

security and addressing malnutrition throughout tropical agroforestry systems. Realizing this potential has advanced now that we have a clearer understanding of breadfruit's nomenclatural odyssey from Oceania to the Caribbean. Still, I can't resist thinking about what's in store regarding this crop's collective knowledge as it gets more widely introduced to new lands, peoples, and cultures.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Ecology: Lifting the curtain on higher-order interactions

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Higher-order interactions — the modification of interactions between a species pair by a third — remain poorly understood in nature. A new study manipulates pairwise and higher-order interactions in the field, offering exciting new insights into how higher-order interactions contribute to coexistence.

Species interactions determine much of the diversity and stability of ecological communities, shaping patterns of abundance and biodiversity across the globe¹. Most empirical work has focused on characterising interactions as they occur between pairs of species², with a host of experimental and theoretical studies exploring how variation in the strength and direction of these pairwise interactions may lead to coexistence or extinction in different contexts. Interactions are, however, not limited to

pairs of species. Higher-order interactions, whereby an interaction occurring between two species is modulated by the presence of a third species (Figure 1A), have the potential to greatly complicate the experimental manipulations required to quantify interactions in nature, as well as our predictions of coexistence. Moreover, higher-order interactions are far less studied than pairwise interactions, which makes it difficult to know whether they are common or rare, and thus how relevant

they might be to maintaining diversity. A new study in this issue of *Current Biology* by Milton Barbosa, Geraldo Wilson Fernandes and Rebecca Jane Morris³ is the first to reveal extensive evidence of higher-order interactions in natural arthropod communities through simultaneous experimental manipulation of multiple interaction types, from competition to cross-trophic interactions between two and more species.

We typically reduce diverse natural communities to a set of pairwise species



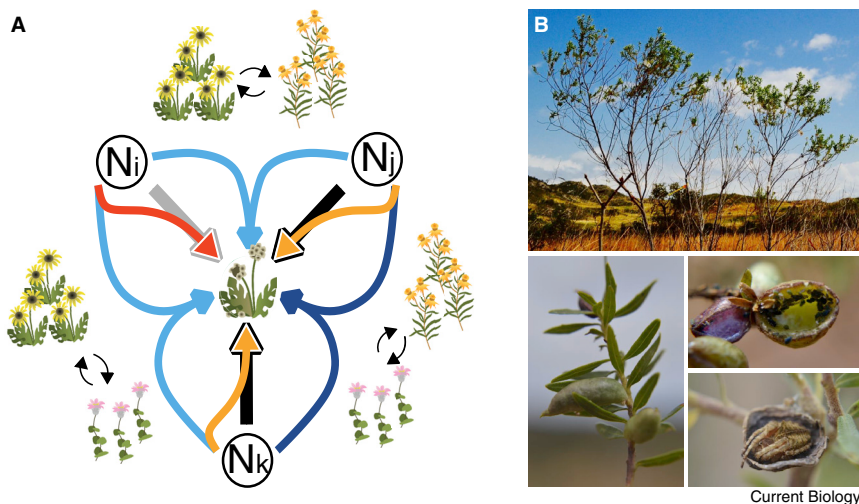


Figure 1. Higher-order interactions in theory and reality.

(A) Illustration of how past field studies have conceived of higher-order interactions. A focal individual (center) is affected by neighbouring species (i, j and k) through direct interactions (straight arrows), whilst density-dependent interactions (N, the number of individuals of each species) occurring between each pair of neighbours (blue arrows) modify the outcomes (yellow and orange arrows) of those direct interactions between focal and neighbour. Despite added complexity, this diagram still collapses multiple co-occurring interactions into a pairwise analysis. Whilst it is mathematically possible to integrate more than two neighbours⁴, current studies do not consider how more than two species at a time might modulate a single focal interaction. (B) Both live and hatched galls provide habitat to many species in this system. *Baccharis dracunculifolia* shrubs (top) with live galls (bottom left) and hatched galls containing aphids (middle right) and a spider (bottom right). Photos: M. Barbosa.

interactions, but it is increasingly appreciated that this simplification is potentially problematic and may obscure some of the processes shaping patterns of diversity^{2,4}. Higher-order interactions offer a partial solution to this problem by adding more biological complexity — and realism — to the study of complex natural communities and have thus been enjoying renewed attention over the last five years. Earlier work in the 1960–80s explored higher-order interactions theoretically⁵ and in experimental microcosms⁶, whereas more recent studies have focused on plant communities at a single trophic level, where such interactions are strongly evident^{4,7,8}. What remains to be answered, however, is how common or rare higher-order interactions might be across a broader range of systems, and across entire communities spanning multiple trophic levels. The study by Barbosa and colleagues³ thus provides an exciting development by including cross-trophic interactions, such as predation or parasitism, as well as single-trophic interactions, such as competition, into their assessment of higher-order interactions.

