Diversity of Interaction Types and Ecological Community Stability

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Ecological theory predicts that a complex community formed by a number of species is inherently unstable, guiding ecologists to identify what maintains species diversity in nature. Earlier studies often assumed a community with only one interaction type, either an antagonistic, competitive, or mutualistic interaction, leaving open the question of what the diversity of interaction types contributes to the community maintenance. We show theoretically that the multiple interaction types might hold the key to understanding community dynamics. A moderate mixture of antagonistic and mutualistic interactions can stabilize population dynamics. Furthermore, increasing complexity leads to increased stability in a "hybrid" community. We hypothesize that the diversity of species and interaction types may be the essential element of biodiversity that maintains ecological communities.

In nature, a number of species coexist to form a complex community network of interspecific interactions, contrary to a theoretical prediction that a complex community is inherently unstable (1). This paradox has stimulated ecologists to try to identify what maintains species diversity in natural communities (2–8). An ecological community has been viewed as a network of species connected by interspecific interactions. For example, a food web is the classical representation of "who eats whom" in the community (9). A mutualistic network, which represents mutualisms within a community, is another interaction network, the structure and dynamics of which are of particular interest in recent studies of community ecology (10). There is no doubt that independently developed studies of these interaction networks have contributed to our understanding of how interspecific interactions are related to population dynamics, what determines community structure, and how species diversity is maintained in nature (2–8). However, the applicability of these insights to real communities remains equivocal, because real communities are "hybrids" composed of different types of interactions (11–15). Mixing different types of interspecific interactions may dramatically alter our view of community dynamics and its relevance to community structure, which has been modeled only in small and simple systems [(16, 17), but see (14, 18, 19)]. Although a recent study showed that interaction type may affect community stability and its relationship with complexity (19), it has remained unanswered how changing relative frequencies of different interaction types, or the diversity of interaction types,

affect community stability and complexity-stability relationships. Here we present a theoretical hybrid community model, which involves both antagonistic and mutualistic interactions in varying proportions, and reveal a role of the multiple interaction types and their composition for the maintenance of complex communities.

Consider an ecological community consisting of N species, in which population dynamics is driven by interspecific interactions. If a Holling type I (linear) functional response is assumed, the population dynamics of species i is described as

$$\frac{dX_i}{dt} = X_i \left(r_i - s_i X_i + \sum_{j=1,\ j\neq i}^{N} a_{ij} X_j \right) \quad (1)$$

where X_i is the abundance of species i, r_i is the intrinsic rate of change in species i, s_i is density-dependent self regulation, and a_{ij} is the interaction coefficient between species i and species j. Of the three different network structures examined, here we describe the results for cascade (20) and bipartite (8) networks. In the cascade model, for each pair of species $i, j = 1,…, n$ with $i < j$, species i never consumes species j, whereas species j may consume species i (20). In the bipartite model, no interactions occur within the same trophic levels (6, 8, 21), and species numbers in each trophic level are the same. We define the proportion of connected pairs P as the proportion of realized interaction links L in the possible maximum interaction links L_{max} of a given network model ($L = P L_{max}$). In the cascade model, $L_{max} = N(N − 1)/2$, and in the bipartite model, $L_{max} = (N/2)^2$. With a biologically feasible assumption that interaction strengths decrease with increasing resource species, due to an allocation of interacting effort, the interaction coefficients a_{ij} ($i \neq j$) are determined as

$$a_{ij} = e_{ij} f_M A_{ij} \Big/ \sum_{k \in \text{resource of mutualist } i,\ k\neq i} A_{ik} \text{ and } a_{ji} =$$

$$e_{ji} f_M A_{ji} \Big/ \sum_{k \in \text{resource of mutualist } j,\ k\neq j} A_{jk} \text{ in a mutualistic}$$

interaction; $a_{ij} = g_{ij} f_A A_{ij} \Big/ \sum_{k \in \text{resource of predator } i,\ k\neq i} A_{ik}$

and $a_{ji} = -a_{ij}/g_{ij} = -f_A A_{ij} \Big/ \sum_{k \in \text{resource of predator } i,\ k\neq i} A_{ik}$

A_{ik} in an antagonistic interaction between consumer i and resource j, where A_{ij} is the potential preference for the interaction partners; f_M and f_A are the relative strengths of mutualistic and antagonistic interactions, respectively; and e_{ij} and g_{ij} are the conversion efficiency when species i utilizes species j in mutualistic and antagonistic interactions, respectively. For a Holling type II (nonlinear and saturating) functional response, we

used $a_{ij} = n_{ij} f_l \left(A_{ij} \Big/ \sum_{k \in \text{resource of sp. } i,\ k\neq i} A_{ik} \right) \Big/ \Big\{ 1 +$

