

Research



Cite this article: Northfield TD, Laurance SGW, Mayfield MM, Paini DR, Snyder WE, Stouffer DB, Wright JT, Lach L. 2018 Native turncoats and indirect facilitation of species invasions. *Proc. R. Soc. B* **285**: 20171936. <http://dx.doi.org/10.1098/rspb.2017.1936>

Received: 28 August 2017

Accepted: 21 December 2017

Subject Category:

Ecology

Subject Areas:

ecology, theoretical biology

Keywords:

biotic resistance, invasion paradox, competition, mutualism, predation, indirect effects

Author for correspondence:

Tobin D. Northfield

e-mail: tobin.northfield@jcu.edu.au

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3969279>.

Native turncoats and indirect facilitation of species invasions

Tobin D. Northfield¹, Susan G. W. Laurance¹, Margaret M. Mayfield², Dean R. Paini³, William E. Snyder⁴, Daniel B. Stouffer⁵, Jeffrey T. Wright⁶ and Lori Lach¹

¹Centre for Tropical, Environmental, and Sustainability Sciences, College of Science and Engineering, James Cook University, Cairns, Australia

²School of Biological Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

³CSIRO, Black Mountain Laboratories, Acton, Australian Capital Territory 2601, Australia

⁴Department of Entomology, Washington State University, Pullman, WA 99164-6382, USA

⁵Centre for Integrative Ecology, University of Canterbury, School of Biological Sciences, Christchurch, Canterbury 8041, New Zealand

⁶Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia

TDN, 0000-0002-0563-485X; DBS, 0000-0001-9436-9674

At local scales, native species can resist invasion by feeding on and competing with would-be invasive species. However, this relationship tends to break down or reverse at larger scales. Here, we consider the role of native species as indirect facilitators of invasion and their potential role in this diversity-driven ‘invasion paradox’. We coin the term ‘native turncoats’ to describe native facilitators of non-native species and identify eight ways they may indirectly facilitate species invasion. Some are commonly documented, while others, such as indirect interactions within competitive communities, are largely undocumented in an invasion context. Therefore, we use models to evaluate the likelihood that these competitive interactions influence invasions. We find that native turncoat effects increase with the number of resources and native species. Furthermore, our findings suggest the existence, abundance and effectiveness of native turncoats in a community could greatly influence invasion success at large scales.

1. Introduction

Understanding the mechanisms driving biological invasions is a fundamental goal of invasion ecology. Dozens of hypotheses have been developed to explain how some species are able to establish and spread [1,2]. Some of these focus on the traits and movement of the would-be invader (e.g. novel weapons, propagule pressure); others on the characteristics of the invaded habitat and its residents (e.g. enemy release, increased resource availability, biotic resistance). Most hypotheses incorporate some consideration of the characteristics of both the would-be invader and the habitat (e.g. evolution of increased competitive ability) [1,2], and thereby implicitly consider species interactions as a vital component in understanding the success of invasive species.

Species interactions have long been recognized as playing a key role in determining species’ range limits [3]. Resident natives can eat or compete with non-native species, forming ‘biotic resistance’ against invasion [3,4]. A corollary to the idea that interactions with native species may prevent invasion is the idea that the absence of predators or other natural enemies improves the chances of invasion. The ‘release’ from enemies reduces mortality and allows the would-be invader to divert resources from defence to growth and reproduction [5], thereby increasing its competitive advantage. Taken together, these two hypotheses suggest that direct, antagonistic interactions that reduce invader success should strengthen resistance to invasion, while the absence of these interactions should enhance invasion success.

Biodiverse communities that include many species of generalist predators capable of recognizing and successfully capturing newly arriving species, or that include a diversity of strong competitors, are thought to be particularly difficult to invade due to a preponderance of species negatively affecting non-native species [3]. This is supported by the common observation that species-depauperate communities are among the most easily invaded. Though both theory [6–8] and some empirical studies (e.g. [4,9,10]) support the hypothesis that the likelihood of successful invasion decreases with increasing biodiversity, other studies [11,12] suggest that the negative effect of biodiversity on invasion success can break down at larger scales, leading to positive relationships between biodiversity and invasion potential, a phenomenon known as the invasion paradox [13–15]. The breakdown of the relationship between biodiversity and biotic resistance at larger scales is generally attributed to changes in spatial processes altering resource availability, reducing direct effects of resistance from competition at larger scales or increasing direct facilitation of non-native species (see [13] for review).