Empirically studying higher-order interactions in natural systems is painstaking and laborious, requiring all actors, both pairwise and modifiers, to be measured under varying densities to confirm the presence of a higher-order interaction⁴. Assessing cross-trophic interactions and cross-trophic higher-order interactions is no small feat either: prior to this work, we are aware of only one other study which has tested for them in a natural field system⁹. In addition to trophic and non-trophic interactions, pairwise interactions and higher-order interactions, Barbosa and colleagues³ explore the potential for several four-way interactions, whereby a higher-order interaction (the modification of an interaction) is itself modified by another species. In order to evaluate all these aspects, the authors present an arduous but rewarding experiment, the first of its kind to manipulate both pairwise and higher-order interactions in the field across an entire cross-trophic community network.

Barbosa and colleagues³ focus on the tropical evergreen shrub *Baccharis dracunculifolia* and its associated

arthropod fauna (Figure 1B). This shrub hosts a wide diversity of arthropod herbivores and predators, as well as multiple gall-inducing species which create further habitats for ants, spiders and aphids. The most common gall-inducing species, the insect *Baccharopelma dracunculifoliae*, creates growths on the plant tissue which harbour its nymphs until they hatch. Hatched and unhatched galls create a living space used by many other arthropods, including parasitoid wasp species which attack live galls. *B. dracunculifolia* is also an important habitat for aphid colonies, which in turn are tended to and protected by various species of ants. Predators and herbivores complete this complex network of interactors.

In previous work¹⁰, reducing the number of *B. dracunculifoliae* galls on the shrubs modified the structure of the remaining galler–parasitoid network, without affecting the abundance or diversity of the galler species themselves, hinting at the presence of indirect pathways through which these changes could propagate. Moreover, experimentally manipulating the number of hatched galls had also been found to modify the aphid–galler–parasitoid three-way relationship¹¹. This suggested that this study system was a great place to look for the kind of complex and indirect effects which characterise higher-order interactions, and that the existence of these interactions could be brought to light through experimental manipulation on an entire interaction network in the field.

In their new study, Barbosa and colleagues³ set up three exclusion treatments and a control: exclusion of ants, exclusion of live (unhatched) galls and exclusion of hatched galls. They then recorded ant, herbivore, predator and aphid densities, gall volume and plant size and wasp parasitism. Using this enormous dataset, they constructed a complex network of pairwise, three-way and four-way interaction effects for this system. This kind of detail is unprecedented in studies of naturally-occurring ecological interaction networks, such as food webs, which typically focus on few interaction types and on pairwise interactions only. By recording all of the arthropod

interactions occurring on these shrubs, Barbosa and colleagues³ were able, for the first time, to unveil how prevalent higher-order interactions can be, as well as to showcase the diversity of mechanisms underpinning them. For example, the aphid–galler interaction was facilitated by ants, which lead or carried aphids into the galls, and by parasitoid wasps, which physically modify the gall and make it easier for aphids to enter. The consequences of these higher-order interactions can be complex: while aphids can kill the nymphs inside the gall and are thus harmful to the galler species, their preference for parasitised galls means they can negatively affect parasitism and thus also benefit gallers. Understanding these kinds of mechanism has been a persistent problem in studies of plant–plant interactions^{4,7,8}, and this study is one of the first to both identify the presence of higher-order interactions and show some of the pathways through which they occur⁹.

Of course, the work of Barbosa and colleagues³ raises further questions about the role of higher-order interactions in natural communities: if they are so common, how do we include them in our models and predictions? Species interactions are already incredibly variable and dynamic because they depend on the biotic and abiotic context — higher-order interactions perhaps even more so than pairwise interactions — and other recent studies have begun to explore the effects of variance in pairwise interactions on coexistence outcomes^{12–15}. Barbosa and colleagues³ provide a key piece to this puzzle by showing that higher-order interactions are likely to be another important source driving variation in the outcomes of species interactions, further challenging our attempts to infer coexistence and ultimately community diversity. Their results highlight the need to move beyond pairwise models of species interactions when seeking to predict local patterns of diversity in natural systems. They also shift our focus towards the complex context-dependent network of interactions operating within and between trophic levels. Whilst this work has recently

begun, and theoretical frameworks are indeed making efforts to include things such as context-dependency^{12,16} and higher-order interactions^{17,18} into multispecies models, new theoretical tools will only be useful if they actually improve our understanding of natural communities¹⁹. This is especially crucial for considering how local communities might respond to common drivers of global change and the resulting modification of interaction networks caused by shifts in species distributions and phenology. As conservation and management action are often implemented locally, it is more urgent than ever that community ecology theory be developed hand-in-hand with these efforts. The new study by Barbosa and colleagues³ serves an important role in this movement and will certainly drive future theoretical developments about the consequences of interactions on diversity and coexistence, whilst keeping such theory grounded in the empirical and changing world we seek to understand²⁰.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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