$\sum_k h_{ik} \left(A_{ij} \Big/ \sum_{k \in \text{resource of sp. } i,\ k\neq i} A_{ik} \right) X_k \Big\}$, where f_l is

f_M or f_A, n_{ij} is e_{ij} or g_{ij}, and h_{ij} is the handling time (6, 8, 21). Parameters, s_i, e_{ij}, g_{ij}, A_{ij}, and h_{ij} are randomly chosen from a uniform distribution between 0 and 1, and there is no correlation between the pairwise parameters (A_{ij} and A_{ji}, e_{ij} and e_{ji}, g_{ij} and g_{ji}, h_{ij} and h_{ji}). The intrinsic rate of change, r_i, is determined to hold $dX_i/dt = 0$ after imposition of an equilibrium density of each species, X_i^*, from a uniform distribution between 0 and 1. Thus, r_i of basal species with no mutualistic interactions should be always positive, whereas that of species with no predators should be negative. Stability analysis is based on a Jacobian community matrix following May's approach (1, 19, 22, 23). Stability is defined as the probability of local equilibrium stability, which is estimated as the frequency of locally stable systems across 1000 sample communities.

The analysis depicts a major effect of interaction type-mixing on population stability (Fig. 1; see the supplementary materials text for analytical results). Consider a food web composed of N species, where a proportion P (≤ 1; the proportion of connected pairs) of all possible species pairs is interacting. Congruent with earlier theoretical studies (24), species may show a stable coexistence under broad P or N ranges (Fig. 1). Yet this is no longer true if a small number of mutualistic interactions is added to the food web. Consider the proportion p_M of randomly chosen antagonistic links that are changed to mutualistic links. The model analysis indicates that in the presence of only a few mutualistic interactions (p_M set to 0.1 to 0.3), virtually no community is stable (Fig. 1) (23). Therefore, even a slight "contamination" of mutualistic interactions can completely destabilize an otherwise stable predator-prey community, clearly demonstrating the potential major effects of interaction type-mixing on population dynamics.

However, this is just half of the story. A further increase in the proportion of mutualism has

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another intriguing consequence. As mutualism (p_M) increases, the population becomes more stable and reaches its peak stability at a moderate mixture of both interaction types (Fig. 1). The same qualitative pattern is observed when resilience, a stability index for transient dynamics (20), is used instead. Although the overall unimodal pattern observed is qualitatively unchanged over a wide range of proportions of connected pairs (Fig. 1), species richness (fig. S2), and parameter variability (fig. S3), the sharp stability peak may not be observed when the dynamics is too strongly stabilized or destabilized at the background so that there is no room for changing p_M to alter stability. For example, with high species richness or strong self-regulation intensity, stability is maximized at a wide range of mutualism proportions (p_M).

The analysis of a hybrid community model provides a different perspective on the ongoing complexity-stability debate (24, 25). Increased complexity (high species richness and more connected pairs) destabilizes, or shows inconsistent effects on, population stability in a nonhybrid community composed of either mutualistic or antagonistic interactions (Fig. 2, A and E). However, positive relationships are consistently observed in hybrid communities with a moderate mixture of interaction types (Fig. 2D) (23). Our model demonstrates a positive complexity-stability relationship, irrespective of the network structure choice (random, cascade, or bipartite) or functional response (fig. S4). This suggests that multispecies coexistence in a hybrid community can be maintained, rather than destabilized, by community complexity. The choice of parameters does not change the pattern as long as it is within the parameter ranges that are not extremely stabilizing or destabilizing (figs. S2 and S3). Furthermore, those results do not change qualitatively even if the interspecific competition between basal species in the communities (figs. S5 and S6) or the varying relative strength of antagonistic and mutualistic interactions f_A and f_M is considered (fig. S7). Our analysis also suggests that the negative relationship between the number of interactions and the interaction strength assumed is crucial for the present patterns. In fact, the violation of this assumption does not create the mixing effect on community stability, as shown in fig. S8 (1, 19).

Under a traditional ecological hypothesis, acutely fragile communities are unlikely to persist under disturbance, and therefore a natural community should be structured to support population stability (26). Based on this hypothesis, an increasing number of empirical studies have been conducted to examine the structural patterns of community networks, such as food webs and mutualistic networks, and predict the network dynamics-related consequences (2–8). Our results show that interaction type-mixing and community network structure synergistically affect population dynamics, and they clearly illustrate the limitations of a single–interaction-type approach.