(a) Indirect interactions

While the positive direct effects of native species on non-native species, such as pollination and beneficial habitat modification, are well documented and relatively easy to observe [16], benefits that native species may provide to arriving non-natives through indirect channels are less documented and appreciated. From work outside of the invasive species literature, it is clear that indirect interactions, where the effect of one species (the donor) on another (the receiver) is passed through a third, intermediate species (the mediator or transmitter) [17], are both exceedingly common and ecologically influential [18]. This use of the term donor is not to be confused with the donor region, which is often used to describe the location from which a non-native species has originated. Indirect interactions are also known to alter selection pressure under some circumstances [19]. For example, predators often indirectly benefit plants by eating herbivores [20–22], and flowering plants can indirectly benefit one another by providing additional resources to pollinators [23,24]. Predators can, of course, also indirectly harm plants by consuming pollinators [25]. Therefore, the indirect effect initiated by the donor species can be either beneficial or harmful to the recipient, and may be difficult to detect if only some of the interacting species are included in a study. When the donor is a native species and the recipient is non-native, indirect effects harmful to the non-native form a recognized component of biotic resistance. By contrast, indirect effects beneficial to a non-native recipient should promote successful invasion, an outcome that is less prevalent in the invasion literature than the reverse (i.e. effects of invaders on native communities). Moreover, as the number of species in a community increases, the number of these indirect interactions can increase dramatically, at a much faster rate than the number of direct interactions (figure 1), and thus may become important in determining biotic resistance or facilitation in species-rich communities. Here, we coin the term ‘native turncoats’ to describe native species that indirectly benefit non-native species by altering the abundance or behaviour of other native species.

Some positive indirect effects of native species on invasive species have been fairly well documented, including chains

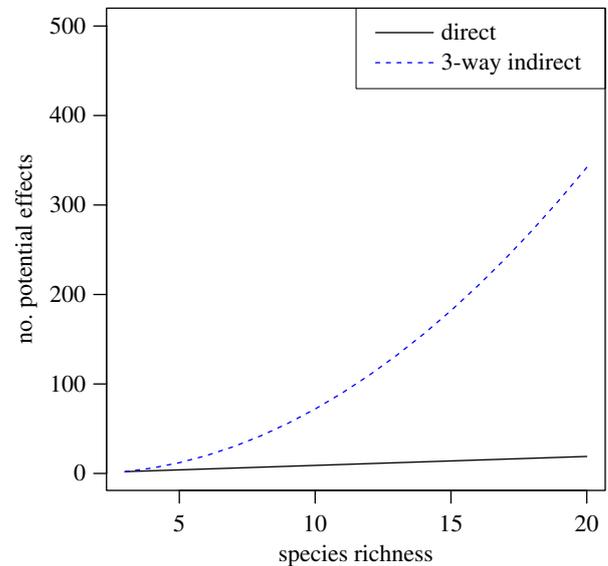


Figure 1. The number of direct and indirect species interaction pathways affecting a given species that include two and three species, respectively, for a saturated (all species competing) competitive community, as they scale with species richness. The number of species indirectly interacting with a focal species is ultimately limited by the number of other species in the community ($n - 1$). However, the types of pathways also depend on the identity of species mediating this interaction, and can therefore be much more diverse. For a saturated community (all species interact with each other), the number of direct interaction pathways increase with species richness (n) as $n - 1$, while indirect interaction pathways comprising three species increase as $(n - 1)! / (n - 3)!$. (Online version in colour.)

of mutualists and/or commensalists, trophic cascades and predators that eat a native competitor of a non-native species [26]. For example, native plants often maintain densities of mutualistic native pollinators or mycorrhizae that can in turn benefit non-native plants [27]. In addition, native predators or parasites often attack other native predators or competitors that would otherwise reduce the densities of non-native species [28,29]. To further clarify the types of potential interactions, we have identified a total of eight possible pathways that may lead native species to indirectly benefit non-native species (table 1). It is often difficult to distinguish between commensalism and mutualism, because the benefits that each receives may be context dependent. Therefore, we group mutualisms with commensalism resulting in benefits received by the native mediator and non-native species (i.e. here we are not concerned with effects on the donor species).

