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Ecological community integration increases with added trophic complexity

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ABSTRACT

The existence of functional biological organization at the level of multi-species communities has long been contested in ecology and evolutionary biology. I found that adding a trophic level to simulated ecological communities enhanced their ability to compete at the community level, increasing the likelihood of one community forcing all or most species in a second community to extinction. Community-level identity emerged within systems of interacting ecological networks, while competitive ability at the community level was enhanced by intense within-community selection pressure. These results suggest a reassessment of the nature of biological organization above the level of species, indicating that the drive toward biological integration, so prominent throughout the history of life, might extend to multi-species communities.

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1. Introduction

A fundamental question in ecology is whether communities of co-existing species are organized by deterministic forces, like competition and consumption, into functional wholes possessing emergent properties (Clements, 1936; Odum, 1969; Pimm, 1991), or are simply random assortments of species with similar environmental requirements (Gleason, 1926; Whittaker, 1962; Hubbell, 2001). Parallel to this question of holism in ecology is the levels of selection debate in evolutionary biology (Reeve and Keller, 1999), where individual selectionists (Williams, 1966) and proponents of selfish gene theory (Dawkins, 1976) have rejected group selection and the idea of the superorganism (Wilson and Sober, 1989).

Over a decade ago, Gilpin (1994) found that Lotka-Volterra communities of competing species could form

entities capable of competing *en masse* against other such entities. Although this finding has been confirmed (Toquenaga, 1997), its potential implications with respect to multi-species ecological organization have not been investigated further. Here I extend Gilpin's theoretical result from competition-only systems to communities containing two trophic levels.

One might imagine community-level competition occurring after some barrier between two separate communities is removed. Indeed, Gilpin's study was motivated by Vermeij's (1991) observation that large-scale biotic interchanges tend to be asymmetric (e.g., movement of species between North America and South America following formation of the Isthmus of Panama), with more species from one assemblage successfully invading newly accessible habitat of another assemblage than vice versa.

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2. Methods

With some modification, I repeated Gilpin's (1994) simulation experiment, and then added a second trophic level (for ease of exposition, two trophic-level systems are referred to as predator-prey communities, but can also be thought of as communities of primary producers and their consumers, or plants and herbivores). Two different types of five-species predator-prey communities were created. The first, what I call 'naïve communities', contained four prey species and one predator species that were mutually compatible with one another *de novo*, i.e., no extinction events occurred when their population trajectories were simulated over time. The second type of five-species community was assembled via a sequence of extinction events. These communities began with eight prey species and two predator species, and only those systems that collapsed to four prey species and a single predator were kept. I call these 'self-organized communities'.

Pairwise community mixing was simulated within source pools of four different community types (one or two trophic levels by naïve or self-organized community assembly). Competitive interactions in the lower trophic level were specified such that, on average, intraspecific competition was twice as strong as interspecific competition—assuming that individuals from the same species, and sharing the same niche, compete more intensely than different species occupying similar, but not identical niches. Among predators, direct intraspecific competition was set to zero, although indirect competition was modeled implicitly by prey depletion. However, direct interspecific competition between predators was allowed, representing behaviors where predators interfere with other species' access to prey, e.g., through territoriality or intra-guild predation. Negative effects of predators on their prey were, on average, an order-of-magnitude greater than reciprocal, positive effects of prey on predators, reflecting intrinsic inefficiencies in converting prey individuals into predator offspring.

Following Gilpin (1994), I simulated the dynamics of single trophic level communities using a normalized version of the Lotka-Volterra equations:

$$\frac{dx}{dt} = \mathbf{x}(\mathbf{b} + \mathbf{A}\mathbf{x}), \tag{1}$$

where population sizes are normalized by their carrying capacities. All elements of the \mathbf{b} vector of intrinsic growth rates, and all diagonal elements (intraspecific competition coefficients) of the community matrix, \mathbf{A} , were set to one. With these parameters fixed, different competition communities were created by randomly specifying interspecific competition coefficients on the off-diagonal elements of \mathbf{A} from the uniform interval $(-1, 0)$.

In five-species predator-prey communities, one prey species in \mathbf{x} was replaced with a predator. Correspondingly, one element in \mathbf{b} was replaced with a density-independent predator death rate of -0.1 . Predator effects on prey species were randomly sampled from the uniform interval $(-1, 0)$, while positive effects of the four prey species on predators were randomly sampled from a smaller uniform interval $(0, 0.1)$. Predator self-limitation, one diagonal element in \mathbf{A} , was set to zero. When more than one predator species was present (during

assembly of self-organized communities, and at the onset of community mixing) interspecific competition coefficients were randomly sampled from the uniform interval $(-1, 0)$.

In assembling naïve and self-organized communities, I simulated population trajectories over 10^4 time steps using a 4th-order Runge-Kutta method. Initial conditions were randomly drawn from a uniform $(0, 1)$ distribution. If a population's size dropped below 10^{-5} , it was set to zero. This threshold reflected the vulnerability of very small populations to stochastic events causing extinction. If communities contained five species after 10^4 time steps, I checked analytically whether they had an interior fixed point where equilibrium population sizes were all greater than zero. Communities that satisfied this criterion were added to source pools for community mixing.

Randomly selected pairs of five-species communities were mixed using an augmented community matrix:

$$\mathbf{A}_{1,2} = \begin{bmatrix} \mathbf{A}_1 & \mathbf{C}_1 \\ \mathbf{C}_2 & \mathbf{A}_2 \end{bmatrix}. \tag{2}$$

The two \mathbf{C} matrices determined the effects of species in one community on species in the other community, and were randomly sampled from the same uniform distributions determining interactions in the original communities. Note that in Gilpin's (11) study the \mathbf{C}_1 and \mathbf{C}_2 matrices were symmetric, i.e. $\mathbf{C}_2 = \mathbf{C}_1'$. This guaranteed that any given pair of species from different communities had identical competitive effects on one another. Although obviously not a realistic simplification, Gilpin (1994) argued that balancing interactions between species from different communities was necessary to establish that asymmetric outcomes of community mixing resulted from within-community, not between-community, properties. I disagreed with this line of reasoning. My question of interest was the effect of building five-species communities in four different ways (one or two trophic levels by naïve or self-organized community assembly) on the outcome of community competition. This was a within-community treatment effect that I varied, all the while keeping the mechanics of community mixing fixed.

Source pools for community mixing contained 20 communities. Within each pool, 2000 mixing trials were conducted, with a new set of between-community interaction coefficients randomly selected at the onset of each trial. Initial conditions for the two communities were the same as their final values at the end of the assembly process. Community dynamics were simulated over 10^4 time steps and final community composition was classified as symmetric or asymmetric. In asymmetric outcomes, the post-mixing community contained four or five species from one community, and zero or one species from the other community. All other post-mixing combinations of species were classified as symmetric. Entire experiments – assembly of 20 communities followed by 2000 mixing trials – were repeated 20 times for each of the four community types (Fig. 1).

3. Results

Community type had a substantial effect on the frequency of asymmetric outcomes (Fig. 2, $F_{3,76} = 175.1$, $P = 4.8E-34$). In

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