The community structure effect on population dynamics may not be correctly evaluated in the absence of interaction type-mixing information. For example, our model indicates that the effect of community complexity on stability can vary largely, depending on interaction types and their diversity. Our study establishes the potential importance of interaction type-mixing in resolving the structure-dynamics relationship. However, empirical data on hybrid community interaction webs are limited. Consequently, additional empirical study of the structure and dynamics of hybrid communities composed of various types of interactions must be pursued. A possible test of our hypothesis is to compare the composition of interaction types between different com-
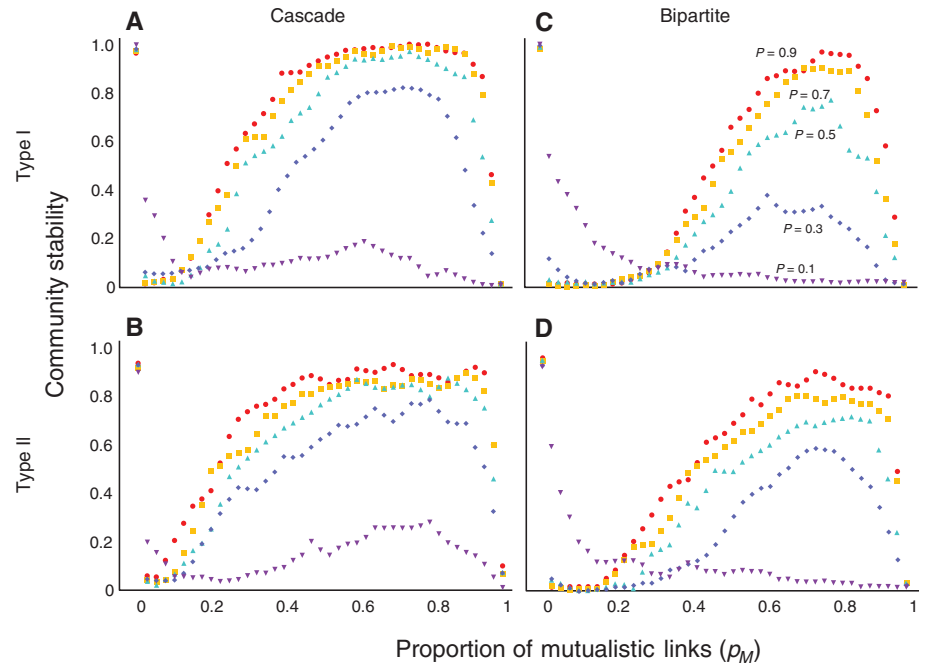
Fig. 1. (**A** to **D**) Relationships between the proportion of mutualistic links (p_M) and stability with varying proportions of connected pairs (P) in four models with different network structures and functional responses. Colors indicate different values of P. We assume $N = 50$.
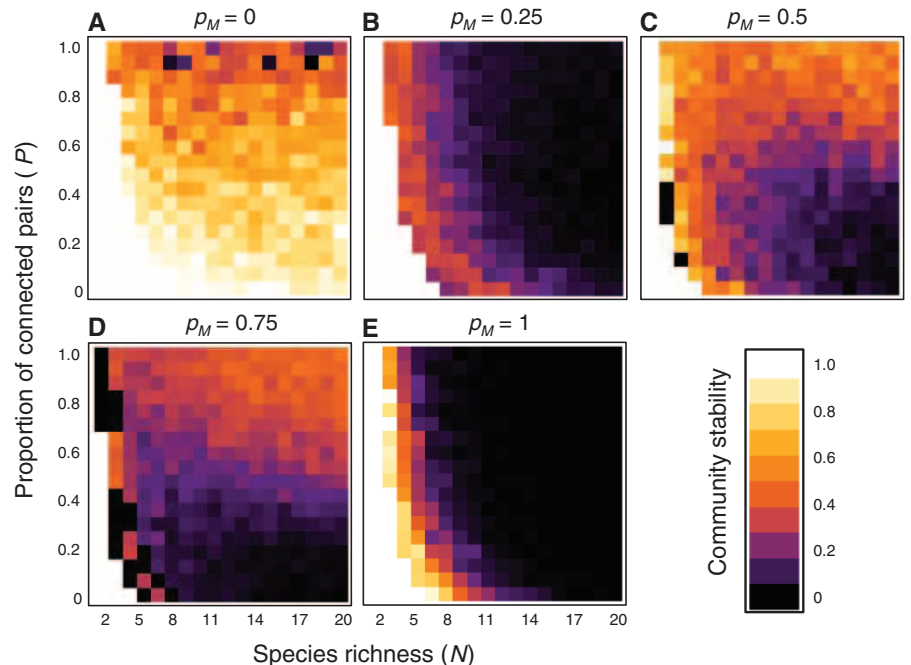
Fig. 2. (**A** to **E**) Complexity-stability relationships with varying proportions of mutualistic links (p_M) in a cascade model with type I functional response.

munities under varying levels of disturbance. An ecosystem under more-intensive disturbance is expected to have a more stabilizing composition of interaction types.

