

Beyond pairwise mechanisms of species coexistence in complex communities

Jonathan M. Levine¹, Jordi Bascompte², Peter B. Adler³ & Stefano Allesina⁴

The tremendous diversity of species in ecological communities has motivated a century of research into the mechanisms that maintain biodiversity. However, much of this work examines the coexistence of just pairs of competitors. This approach ignores those mechanisms of coexistence that emerge only in diverse competitive networks. Despite the potential for these mechanisms to create conditions under which the loss of one competitor triggers the loss of others, we lack the knowledge needed to judge their importance for coexistence in nature. Progress requires borrowing insight from the study of multitrophic interaction networks, and coupling empirical data to models of competition.

The goal of ecological research on species coexistence is to explain how the tremendous diversity of species that we see in nature persists despite differences between species in competitive ability^{1,2}. However, empirically evaluating the interactions between a large set of competitors is logistically challenging, and many of the mathematical tools for analysing the interaction between a pair of competitors do not translate readily to large networks of competing species³. As a consequence, coexistence research has focused overwhelmingly on mechanisms that operate between pairs of competitors. Although the emphasis on pairwise coexistence may prove valid, and great progress in understanding the maintenance of species diversity has been achieved through a pairwise approach² (Box 1), ecologists have had difficulty showing that the coexistence of many species in diverse ecosystems results from pairwise mechanisms. How probable is it that the more than 1,000 tropical tree species found in a 25-hectare plot in the Amazon rainforest coexist because of countless pairwise niche differences between the competitors^{4,5}?

A tantalizing explanation for coexistence in species-rich communities involves mechanisms that emerge only in diverse systems of competitors. Indeed, systems of more than two competitors form a network of competitive relationships, the structure of which should influence the dynamics of the system as a whole^{3,6}. The degree to which studying coexistence between pairs of species in isolation can help us to understand the dynamics of complex competitive networks is simply not known^{7,8}. However, it is known that network structure can strongly determine the robustness of mutualistic and multitrophic networks to perturbations, as well as radically change the outcome of the pairwise interactions^{9–11}. We might therefore expect similarly powerful consequences of network structure for the dynamics of diverse competitive systems.

In this Review, we propose that to understand the maintenance of species diversity, ecologists must better explore the coexistence mechanisms that result from the structure of diverse competitive networks. We further suggest that this understanding can be accelerated by applying lessons from the study of mutualistic and multitrophic networks to competitive systems. Importantly, a better understanding of coexistence mechanisms that emerge only in diverse systems would shed light on the stability of biodiversity. By definition, these coexistence mechanisms erode as species are lost. As a consequence, the loss of one competitor may lead to the subsequent loss of others, an extinction cascade well known from the theoretical study of trophic¹²

and mutualistic^{13,14} networks, but studied rarely in competitive systems (see ref. 15 for an example).

Here, we discuss the theoretical and empirical literature on mechanisms of coexistence that emerge only in networks of more than two competitors. Despite these mechanisms being demonstrated with mathematical models almost fifty years ago, convincing empirical tests of their operation remain rare, which leaves the implications of these interactions for coexistence in nature unknown. Although we focus exclusively on the interactions between competitors, throughout the Review we highlight findings from the study of trophic and mutualistic networks that help to show how diverse competitive networks operate and can be analysed. We then lay out a roadmap for advancing the understanding of coexistence mechanisms that emerge only in systems of more than two species. This involves developing a predictive understanding of when such mechanisms are likely to operate, empirically evaluating their prevalence and importance in nature and demonstrating theoretically how they influence coexistence in truly diverse systems.

Coexistence between more than two competitors

Theory shows that two kinds of competitive dynamics — interaction chains and higher-order interactions — emerge only in networks of three or more species (Fig. 1). Such interactions do not necessarily stabilize, and can in fact destabilize, coexistence. Therefore, first we define these interactions and then we explain the conditions under which they promote species richness — our measure of diversity in this Review.

Interaction chains emerge when pairwise competitive interactions are embedded in a network of other (still pairwise) interactions. As in a trophic cascade, the indirect effects that result arise from changes in the density of a third (or further) species that interacts with both species of the focal pair (Fig. 1b). Even when all direct pairwise interactions are negative, these indirect effects are often positive¹⁶. The best-studied stabilizing competitive network involves intransitive competition among three species, as underpins a game of rock–paper–scissors^{6,17}. Although the interactions between the species remain fundamentally pairwise, the stabilized dynamics emerge from stringing these pairwise interactions together, so that changes in density propagate through the network to form a negative feedback loop that counteracts the initial perturbation.

Higher-order interactions emerge when the interactions between species are no longer fundamentally pairwise. Instead, the per capita effect

¹Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland. ²Department of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland. ³Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322, USA. ⁴Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637, USA.

BOX 1

Controls over coexistence in systems of two competitors

Coexistence between two species is commonly evaluated according to a mutual invasibility criterion, which means that each species has a positive growth rate when it is at low density (rare) and its competitor is at its single-species equilibrium (carrying capacity). Such a criterion can be met only if species have a greater growth rate when rare than when they are common, as arises when individuals are more strongly limiting to individuals of their own species than to individuals of other species². One advantage of this framework is that it can be applied flexibly to systems with stochastic fluctuations in the environment, through calculations of the low-density growth rate averaged over time².

Chesson² showed how the growth rates of species when they are rare can be decomposed into an average fitness difference and a stabilizing niche difference between competitors. The average fitness difference describes the degree to which one competitor is superior, on average, to the other. Although the precise definition depends on the model that is being examined, in general, it reflects a combination of the innate reproductive capacity of species in the absence of neighbours and the degree to which species resist the potentially suppressive effect of their neighbours (Supplementary Note). In the absence of processes that give advantages to species when rare, the average fitness difference causes positive growth for the species with superior fitness and negative growth for the inferior species. Trade-offs that make these growth rates more similar are called equalizing mechanisms². However, such mechanisms can never cause both species to have a positive growth rate when suppressed to the invader state, as required for mutual invasibility. This condition can be met only with stabilizing mechanisms that arise from niche differences

between competitors.

Stabilizing niche differences include all factors that cause species to limit their own individuals more than they do those of other species^{2,83}. Such factors increase the population growth rate of a species that drops to a low relative abundance^{2,83}. Coexistence therefore depends on the magnitude of the stabilizing niche difference exceeding that of the average fitness difference, such that even species with an average fitness disadvantage can invade the system. Stabilizing niche differences can arise in well-mixed systems when, for example, the two species are limited by different resources or by specialist consumers or pathogens. Alternatively, they can occur when species specialize on different locations in a spatially heterogeneous environment or on different types of climatic conditions in stochastically fluctuating environments².

