, Research and Training (IGERT).

18 April 2003; accepted 8 July 2003