Species diversity has been of primary interest in understanding the role of biodiversity in ecosystem maintenance (24, 27), and a major focus of biodiversity conservation. The present study sheds new light on another aspect of biodiversity: diversity in interaction types. We determined that biodiversity in species and interactions is integral to stabilizing biological communities, which has important implications for biodiversity conservation. Species loss is of vital conservation concern; however, we may also need to identify the interaction types lost or maintained for two primary reasons. First, a complex community may be self-sustaining only in the presence of different interaction types. Therefore, a biased loss of one interaction type may critically destabilize the complex ecosystem. Second, the multiple interaction types can change the complexity-stability effect. The positive complexity-stability relationship of hybrid communities implies that a hybrid community is self-sustaining. However, it should be noted that such a self-sustaining community is more vulnerable to cascading biodiversity losses;

a simplified community can destabilize population dynamics and enhance additional species losses.

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LAAT-1 Is the Lysosomal Lysine/Arginine Transporter That Maintains Amino Acid Homeostasis

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Defective catabolite export from lysosomes results in lysosomal storage diseases in humans. Mutations in the cystine transporter gene *CTNS* cause cystinosis, but other lysosomal amino acid transporters are poorly characterized at the molecular level. Here, we identified the *Caenorhabditis elegans* lysosomal lysine/arginine transporter LAAT-1. Loss of *laat-1* caused accumulation of lysine and arginine in enlarged, degradation-defective lysosomes. In mutants of *ctns-1* (*C. elegans* homolog of *CTNS*), LAAT-1 was required to reduce lysosomal cystine levels and suppress lysosome enlargement by cysteamine, a drug that alleviates cystinosis by converting cystine to a lysine analog. LAAT-1 also maintained availability of cytosolic lysine/arginine during embryogenesis. Thus, LAAT-1 is the lysosomal lysine/arginine transporter, which suggests a molecular explanation for how cysteamine alleviates a lysosomal storage disease.

Defects in exporting hydrolytic degradation products from lysosomes cause lysosomal storage diseases such as cystinosis, which is characterized by intralysosomal accumulation of free cystine because of mutations in the lysosomal cystine transporter gene *CTNS* (cystinosin) (1–4). The most effective therapeutic agent for cystinosis, cysteamine (an aminothiol), converts lysosomal free cystine to cysteine and the mixed disulfide of cysteine-cysteamine, which is thought to be exported from lysosomes as a lysine analog through a lysine/cationic amino acid transporter (5–7). The molecular identity of the transporter remains unknown. Although biochemically detected, most mammalian lysosomal amino acid transporters have not been molecularly characterized (1).

From a forward genetic screen for *Caenorhabditis elegans* mutants with increased embryonic cell corpses, we isolated a recessive mutant *qx42* that accumulated many refractile corpse-like objects and lysotracker-positive puncta, suggestive of abnormal lysosomes (fig. S1, A to G). Using NUC-1::mCherry, which labels lysosomes (8, 9), or lysotracker staining, we found that *qx42* lysosomes were on average twice the volume of wild type (1.3 versus 0.5 μm³) (Fig. 1, A to F‴, and fig. S1, H to K).

We next examined whether *qx42* affected lysosomal cargo degradation. Apoptotic cells are phagocytosed, then degraded in lysosomes. Cell death and cell corpse engulfment were normal in *qx42* mutants (fig. S2). However, degradation of apoptotic cells in phagolysosomes (indicated by GFP::RAB-7 or NUC-1::mCherry) as measured by loss of HIS-24::GFP or H2B::GFP (which label chromatin in all somatic and germ nuclei, including cell corpses, respectively) was severely affected in *qx42* mutants, with HIS-24::GFP persisting >4 times as long as in wild type (Fig. 2A and fig. S2, L to O). Yolk lipoprotein is degraded throughout embryogenesis to nourish developing cells (10, 11). In *qx42* mutants, intestinal secretion of yolk reporter VIT-2::GFP and uptake by oocytes were normal (fig. S3, A to B′). However, *qx42* embryos accumulated significantly more VIT-2::GFP in enlarged puncta, which overlapped with NUC-1::mCherry, suggesting defective lysosomal yolk degradation (Fig. 2, B to D, and fig. S3, C to H′). Cell surface proteins CAV-1 and RME-2, which are internal-

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Diversity of Interactions
The diversity in interactions that occur between different species−−such as predation, competition, and mutualism
−−is a fundamental feature of natural ecological systems. Using a theoretical model, **Mougi and Kondoh** (p. 349; see the
Perspective by **Boyd**) show that the diversity of ecological relationship helps a biological community to be stable and
thus may be key to the maintenance of biodiversity itself.

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