One challenge that arises when applying the principles of coexistence theory developed from the mutual invasibility criterion to systems of three or more competitors is that satisfying this condition is no longer sufficient for predicting coexistence. Even when all species are able to invade, they may be invading systems that lack the full complement of resident species if the persistence of some residents depends on the invader being common³ (as occurs in rock–paper–scissors competition). By contrast, in a competitive system of two species, the resident species always persists when its competitor is suppressed to the invader state. For this reason, alternative frameworks for understanding coexistence (outlined in Box 2) are particularly important for studying mechanisms that emerge when more than two species are involved.

of one competitor on another depends on the population density of a third, fourth or fifth (or potentially an even greater number of) species (Fig. 1c). These interactions are analogous to the trait-mediated indirect interactions described in the trophic literature, in which higher-order interactions occur when a predator, for example, modifies the behaviour of its prey with cascading effects on even lower trophic levels¹⁸. Higher-order interactions between competitors are less intuitive than interaction chains, but can emerge when one species has a plastic morphological or behavioural response to another, such as the reduction in forb rooting depth shown in Fig. 1c, which alters the forb's competition with a third species. In a less hypothetical example, plantain (*Plantago lanceolata*) suppresses the root growth of red fescue (*Festuca rubra*), an otherwise efficient competitor for soil nutrients¹⁹. This plastic response would, in turn, weaken the per capita effect of red fescue on the performance of other nutrient-limited competitors. More generally, higher-order interactions might stabilize coexistence when the presence of one species weakens the interspecific interaction of another two.

The distinction between interaction chains and higher-order interactions is determined by whether the indirect effect emerges from a change in competitor density (interaction chain) or a change in the per capita competitive effects (higher-order interaction). As a consequence, interaction chains and higher-order interactions differ in the timescale of their operation. In a higher-order interaction, one competitor immediately modifies the competition between another two (for example, by changing individual traits). By contrast, in interaction chains, the competitor modifies the interaction between another two species by changing the density of other competitors, and should therefore emerge after a greater time lag. Although distinct in how they are defined, interaction chains and higher-order interactions require diversity to operate, and both can therefore make systems vulnerable

to extinction cascades. The simplest example of this dynamic involves the loss of one competitor from a system that is stabilized by intransitive competitive loops, which leads to the loss of other competitors (Fig. 2).

Theoretical insights into interaction chains

Theoretical ecologists have long been aware that the outcome of pairwise competitive interactions can change when species are embedded in a diverse competitive network. Much of this understanding was inspired initially by studies of Lotka–Volterra systems describing the interactions between a diverse set of species — often modelling the response of entire communities to small perturbations around an equilibrium^{15,20,21} (Box 2). Subsequent work showed that when interspecific competitive interaction strengths are sampled randomly from a distribution, more diverse communities are less likely to be stable²². Although this finding suggests that coexistence opportunities are reduced by increasing the number of species, it is partly a function of the random network structure — intransitive competitive structures can alter this expectation.

A parallel course of study has explored the specific competitive relationships (network structure) that enable the outcome of competition between two species to be altered by the inclusion of additional competitors^{16,23–25}. The inclusion of a third competitor can benefit coexistence by having an equalizing or stabilizing effect (as defined in Box 1). For example, a superior competitor can favour the coexistence of two others by differentially harming the fitter of the two²⁴. With this interaction structure, the superior species equalizes the average fitness of the other two competitors, but does not stabilize their dynamics through the introduction of a new mechanism of coexistence. Any long-term coexistence would still require pairwise niche differences, as defined in Box 1. By contrast, when the three species form an intransitive competitive loop, this structure can stabilize coexistence^{23,25}.

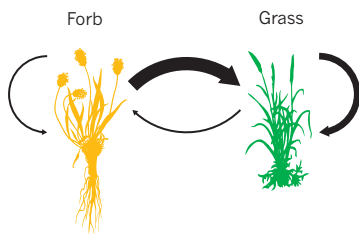
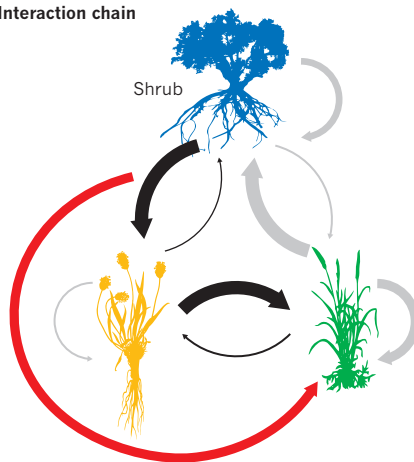
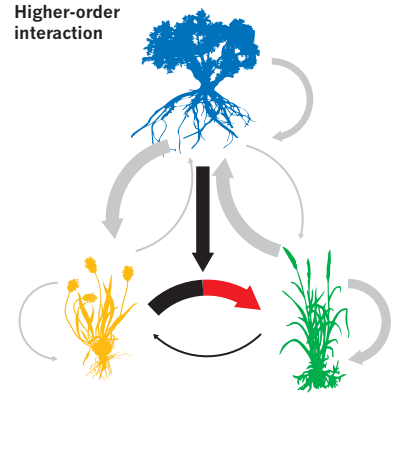
a Pairwise interaction**b** Interaction chain**c** Higher-order interaction

Figure 1 | Coexistence mechanisms that emerge only with more than two competitors. **a**, Strictly pairwise competition between a forb and a grass, showing both interspecific and intraspecific interactions. **b**, An interaction chain in which a shrub provides indirect benefits (red arrow) to a grass through the suppression of a forb. Grey arrows indicate pairwise interactions that are not directly involved in the interaction chain or

higher-order interactions. **c**, A higher-order interaction in which a shrub alters the per capita effect of a forb on a grass. In this case, the shrub induces a plastic change in the forb that leads it to root at more shallow depths of soil, bringing it into greater competitive contact with the grass. Arrow widths in **a–c** indicate the strength of the per capita competitive effect.

Intransitive competition occurs whenever species cannot be ranked in a simple linear competitive hierarchy. This mechanism is stabilizing because decreasing the abundance of any competitor in the loop propagates through the network in a way that feeds back to favour the recovery of the perturbed species. These stabilized dynamics, however, emerge only in systems with an odd number of species⁶; this mechanism cannot produce coexistence when there is an even number of competitors, which raises interesting questions about how these systems assemble. The most basic models of this type of interaction encode competitive dominance between species in a directed graph, in which nodes represent species and, for each pair, an arrow termed an ‘edge’ connects the competitive winner to the loser²⁶ (Fig. 2a). The simplest case of intransitive competition, in which three species form a rock-paper-scissors intransitive loop, has been shown to generate possible coexistence of the three competitors, albeit with cycles²⁶. Larger networks containing many species have been explored by simulation²⁷ or by writing deterministic equations⁶, such as the replicator equation that is central to evolutionary game theory²⁶ (Fig. 2b).

In other modelling approaches applied to interaction chains, competition is less asymmetric, yet intransitivity between three competitors still strongly stabilizes the dynamics. For example, May and Leonard²³ studied a Lotka–Volterra model for three species (here termed A, B and C) in which competition coefficients were chosen such that A is more affected by B than B is by A, B is more affected by C than C is by B, and C is more affected by A than A is by C. All coefficients are therefore negative, but those with the largest magnitude are arranged in a rock-paper-scissors loop. Such a model can produce robust limit cycles of all three species rather than the monodominance that is expected under transitive competition. Similar mechanisms promote coexistence in models with explicit consumer–resource interactions²⁸, successional replacement²⁹ or a trade-off between competition, colonization and space pre-emption³⁰.

Although the specific effects of intransitive competition on coexistence highlight the importance of embedding pairwise competitive interactions into a diverse network of competitors, how network structure affects the dynamics of diverse competitive communities more generally is rarely explored explicitly. However, an implicit acknowledgement of the importance of network structure comes from the common practice by theoretical ecologists of building communities of competitors from rules that generate specific interaction structures³¹. Models often assume, for example, that the per capita effect of one species on another is a function of their overlap in the use of resources along a common niche axis³¹.