The competition chain occurs when one native species (the donor) competes strongly with another native species (the mediator) that would otherwise competitively resist the non-native species (table 1a). For this type of interaction to have strong effects relative to direct competition, competition between the donor and non-native species must be weak, and this may occur when there is large niche overlap between the donor and the mediator and between the mediator and non-native species, but low between the donor and non-native species (figure 2). Although examples of indirect interactions within competition chains involving invasive recipients are rare, they have often been identified in the plant and animal community assembly literature (e.g. [30–32,34]). Though their focus was not biological invasion *per se*, Mayfield & Stouffer [39] provide one of the few empirical

Table 1. Description of possible indirect interactions between native (open symbols) and non-native species (solid circle) that result in a net facilitation of a non-native species. Species involved include the facilitator (star), mediator (square) and the non-native recipient (filled circle). + and – indicate, respectively, positive and negative effects of one species on another in the direction of the arrow, with solid arrows indicating direct effects and dotted arrows indicating indirect effects.

interaction type	interaction description	published examples	references
(a) 	Competition chain: native species competes with another native that competes with a non-native species.	None identified from invasive species literature, but common in community assembly literature within native communities.	[30–32]
(b) 	Mutualism or commensalism chain: native species has a mutualism or commensalism with another native species that also has a mutualism or commensalism with a non-native species.	Native plant (mediator) has a mutualism with soil biota that also benefits the non-native species. Native plant has a mutualism with a pollinator that also pollinates the non-native species.	[27,33]
(c) 	Trophic cascade: native species preys on or parasitizes a native species that preys on or parasitizes a non-native species.	Crabs feed on urchins, which in turn feed on a non-native ascidian.	[29]
(d) 	Predation or parasitism of a competitor: native species preys on or parasitizes a native species that competes with a non-native species.	Vertebrate herbivores consume native woody plants that compete with non-native understory plants.	[28]
(e) 	Competition with a predator or parasite: native species competes with a native species that preys on, or is hosted by, a non-native species.	We are not aware of any published examples. However, this is similar to the enemy of my enemy hypothesis [34,35].	
(f) 	Prey (or host) of a commensalist or mutualist: native species is prey or host for another native species that benefits a non-native species via mutualism or commensalism.	Beech trees host native scale insects that provide honeydew to invasive wasps.	[36]
(g) 	Mutualist or commensalist of a prey or host: native species has a mutualism or commensalism with another native species that is prey or host for a non-native species.	Native nutcrackers disperse seeds of native white pines that serve as hosts of invasive fungal pathogens.	[37]
(h) Trait-mediated interaction	Predator or parasite preys on or is hosted by a prey or host of an non-native species that indirectly improves a non-native species' attack rate.	Tuberculosis parasitism risk is higher for buffalo in Africa when they have been parasitized by nematodes, due to a weakened Th1 response.	[38]

examples of indirect interactions significantly altering the fitness of specific non-native species. The authors used mathematical models to evaluate the effects of species interactions on fecundity of annual woodland plants and found that non-additive, higher-order (i.e. species interacting indirectly) interactions strongly influenced species performance. Similarly, recent theoretical analyses suggest these types of interactions can strongly influence species coexistence and diversity in competitive communities [40], leading to calls for increased consideration of indirect interactions in ecological theory [41]. Indirect interactions are particularly strong in intransitive competition chains, which represent a special case of competition chain when there is no single dominant competitor, such that species A can outcompete species B,

which can outcompete species C, which in turn outcompetes species A. Intransitive competition chains have most commonly been observed in microbial systems [42] with more limited and more mixed evidence for them in environmentally heterogeneous plant communities [43,44]. That said, research on intransitivity in invaded systems is quite uncommon in all but microbial systems.

Here, we consider the potential for indirect interactions to affect invasion success within competitive communities. These indirect interactions are very amenable to theoretical modelling due to the simplicity of competitive communities relative to other network types [45]. Therefore, we use theoretical models to evaluate the potential for these interactions to alter invasion processes.

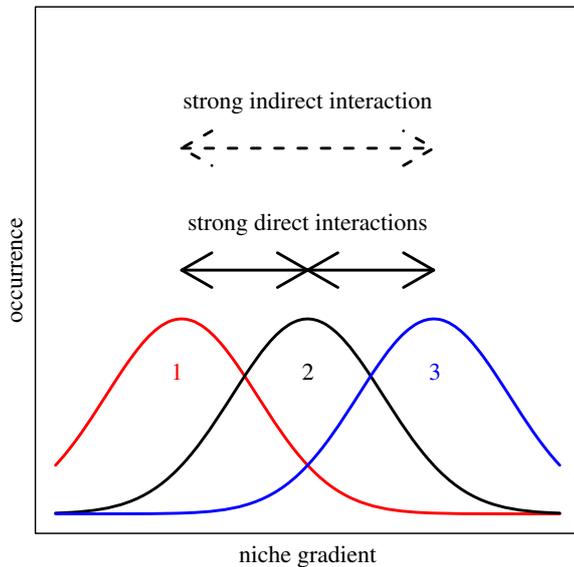


Figure 2. Depiction of how strong indirect interactions can emerge from pairwise direct interactions. If interaction strength depends on niche overlap, we would expect species 2 (black lines) to strongly interact with each species 1 (red lines) and 3 (blue lines). The low niche overlap between 1 and 3 would suggest little direct interaction between them, but as they both interact strongly with species 2, they would interact indirectly. (Online version in colour.)