Moreover, network architecture is well known to strongly influence species persistence in other types of interaction networks. Food webs, for instance, tend to be organized in compartments, in which species within a compartment interact more frequently with each other than they do with species from other compartments^{32–36} (but see ref. 37 for an alternative perspective). Interestingly, this block structure can buffer the spread of perturbations across the entire network^{12,22} and could play a similar part in networks that are stabilized by intransitive competitive relationships. Networks of mutualistic interactions, such as those that form between flowering plants and their animal pollinators or seed dispersers, tend to be organized in a nested manner, which means that specialist animals interact with proper subsets of plant species that also interact with more generalist animals³⁸. This nested network structure can increase the number of coexisting species in mutualistic networks³⁹.

In one of the few contemporary studies to explicitly ask how network structure affects competitor dynamics, Barabas *et al.*³ explored how the arrangement of coefficients in the interaction matrix (Box 2) affects the stability and feasibility of diverse competitive systems. They found that both maximal and minimal stability are achieved by arranging the interaction coefficients in a nested manner, and by arranging them in blocks. This work shows that macroscopic network properties such as compartmentalization and nestedness probably have important effects in competitive communities, as is already known for other interaction types.

Empirical evidence for intransitive competition

Interaction chains between competitors can have a range of effects on the dynamics of competitive networks²⁴, although interaction chains that act specifically to stabilize coexistence — intransitive competitive loops — are of particular relevance here. Direct empirical evidence that intransitive competition operates in nature is generally sparse, and studies reporting strong support for transitivity or pervasive intransitivity have underlying problems. The two most convincing examples of intransitive interactions actually concern competition within a species, rather than between species. Kerr *et al.*¹⁷ showed that intransitive interactions occur between engineered strains of the bacterium *Escherichia coli*, whereas Sinervo and Lively⁴⁰ demonstrated that these interactions exist between individuals with different mating strategies in a population of lizards. Bridging the ‘within species’ and ‘between species’ evidence for intransitivity are data presented by Lankau and Strauss⁴¹, who showed that intransitive competition occurs between two selectively bred populations of black mustard (*Brassica nigra*) and a third,

heterospecific, plant competitor. However, the authors' mathematical models suggest that selection should drive the mustard population to a single optimal strategy, collapsing the system to pairwise, between-species coexistence⁴². The best species-level evidence for intransitive competition comes from patterns of colony overgrowth in marine sessile organisms^{43–45}. Even in these systems, however, the observed intransitive competition between triplets of species is embedded in a larger matrix of mostly transitive interactions.

An alternative approach to evaluating the prevalence of intransitivity involves analysing the results of experiments in which many species, typically plants in a greenhouse setting, compete against each other in pairwise trials. Although these studies generally conclude that intransitivity is rare^{46–51}, they usually measure competitive dominance through relative yield or related measures, in which the growth of an individual plant with a heterospecific neighbour or neighbours is scaled by its growth with neighbours of its own species. This approach measures differences between species in their per capita competitive effect on the common target individual plant (see Supplementary Note). However, both mechanistic and phenomenological models show that competitive dominance arises not from differences in the per capita competitive effect of species, but instead from the differential ability of species to tolerate the effects of intraspecific and interspecific competitors^{2,52}. Relative yield provides no insight into how species tolerate competition and therefore cannot reveal competitive outcomes (Supplementary Note).

A further approach infers the network of pairwise competitive dominance from patterns of species abundance in field plots⁵³. Applications of this approach suggest that widespread intransitivity exists in plant communities and that there is a positive relationship between the degree of intransitivity and species richness⁵⁴. However, the method is built on assumptions of low spatial environmental heterogeneity and density-independent probabilities of species replacement, and therefore the inferred competition matrix does not allow for pairwise niche differences (Box 1). Although the approach may be appropriate for asking which intransitive network structure is most consistent with patterns of abundance under the assumption that there are no other controls on species abundance, it is not well suited for evaluating whether intransitivity is a more parsimonious explanation for abundance patterns or coexistence than pairwise mechanisms.

Overall, the existing empirical literature on intransitive competition consists of several well-resolved examples of intransitive loops within species (but not between species), analyses of experiments with improper estimates of competitive dominance, and inverse modelling built on the premise that there is an absence of pairwise niche differences. The evidence provided by these approaches makes it difficult to resolve the true prevalence of intransitive competition in nature. However, prevalence is only part of the problem because there is an even more glaring absence of evidence to evaluate the degree to which observed intransitivity stabilizes coexistence in nature.

Theoretical insights into higher-order interactions

The assumption that the interaction between species is fundamentally pairwise is central to almost all coexistence theory. Yet from an empirical standpoint, we have little idea of whether this assumption is correct. Species interactions may actually result from multiway relationships between more than two competitors (three-way, four-way or even higher-order interactions). Abrams⁵⁵ showed that higher-order interactions often emerge in classic models of resource competition with non-logistic resource growth or non-linear functional responses of the consumer to the resource density. This result raises the important point that the designation of higher-order interactions as being fundamentally different to pairwise competition is partly an artefact of a phenomenological approach to studying species coexistence. Such an approach uses interaction coefficients to describe the negative effects of one competitor on the other, rather than using explicit interactions with shared resources or consumers, as occurs in more mechanistic models of competition (for example, ref. 52). In the mechanistic models, higher-order interactions

can emerge organically from the underlying biology without the addition of special higher-order terms⁵⁵. However, regardless of whether phenomenological or mechanistic models of competition are considered, how much the interaction between any two species is dictated by other species in the system remains a relevant question.

Another theory has shown how a network framework can be used to study higher-order interactions⁵⁶. Rather than a graph in which arrows connect species (nodes), as in networks of pairwise interactions, higher-order interactions are represented in a hypergraph in which arrows connect nodes to other arrows (as in Fig. 1c). Just as an $n \times n$ matrix (n = number of species) of competition coefficients is used to parameterize a system of equations assuming pairwise interactions, an $n \times n \times n$ tensor (a multidimensional array) can be used to describe three-way interactions, in which each element describes the joint effect of two species on the third⁵⁷. Although such a tensor describes all higher-order interactions that can potentially operate, the actual operation of these interactions in nature is complicated by the finite nature of individual organisms and the fact that sessile organisms interact only with those in their neighbourhood⁴. At the same time, the stabilizing effects of higher-order interactions (and interaction chains) could potentially compensate for the depressive effects of demographic stochasticity on species richness.

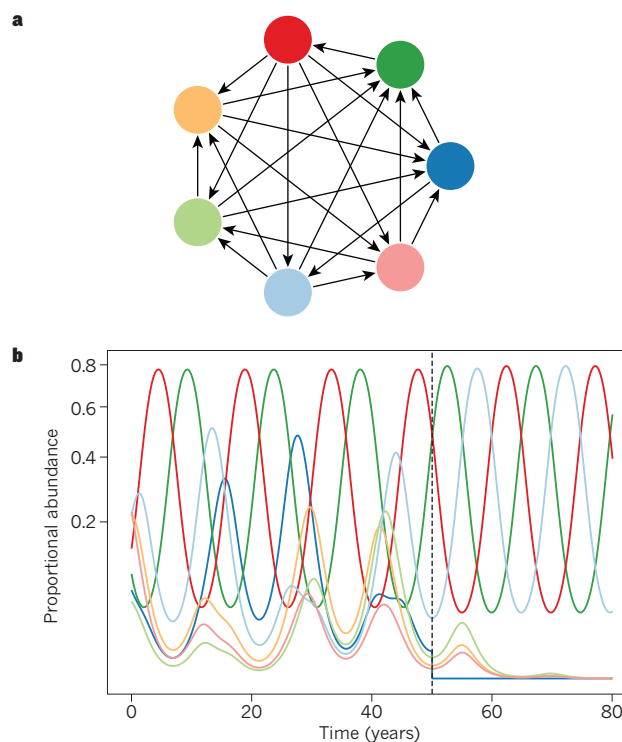


Figure 2 | A competitive network and an extinction cascade. **a**, An intransitive competitive network or 'tournament', in which arrows point from the winner to the loser in pairwise competition. The system is composed of a number of smaller intransitive loops (for example, between the light blue, the dark blue and the pink species) that are nested in larger loops that include all seven species (see ref. 3 for examples of competitive network structure). **b**, Simulation of the dynamics of the system following the methods of ref. 6. Owing to intransitive competitive relationships, the seven species shown would coexist indefinitely, cycling around an equilibrium in which the red and dark-green species have a proportional abundance (the proportion of individuals that belong to each species) of 1/3, the light and dark blue species have a proportional abundance of 1/9 and the light green, orange and pink species have a proportional abundance of 1/27. At year 50, the dark blue species is sent to extinction, which causes a further 3 species to become extinct owing to the disruption of the intransitivity that stabilized their dynamics. The remaining three species oscillate in a rock–paper–scissors fashion around a proportional abundance of 1/3. The y-axis is presented on a square-root scale to improve the visibility of species with low abundance.

BOX 2

Evaluating the stability of coexistence in diverse ecological networks

Ecological stability is a multifaceted concept, but theoretical approaches commonly evaluate the stability of species coexistence on the basis of the local or global stability of a multispecies equilibrium with specific parameters. An equilibrium is locally stable, for example, if the system returns to it following an infinitesimally small perturbation in species density, and this is determined from the eigenvalues of the Jacobian matrix when evaluated at the equilibrium point. For models with a linear functional response, the Jacobian matrix is defined as the product of two terms, the first of which is a matrix in which diagonal elements represent the equilibrium abundances of each species and off-diagonal elements are zero. The second term is the interaction matrix, whose ij th entry describes the per capita effect of changes in the abundance of species j on the rate of change of the abundance of species i . May²⁰, for example, modelled this matrix as a random matrix in his efforts to define the relationship between diversity and stability in ecological communities. This general approach enables the ecological concept of stability to be related to a well-defined mathematical framework that is used widely throughout the natural sciences. Higher-order interactions can affect local stability by altering the value of the elements of the Jacobian matrix. Global stability, in turn, is a more general concept that quantifies the stability of any potential feasible equilibrium solution after a perturbation of any given magnitude⁸⁴.

Although knowledge of local and global stability has provided important insight into the behaviour of model communities, these concepts have a number of limitations. For instance, stability conditions are often derived for equilibrium solutions that are not

necessarily feasible, meaning that they involve populations with negative abundances. The conditions for feasibility therefore may be stronger than those for local stability, and both have to be considered when studying species coexistence^{85–90}. Another limitation of the local stability approach is the assumption that perturbations affect only species density. In nature, however, many perturbations will change species' growth rates or interaction coefficients⁹¹.

Structural stability offers an alternative approach that is better suited to evaluating multispecies coexistence^{91,92}. Rather than addressing only the stability of the dynamical variables for a given set of parameters, this approach quantifies the range of parameters that are compatible with the stable coexistence of all species, as determined by the existence of a fixed point that is both fully feasible and globally stable^{71,88,90}. Structural stability simultaneously considers dynamical stability and feasibility, assumes that perturbations may affect demographic parameters and is not constrained to small perturbations. It is therefore better suited to studies of global environmental change, which often involves large and directional changes. Although it exerts less influence on ecology than it does on other fields, structural stability has been advocated by several ecological theoreticians^{39,71,88–90,93} and was used to quantify the contribution of indirect interaction chains to multispecies coexistence⁹⁴. More generally, it is important to consider how conclusions about the dynamical consequences of interaction chains and higher-order interactions depend on the chosen definition of coexistence and stability.

Despite common arguments that higher-order interactions should be pervasive in ecosystems^{58,59}, they are generally excluded from models of competition. Ecologists therefore lack clear expectations of how such interactions should affect the outcome of competition. Moreover, given the dearth of empirical evidence for how these interactions are structured, theory has few anchors from which to work. Therefore, a reasonable starting point is to consider the implications of random higher-order interactions — as incorporated into the models of Bairey *et al.*⁵⁷. The authors show that including interactions of increasingly high order, and with randomly assigned values, reverses the classic result of May²⁰, in which community diversity destabilizes ecological systems. With strictly four-way interactions, more diverse communities can better withstand the destabilizing effects of stronger interactions and, as a consequence, the loss of a species makes the remaining system more vulnerable to extinctions. Bairey *et al.*⁵⁷ explore the stability of communities that are a mix of competitors, consumers and mutualists, although similar results might hold for purely competitive systems. However, the Bairey *et al.* study⁵⁷ should not be interpreted to suggest that higher-order interactions are necessarily stabilizing. As with interaction chains, the consequences of higher-order interactions should depend on the structure of the network and the sign of the higher-order effects — topics yet to receive considerable empirical attention (although see ref. 59).

Empirical evidence for higher-order interactions

Although higher-order interactions between species in different trophic levels are the subject of a considerable level of research⁵⁶, such interactions between competitors are much less understood. The classic approach for evaluating the operation of higher-order interactions between three species — and the scope of most existing work — involves evaluating the performance of species in all two-way and three-way combinations^{60–63}. The number of treatments typically restricts these

experiments to tractable laboratory model systems such as fruit flies, protists and pond microcrustaceans. Using this design, it can be tested how well the response of a focal species to each of the others in isolation (pairwise competition) predicts the focal species' response to multiple competitors (in triplet combination), typically through an analysis of variance (ANOVA). However, ANOVA tests can also generate a significant statistical interaction between the effect of two competitors on a focal species, and therefore indicate the presence of higher-order interactions, even when the effect of each competitor on the focal species is independent of the other^{7,64,65}. Moreover, in experiments conducted across a time frame that is long enough for competitor densities to change, it is difficult to prove that the apparent higher-order interaction is not caused by a change in the abundance of the competitors, which would make it a 'misdiagnosed' interaction chain^{62,64}. As a consequence of this, as well as the laboratory settings in which they take place, these experiments generally have not provided definitive tests of whether higher-order interactions are prevalent in ecological communities in nature.

A related approach involves fitting models of population dynamics or biomass accumulation to competition experiments and evaluating how well a model with purely pairwise interactions can predict the performance of individuals or the dynamics of multispecies systems^{59,66,67}. Quantifying higher-order interactions with this approach is a formidable empirical and statistical challenge. Although characterizing all pairwise interactions between n species requires the empirical estimation of n^2 coefficients, estimating all triplet interactions requires up to n^3 coefficients. To simplify the design, Weigelt *et al.*⁶⁷ grew focal plants of a single species in experimental arrays surrounded by conspecific individuals, or individuals from one, two or three other species. They then fitted a series of models to describe how the biomass of the focal plant is reduced by neighbours. In one-third of the three or more

competitor combinations tested, a model with both pairwise effects and an interaction term could best describe individual biomass declines with neighbour density, which suggests the presence of higher-order interactions. More direct statistical tests for higher-order interactions were developed by Mayfield and Stouffer⁵⁹, who then applied their method to observational data collected in a community of annual plants in south-western Australia. They found that higher-order interactions significantly affected the fecundity of three of six focal species, often weakening the suppressive effect of neighbours.