(b) Background theory

Theory of indirect, positive interactions is most developed for single guild competitive communities where all direct interactions are negative, and thus positive interactions are all indirect net effects of competition and easily distinguishable from direct effects [18]. The donor species in these cases are generally referred to as ‘advantageous in a community context’ to the receiver species to describe the competitive advantage gained by the receiver species due to the donor reducing the density of a key competitor [45,46]. These types of interactions are more prevalent in communities where competitive interactions are generally strong, but highly variable among members of a community [45,46]. It is still unclear, however, how community size or spatial scale alters the probability that species are advantageous in a community context, or how likely these interactions are to alter resistance to a would-be invader.

Our model analyses evaluate the potential for positive indirect effects of native donors on non-native recipients. We focus on the identification of positive indirect effects because, as described above, they are identifiable in competitive communities, and because the number of indirect interactions increases with increasing diversity (figure 1). These indirect interactions may also be an as yet unacknowledged mechanism by which invasion can increase with species richness. We begin by using competition models to identify native turncoat species that indirectly benefit non-natives. We also evaluate their influence on the relationship between biodiversity and biotic resistance, and in general, on the likelihood of species invasion. In our models, competition is determined by resource use patterns (as in [6,47]), allowing us to evaluate the effect of spatial scale and biodiversity on the presence of indirect interactions. We do not model spatial scale explicitly, but rather we model the number of resources available to the community, which we assume alters niche overlap and competition. This can also

be viewed as equivalent to niche dimensionality. We focus on the increase in the number of resources with scale, as this has often been proposed as the basis for why biodiversity–invasibility relationships break down or reverse at large scales (see [13] for review).

To quantify indirect interactions, we construct a community interaction matrix and solve for the algebraic inverse of this matrix, often referred to as the ‘inverse’ method [48–50]. We use this method to measure the magnitude of direct competitive interactions and positive indirect interactions from particularly competitive and beneficial species, respectively, and evaluate the influence of removing each on invasion success. We do not focus on negative indirect interactions (i.e. indirect interactions containing 4, 6, 8, etc., species), due to difficulties in distinguishing them from direct interactions (which are also negative). We find that positive indirect effects provide a counteracting force against biotic resistance that becomes stronger at larger scales, implicitly altered by increasing niche dimensionality and species richness. Therefore, these positive indirect effects may help explain the invasion paradox: why the relationship between invasibility and biodiversity depends on scale.

2. Theoretical analysis

(a) Model description

We use a Lotka–Volterra model to describe competition between n species, where the changes in abundance (N_i) of species i is determined by its growth rate (r_i), carrying capacity (K_i), the vector of competition coefficients acting on species i (a_i) and the vector of all the densities in the community (N). We can arrange the vectors of competition coefficients in a matrix A , where the element in the i th row and j th column represents the *per capita* effect of species j on species i and describe the changes in the vector of densities as

$$\frac{dN}{dt} = D(K - AN), \quad (2.1)$$

where D is an n by n matrix with diagonal elements $r_i N_i / K_i$ and zeroes for all off-diagonal elements, and K is the vector of carrying capacities. We assume each element of A is described by resource use overlap between two species for m resources, such that each competition coefficient (each element of A) is determined by the resource utilization overlap method [6,47,51]. Thus, to describe resource use patterns for n species and m resources, we use the resource utilization matrix U , an $m \times n$ matrix containing elements u_{ik} that describe the rate at which the i th species uses the k th resource. To define each element of U , we follow Byers & Noonburg [47] in drawing m random numbers from a uniform distribution between 0 and 1 for each species i , and add each number that is greater than a threshold value t to u_{ik} , where the resource k assigned is drawn from a uniform distribution between 0 and m .

We consider two models that differ only in their value for t , which describes resource use limitation. We consider a model (termed RU_{fixed} by Byers & Noonburg [47]) inspired by species with limitations on the numbers of resources that can be used (i.e. more specialized species), where the number of resources used by each species is independent of m . We then relax these limitations to allow species to be more generalized in their resource use patterns, by increasing the average number of resources used by a given species, m_u .