Aside from the technical challenges of quantifying higher-order interactions, a central problem is that few empirical studies actually evaluate the ecological importance of these interactions. Indeed, it has been proposed that because higher-order interactions almost certainly operate in nature, and that demonstrating them just requires having enough degrees of freedom, the real question is whether higher-order interactions have consequences that are noticeable against a background of other sources of ecological uncertainty⁶⁸. Unfortunately, it is difficult to assess how such interactions influence coexistence because few studies measure response variables that can be translated into dynamics through a competitive population-dynamics model. Ecologists may have modestly better evidence with which to evaluate higher-order interactions than they do for interaction chains, but the evidence is still sparse and it is hard to evaluate through current work how these interactions modulate community dynamics in nature.

Moving forward with n species

Advancing our understanding of coexistence mechanisms that operate only in systems with more than two competitors requires the gain of three types of knowledge. First, we need to build better expectations of when and how intransitive competitive relationships and stabilizing higher-order interactions emerge in competitive communities. Second, we need to obtain definitive empirical evidence concerning the prevalence and importance of these interactions in nature. Last, we need to develop theoretical guidance for how these mechanisms influence coexistence in truly diverse communities. Here, we lay out a research agenda that should resolve these main outstanding questions.

When to expect complex coexistence mechanisms

Much of the work on interaction chains and higher-order interactions has involved phenomenological models of competition. For theoreticians, these models enable the consequences of these interactions for coexistence to be evaluated efficiently, and for empiricists, the models present a limited number of parameters for fitting to data. However, inserting higher-order terms or intransitive competitive loops into phenomenological models does not help to build a predictive understanding of when intransitive competition and higher-order interactions emerge in nature. Developing such an understanding is important because the quantification of these mechanisms is challenging and something that we would only want to undertake when we have reason to think that they operate strongly. Moreover, higher-order interactions need to be demystified to become a regular part of how ecologists envision coexistence, and identifying their mechanistic basis is one way of doing so. As an example of the extent of the problem, even empirical studies that propose the presence of higher-order interactions have rarely provided a mechanism for the observed interaction (for exceptions, see refs 63 and 67). We therefore advocate the exploration of mechanistic models of competitive interactions in diverse networks that explicitly incorporate the dynamics of resources or predators.

The value of a more mechanistic approach to understanding intransitive competitive relationships has already been demonstrated by Huisman and Weissing⁶⁹. They built consumer–resource models and demonstrated the conditions under which transitive competition and intransitive competition emerge in systems comprising three species. Multiple limiting resources, an important condition for coexistence through pairwise niche differences, were shown to also be required for the emergence of intransitive loops. With only a single limiting resource,

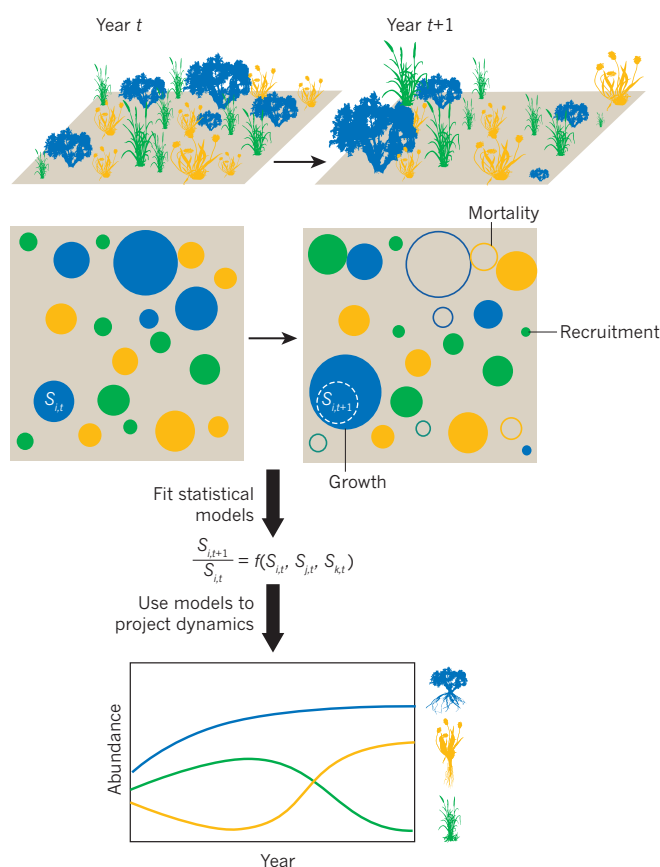


Figure 3 | A data-driven approach to modelling species

dynamics. Observational or experimental data can be fitted to models, which are then used to analyse the effects of interaction chains or higher-order interactions on dynamics. Between-year patterns of abundance (top) are converted into demographic transitions as a function of size (middle). For a size-based model, all individuals may be considered as circles of a given area. The change in size of species i (S_i) from one year to the next can be modelled as a function of the abundance or collective size of other individuals within a given radius or neighbourhood, assuming pairwise or higher-order interactions. Similar models can be built for survival and reproduction. The fitted functions can then be used to inform individual-based or integral projection models of community dynamics (bottom). These models and their parameters can be manipulated to add or remove particular mechanisms of coexistence, which enables their contribution to diversity maintenance to be evaluated.

species are ranked simply by their ability to depress the resource, which generates purely transitive competitive relationships (a point that is reinforced by ref. 6). Similar approaches could be applied to understanding the conditions that are necessary for the emergence of higher-order interactions, and whether these interactions benefit or harm coexistence. Initial progress towards this goal could be achieved by modifying existing models of resource competition, such as Tilman's R^* model⁵². This would enable ecologists to explore when higher-order interactions emerge in a system with more than two competitors and, if they do emerge, how the interactions affect coexistence and extinction cascades. Assumptions about trait plasticity in such models may prove to be important; existing eco-evolutionary models in which trait values respond to and affect competitive interactions⁷⁰ might therefore be a useful starting point.

The addition of resources or higher trophic levels to models with a diverse guild of competitors both enhances network complexity and deepens the associated quantitative challenges. Fortunately, techniques exist to simplify the structure of multitrophic systems by correcting competition coefficients so that they include both 'within' and 'between' trophic-level interactions. Bastolla *et al.*⁷¹ developed such a framework,

which enabled the calculation of an upper limit to the number of coexisting species in competitive systems. This framework was later extended to address systems of species that compete and engage in mutualistic interactions, and the structure of the mutualistic interactions was found to affect species coexistence by modulating the relative effects of facilitation and competition³⁹. Methods also exist for reframing the effects of network structure in terms of average fitness differences and stabilizing niche differences (as defined in Box 1) — metrics that are used commonly to understand pairwise coexistence. For example, Jabot and Bascompte⁷² showed how the balance between the stabilizing effects of interactions with higher trophic levels and the effects of interactions that drive fitness differences is mediated through the structure of the multitrophic interaction network.

Obtaining empirical evidence

The general absence of evidence with which to evaluate the prevalence and importance of interaction chains and higher-order interactions in nature may be one of the greatest knowledge gaps in our study of species coexistence. Filling this gap will require two efforts of equal importance: quantifying the operation of such mechanisms in natural communities; and evaluating their importance for species coexistence. We think that moving forwards on both of these fronts requires that multispecies population models are fitted to observational or experimental data. We acknowledge that a model-based approach may not be necessary for laboratory populations of microorganisms, which more readily provide the option of comparing the long-term competitive outcome in pairwise and more complex competition trials⁸. Nonetheless, without fitted models, it will remain difficult to resolve the exact reasons for why outcomes change as community complexity increases.

The model-based approach can be implemented in several ways, but it uses two steps at its core (Fig. 3). The first involves using statistical models to quantify how the demographic performance of individual organisms depends on naturally occurring (or experimentally imposed) variation in the abundance and identity of neighbours^{73–75}. The fitted models can then be used to quantify the prevalence of intransitive competition⁷⁶ or the significance of higher-order terms⁵⁹. The second step involves using models to project community dynamics on the basis of the fitted relationships^{75,77} (Fig. 3). These projections can be built on analytical expressions or multispecies simulations of demographic models structured by organism stage (size) or age. The importance of a particular mechanism for coexistence can then be quantified by projecting the outcome of competition in the presence or absence of that mechanism. An alternative option is to construct dynamical models that differ in the mechanisms that they include and then to fit these models directly to observed changes in abundance. However, some coexistence mechanisms with only weak statistical support may strongly influence dynamics⁷⁷, necessitating the approach advocated here that uses model fitting followed by projection.

For an example of how fitted models might be projected to quantify the consequences of higher-order interactions (something that no empirical study has yet accomplished), community dynamics projected under the assumption of purely pairwise interactions can be compared to the dynamics that are observed when fitted higher-order interactions also operate. Similarly, to understand how well intransitive competition stabilizes coexistence, the pairwise intraspecific interactions can be forced to match the interspecific interactions (as performed in refs 75 and 76), which leaves only the intransitivity to stabilize the dynamics.

Despite the need for mathematical models that are fitted to empirical data, building them presents formidable challenges — the most obvious of which is parameter estimation and the risk of overfitting the models⁵⁹. As well as parameters that describe the intrinsic demographic performance, which may vary with size, stage or age, and also in space and time, we require parameters to describe the intraspecific and interspecific density dependence. As noted previously, the number of pairwise interactions increases by the square of the number of species in the system, and the number of higher-order interactions expands

even more rapidly. Ideally, to estimate these parameters properly, we would observe the per capita growth rate of each species in the community when growing with all density combinations of the competitor species — essentially, an n -dimensional response surface design. Observational data sets often fall short of this ideal (with a high risk of overfitting), especially if stabilizing mechanisms maintain populations close to some equilibrium. Experiments that manipulate the densities of several competitors in a factorial design, and that examine the pairwise and interactive effects of competitors on individuals of a target species, probably represent the most convincing option for fitting higher-order interactions in nature.

Coexistence in diverse competitive networks

Further theoretical attention is required to determine how intransitive competition and higher-order interactions influence coexistence and the robustness of competitive networks to species loss in systems larger than those that can be parameterized empirically. Progress towards this goal is hindered by the fact that, although the stability of systems with n competitors (the classic focus of theory; see Box 2) can be evaluated, it is not easy to evaluate how many of the competitors can coexist if the full system is unstable. We therefore advocate a shift in focus from the probability that n species coexist to questioning what fraction of species will coexist if we start with a certain value of n . This would enable us to ask, for example, how higher-order or intransitive interactions dictate the fraction of species that can coexist after community disruption and recolonization, a common scenario in some ecological systems^{78,79}.

Simulation cannot be used easily to achieve such aims due to the tremendous number of subcommunities that can be derived from a truly diverse system. Quantifying the fraction of species that can coexist therefore requires new theory to be built, different experimental protocols to be designed and the use of mathematical tools that are new to ecology. Currently, this coexisting fraction has been determined only for highly idealized models of competition in which all pairwise interactions result in exclusion so that coexistence is possible only through intransitive competition. If the pairwise winner and loser are determined at random, to build what is called a random tournament graph, the number of coexisting species when starting with n can be calculated analytically⁶. Although the probability of achieving the coexistence of all species becomes vanishingly small as n increases, on average $n/2$ species can coexist. A very diverse system can therefore exist despite the loss of a considerable number of species to extinction.

A theoretical framework that predicts the fraction of species that can coexist would be particularly useful for evaluating how network structure influences the extent of extinction cascades. Formally, if n species stably coexist but $n - 1$ do not (owing to the loss of a key competitor), ideally, we could predict the fraction of the $n - 1$ species that do persist. Moreover, how this fraction depends on the structure of the competitive network, which includes the structures of both interaction chains and higher order interactions, provides an important question for future research. Analyses already developed for the study of mutualistic and multitrophic networks^{9,10,39,80} could be of particular value here.

A word of caution

We have presented the argument that ecologists lack the empirical data to evaluate the stabilizing role of intransitive competition and higher-order interactions in shaping species coexistence. Although theory shows that these types of interactions play potentially crucial parts in shaping species coexistence^{6,57}, our call for appropriate empirical tests should not be taken as an expectation that these factors have important roles in nature — simply, we do not know. Moreover, other types of evidence can be used to constrain their potential importance. As noted at several points in this Review, a unifying feature of coexistence mechanisms that depend on either intransitivity or higher-order interactions is that both rely on the presence of a sufficient number of species to operate. However, findings from the large body of studies that have manipulated species diversity suggest that as the number of species that

are assembled into a community increases, it becomes more difficult for new species to enter⁸¹. This finding may reflect the fact that conventional pairwise niche mechanisms, which would generate this pattern, overwhelm the operation of coexistence mechanisms that emerge only with larger sets of competitors.

A further reason for caution is that ecologists do have reasonable alternatives that rely purely on pairwise mechanisms to explain the very high diversity that is seen in many ecosystems. Spatial environmental heterogeneity is a powerful force for maintaining species diversity, even at surprisingly small scales⁸². Although it may seem improbable that each species in a diverse community has specific environmental preferences, modest differences between species can maintain coexistence as long as the average fitness of the species is similar (Box 1). Coexistence in nature may also result from the interaction between pairwise mechanisms and those that require more than two species. Spatial heterogeneity in intransitive competitive relationships⁶, or heterogeneous mutualistic or antagonistic network structure⁷², can strongly benefit regional-scale coexistence. Furthermore, the cyclical nature of coexistence under intransitive competitive loops creates temporal variation in the environment, through which many other species can specialize and ultimately coexist²⁸.

Outlook

In this Review, we suggest that coexistence mechanisms that emerge only in systems with more than two competitors exert a largely unexplored control over the maintenance of diversity in species-rich communities. We also highlight that when studying more than two competitors, ecologists necessarily confront an ecological network. However, it remains largely unknown how the structure of the network influences coexistence. The sparseness of evidence results from the intractability of empirically evaluating competition between many species and the technical difficulties that are inherent in tightly coupling theory to data. Despite these challenges, there are compelling reasons to deepen our understanding of these more complex mechanisms of coexistence. Armed with advances in data-driven modelling and network analyses that have been developed for multitrophic systems, ecologists are well-positioned to determine, for at least some species-rich communities, how much of the coexistence results from mechanisms that emerge only in diverse systems. Few other questions in ecology have such great potential to radically shift how we think about the maintenance and fragility of biodiversity. ■

Received 25 November 2016; accepted 23 March 2017.

Supplementary Information is linked to the online version of the paper at go.nature.com/2rphvxn.

- Hutchinson, G. E. The paradox of the plankton. *Am. Nat.* **95**, 137–145 (1961).
- Chesson, P. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
- Barabás, G., Michalska-Smith, M. J. & Allesina, S. The effect of intra- and interspecific competition on coexistence in multispecies communities. *Am. Nat.* **188**, E1–E12 (2016).
- This paper investigates how the specific arrangement of competition coefficients in a network structure affects stability.**
- Hubbell, S. P. Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* **19**, 166–172 (2005).
- Kraft, N. J. B., Valencia, R. & Ackerly, D. D. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* **322**, 580–582 (2008).
- Allesina, S. & Levine, J. M. A competitive network theory of species diversity. *Proc. Natl Acad. Sci. USA* **108**, 5638–5642 (2011).
- This paper uses mathematical theory to show how intransitive competitive loops emerge and stabilize coexistence in diverse competitive networks.**
- Billick, I. & Case, T. J. Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* **75**, 1529–1543 (1994).
- Friedman, J., Higgins, L. M. & Gore, J. Community structure follows simple assembly rules in microbial microcosms. *Nature Ecol. Evol.* 0109 (2017).
- Thébault, E. & Fontaine, C. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856 (2010).
- Stouffer, D. B. & Bascompte, J. Compartmentalization increases food-web persistence. *Proc. Natl Acad. Sci. USA* **108**, 3648–3652 (2011).
- Montoya, J. M., Woodward, G., Emmerson, M. C. & Solé, R. V. Press perturbations and indirect effects in real food webs. *Ecology* **90**, 2426–2433 (2009).

- Solé, R. V. & Montoya, J. A. Complexity and fragility in ecological networks. *Proc. R. Soc. B* **268**, 2039–2045 (2001).
- Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B* **271**, 2605–2611 (2004).
- Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jr, Jordano, P. & Bascompte, J. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925–928 (2007).
- Case, T. J. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biol. J. Linn. Soc.* **42**, 239–266 (1991).
- Stone, L. & Roberts, A. Conditions for a species to gain advantage from the presence of competitors. *Ecology* **72**, 1964–1972 (1991).
- Kerr, B., Riley, M. A., Feldman, M. W. & Bohannan, B. J. M. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* **418**, 171–174 (2002).
- This paper shows how a rock-paper-scissors competitive loop can stabilize the dynamics of multiple strains of *E. coli* in the laboratory.**
- Wootton, J. T. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *Am. Nat.* **141**, 71–89 (1993).
- Padilla, F. M. et al. Early root overproduction not triggered by nutrients decisive for competitive success belowground. *PLoS ONE* **8**, e55805 (2013).
- May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).
- Yodanis, P. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**, 508–515 (1988).
- Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
- May, R. M. & Leonard, W. J. Nonlinear aspects of competition between three species. *SIAM J. Appl. Math.* **29**, 243–253 (1975).
- Levine, S. H. Competitive interactions in ecosystems. *Am. Nat.* **110**, 903–910 (1976).
- Vandermeer, J. Indirect and diffuse interactions: complicated cycles in a population embedded in a large community. *J. Theor. Biol.* **142**, 429–442 (1990).
- Hofbauer, J. & Sigmund, K. Evolutionary game dynamics. *Bull. Am. Math. Soc.* **40**, 479–519 (2003).
- Laird, R. A. & Schamp, B. S. Competitive intransitivity promotes species coexistence. *Am. Nat.* **168**, 182–193 (2006).
- Huisman, J. & Weissing, F. J. Biodiversity of plankton by species oscillations and chaos. *Nature* **402**, 407–410 (1999).
- Benincà, E., Ballantine, B., Ellner, S. P. & Huisman, J. Species fluctuations sustained by a cyclic succession at the edge of chaos. *Proc. Natl Acad. Sci. USA* **112**, 6389–6394 (2015).
- Edwards, K. & Schreiber, S. Preemption of space can lead to intransitive coexistence of competitors. *Oikos* **119**, 1201–1209 (2010).
- MacArthur, R. & Levins, R. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–385 (1967).
- Pimm, S. L. The structure of food webs. *Theor. Popul. Biol.* **16**, 144–158 (1979).
- Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E. & Taylor, W. W. Compartments revealed in food-web structure. *Nature* **426**, 282–285 (2003).
- Olesen, J. M., Bascompte, J., Dupont, Y. L. & Jordano, P. The modularity of pollination networks. *Proc. Natl Acad. Sci. USA* **104**, 19891–19896 (2007).
- Allesina, S. & Pascual, M. Food web models: a plea for groups. *Ecol. Lett.* **12**, 652–662 (2009).
- Guimerà, R. et al. Origin of compartmentalization in food webs. *Ecology* **91**, 2941–2951 (2010).
- Grilli, J., Rogers, T. & Allesina, S. Modularity and stability in ecological communities. *Nature Commun.* **7**, 12031 (2016).
- Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. The nested assembly of plant–animal mutualistic networks. *Proc. Natl Acad. Sci. USA* **100**, 9383–9387 (2003).
- Bastolla, U. et al. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020 (2009).
- Sinervo, B. & Lively, C. M. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380**, 240–243 (1996).
- Lankau, R. A. & Strauss, S. Y. Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* **317**, 1561–1563 (2007).
- This paper shows how genetic diversity in a species of mustard helps to stabilize between-species coexistence through an intransitive competitive relationship.**
- Lankau, R. A. Genetic variation promotes long-term coexistence of *Brassica nigra* and its competitors. *Am. Nat.* **174**, E40–E53 (2009).
- Buss, L. W. & Jackson, J. B. C. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.* **113**, 223–234 (1979).
- Buss, L. W. Competitive intransitivity and size-frequency distributions of interaction populations. *Proc. Natl Acad. Sci. USA* **77**, 5355–5359 (1980).
- Paine, R. T. Ecological determinism in the competition for space: the Robert H. MacArthur Award lecture. *Ecology* **65**, 1339–1348 (1984).
- Keddy, P. A. & Shipley, B. Competitive hierarchies in herbaceous plant communities. *Oikos* **54**, 234–241 (1989).
- Grace, J. B., Guntenspergen, G. R. & Keough, J. The examination of a competition matrix for transitivity and intransitive loops. *Oikos* **68**, 91–98 (1993).
- Shipley, B. A null model for competitive hierarchies in competition matrices. *Ecology* **74**, 1693–1699 (1993).
- Diez, H., Steinlein, T. & Ullmann, I. The role of growth form and correlated traits in competitive ranking of six perennial ruderal plant species grown in unbalanced mixtures. *Acta Oecol.* **19**, 25–36 (1998).

50. Cameron, D. D., White, A. & Antonovics, J. Parasite–grass–forb interactions and rock–paper scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities. *J. Ecol.* **97**, 1311–1319 (2009).
51. Zhang, S. & Lamb, E. G. Plant competitive ability and the transitivity of competitive hierarchies change with plant age. *Plant Ecol.* **231**, 15–23 (2012).
52. Tilman, D. *Resource Competition and Community Structure* (Princeton Univ. Press, 1982).
53. Ulrich, W., Soliveres, S., Kryszewski, W., Maestre, F. T. & Gotelli, N. J. Matrix models for quantifying competitive intransitivity from species abundance data. *Oikos* **123**, 1057–1070 (2014).
54. Soliveres, S. *et al.* Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett.* **18**, 790–798 (2015).
55. Abrams, P. A. Arguments in favor of higher-order interactions. *Am. Nat.* **121**, 889–891 (1983).
56. Golubski, A. J., Westlund, E. E., Vandermeer, J. & Pascual, M. Ecological networks over the edge: hypergraph trait-mediated indirect interaction (TMII) structure. *Trends Ecol. Evol.* **31**, 344–354 (2016).
57. Bairey, E., Kelsic, E. D. & Kishony, R. Higher-order species interactions shape ecosystem diversity. *Nature Commun.* **7**, 12285 (2016).
- This paper uses mathematical models to show that higher-order interactions can cause communities with greater diversity to be more stable than their species-poor counterparts, contrary to classic theory that is based on pairwise interactions.**
58. Vandermeer, J. H. A further note on community models. *Am. Nat.* **117**, 379–380 (1981).
59. Mayfield, M. M. & Stouffer, D. B. Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecol. Evol.* **1**, 0062 (2017).
60. Vandermeer, J. H. The competitive structure of communities: an experimental approach with protozoa. *Ecology* **50**, 362–371 (1969).
61. Neill, W. E. The community matrix and interdependence of the competition coefficients. *Am. Nat.* **108**, 399–408 (1974).
62. Worthen, W. B. & Moore, J. L. Higher-order interactions and indirect effects: a resolution using laboratory *Drosophila* communities. *Am. Nat.* **138**, 1092–1104 (1991).
63. Morin, P. J., Lawler, S. P. & Johnson, E. A. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* **69**, 1401–1409 (1988).
64. Pomerantz, M. J. Do ‘higher order interactions’ in competition systems really exist? *Am. Nat.* **117**, 583–591 (1981).
65. Adler, F. R. & Morris, W. F. A general test for interaction modification. *Ecology* **75**, 1552–1559 (1994).
66. Dormann, C. F. & Roxburgh, S. H. Experimental evidence rejects pairwise modelling approach to coexistence in plant communities. *Proc. R. Soc. B* **272**, 1279–1285 (2005).
67. Weigelt, A. *et al.* Identifying mechanisms of competition in multi-species communities. *J. Ecol.* **95**, 53–64 (2007).
68. Vandermeer, J. H. A further note on community models. *Am. Nat.* **117**, 379–380 (1981).
69. Huisman, J. & Weissing, F. J. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology* **82**, 2682–2695 (2001).
70. Vasseur, D. A., Amarasekare, P., Rudolf, V. H. W. & Levine, J. M. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am. Nat.* **178**, E96–E109 (2011).
71. Bastolla, U., Lässig, M., Manrubia, S. C. & Valleriani, A. Biodiversity in model ecosystems. I: coexistence conditions for competing species. *J. Theor. Biol.* **235**, 521–530 (2005).
72. Jabot, F. & Bascompte, J. Biotrophic interactions shape biodiversity in space. *Proc. Natl Acad. Sci. USA* **109**, 4521–4526 (2012).
73. Lasky, J. R., Uriarte, M., Boukili, V. K. & Chazdon, R. L. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proc. Natl Acad. Sci. USA* **111**, 5616–5621 (2014).
74. Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci. USA* **112**, 797–802 (2015).
75. Chu, C. & Adler, P. B. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.* **85**, 373–392 (2015).
- This paper describes state-of-the-art approaches for combining observational data with mathematical models to project the importance of particular coexistence mechanisms in nature.**
76. Godoy, O., Stouffer, D. B., Kraft, N. J. & Levine, J. M. Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology* <http://dx.doi.org/10.1002/ecy.1782> (2017).
77. Ellner, S. P., Snyder, R. E. & Adler, P. B. How to quantify the temporal storage effect using simulations instead of math. *Ecol. Lett.* **19**, 1333–1342 (2016).
78. Antonopoulos, D. A. *et al.* Reproducible community dynamics of the gastrointestinal microbiota following antibiotic perturbation. *Infect. Immun.* **77**, 2367–2375 (2009).
79. Costello, C. *et al.* Status and solutions for the world’s unassessed fisheries. *Science* **338**, 517–520 (2012).
80. Eklof, A. & Ebenman, B. Species loss and secondary extinctions in simple and complex model communities. *J. Anim. Ecol.* **75**, 239–246 (2006).
81. Levine, J. M., Adler, P. B. & Yelenik, S. G. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* **7**, 975–989 (2004).
82. Silvertown, J., Dodd, M. E., Gowing, D. J. G. & Mountford, J. O. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* **400**, 61–63 (1999).
83. Adler, P. B., HilleRisLambers, J. & Levine, J. M. A niche for neutrality. *Ecol. Lett.* **10**, 95–104 (2007).
84. Goh, B. S. Global stability in many-species systems. *Am. Nat.* **111**, 135–143 (1977).
85. Roberts, A. The stability of a feasible random ecosystem. *Nature* **251**, 608–609 (1974).
86. Vandermeer, J. H. Interspecific competition: a new approach to the classical theory. *Science* **188**, 253–255 (1975).
87. Stone, L. *Some Problems of Community Ecology: Processes, Patterns and Species Persistence in Ecosystems*. PhD thesis, Monash Univ. (1988).
88. Logofet, D. O. *Matrices and Graphs: Stability Problems in Mathematical Ecology* (CRC, 1992).
89. Case, T. J. *An Illustrated Guide to Theoretical Ecology* (Oxford Univ. Press, 2000).
90. Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497 (2014).
91. Justus, J. Ecological and Lyapunov stability. *Philos. Sci.* **75**, 421–436 (2008).
92. Thom, R. *Structural Stability and Morphogenesis* (Addison-Wesley, 1994).
93. Solé, R. V. & Valls, J. On structural stability and chaos in biological systems. *J. Theor. Biol.* **155**, 87–102 (1992).
94. Saavedra, S. *et al.* A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* <http://dx.doi.org/10.1002/ecm.1263> (2017).

Acknowledgments Comments from the Plant Ecology group at ETH Zürich improved the manuscript. We thank R. Freckleton for feedback on the limitations of relative-yield approaches and A. Ferrera for insightful discussions on stability. Conversations with S. Pacala, S. Levin, A. Hastings and A. Ives helped to clarify our thoughts on higher-order interactions. J.M.L. is supported by US National Science Foundation (NSF) grant 1644641, J.B. is funded by the European Research Council through an Advanced Grant, P.B.A. is supported by NSF grant 1353078 and S.A. is supported by NSF grant 1148867.

Author Contributions All authors researched the literature to assemble the review. J.M.L. assembled the first draft of the paper, with all authors contributing individual sections and revisions.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this paper at go.nature.com/2rphvnm. Correspondence should be addressed to J.M.L. (jlevine@ethz.ch).

Reviewer Information *Nature* thanks A. Golubski, E. Thebault and the other anonymous reviewer(s) for their contribution to the peer review of this work.