The value of t then varies with m , such that $m(1 - t) = m_u$. Once we have the resource utilization matrix U , we can set competition coefficients, a_{ij} , according to the resource use overlap between species j and i such that [6,47,51]

$$a_{ij} = \frac{\sum_{k=1}^m u_{ik}u_{jk}}{\sum_{k=1}^m u_{ik}^2}. \quad (2.2)$$

We set the vector K to determine positive equilibrium densities for all species, for our competition matrix A . Using this approach, there is an n -dimensional set of K vectors that will allow coexistence [52], which can be found through linear programming (see electronic supplementary material). We used the midpoint of the feasible K space as our vector of carrying capacities (as in [47,52]). Once the competition matrix, A , and the vector of carrying capacities, K , was defined, the vector of equilibrium densities of the native competitors was defined as

$$N^* = A^{-1}K. \quad (2.3)$$

As described in the above equation, the inverse community matrix A^{-1} translates the vector of competitor carrying capacities into the vector of equilibrium densities for the community. Therefore, this matrix can be used to describe the effects of changes in j th species equilibrium density, on the equilibrium density of the i th species [48–50]. These effects include both direct and indirect effects, and because all the direct competitive effects are negative in sign, any positive values can be attributed to strong, positive indirect effects between species [45].

(b) Simulations

We use the Lotka–Volterra modelling framework presented above to evaluate the ways variation in resource abundance and species richness alter resistance to non-native species via indirect pathways. We do this by using the inverted competition matrix including all species (including the non-native species) to identify ‘native turncoats’. We vary the number of resources available to the competitor community, m and evaluate its effects on invasion success.

To implicitly model changes in spatial scale, we assume that the number of species (n) increases linearly with the number of resources (m), such that $n = m - 1$. We also evaluate variation in either n or m individually, and present them in the electronic supplementary material. After assembling the native community as described above, we assigned resource use values, u_{ik} , for a non-native species. We set Mu (mean number of resources used per species) to either 15 or 30 to describe species that are more specialized or generalized in their resource use patterns, respectively. We set the non-native species’ carrying capacity equal to 1, the midpoint of the carrying capacity vector K for the native community [47]. All intrinsic rates of increase r_i were set to 0.5, although this term does not alter the final equilibrium densities (equation (2.3)). For the simulations, we set the initial density for the non-native species to 0.0001 (0.01% of the single species carrying capacity) and the vector of native species densities to their equilibrium values in the absence of the non-native species (N^*). We used the differential equation solver package *desolve* in R [53] to model the population dynamics of the invasion for 1000 time steps, which preliminary analyses suggested was sufficient to bring the system to equilibrium. We consider a successful invasion to have

occurred when the equilibrium density is greater than the initial starting density, suggesting that the non-native has established and spread.

To evaluate how variation in combined changes in resource number and species richness alters patterns of indirect interactions, direct competitive interactions and invasion success, we simulated 1000 invasions at each number of resources ranging from 10 to 48 by increments of two, for each level of mean resources used per species, $Mu = 15$ and 30, and varied species richness with the number of resources as described above. This approach implicitly evaluates one aspect of scale on the invasion process [14,47]. The effects of separate variation in species richness and resource number on invasion success are presented in the electronic supplementary material. We evaluated the effects of scale on the magnitude of the positive indirect effects from the five native species most beneficial to the non-native species. We estimate the benefit of these species by calculating the mean of the five largest values in the inverted matrix row corresponding to the effects of native species on the non-native species. We took the \log_{10} of these values before calculating the mean to reduce the effects of particularly beneficial species, because unlike competition coefficients, they are not bound between zero and one. In the rare case where there were fewer than five species that indirectly benefited the non-native species, we considered only the species that were beneficial. Similarly, we evaluated the effects of scale (i.e. number of resources and species) on the mean competitive resistance to the non-native species from the five native species most detrimental to the non-native species.

To identify native turncoats, we consider indirect interactions within communities present at the beginning of the invasion, before any species have gone extinct. Because the inverted matrix approach depends on the species included in the analysis, it can either be considered within the full community, which is present at the initiation of the invasion, or the final community, which will reflect changes in community composition due to species extinction or invasion failure. While it would be interesting to also evaluate indirect interactions within the final community after accounting for compositional changes, evaluating indirect effects on the non-native species necessitates invasion success (i.e. the non-native species must be present to interact with other species), and thus it is not possible to compare the interactions in this community for cases in which the invasion was not successful. Nonetheless, we find the inverted matrix approach to be useful for identifying particularly impactful native turncoats that influence the invasion process (see Results).

To evaluate the effects of the most influential turncoats and direct competitor species on invasion success, we conducted grouped simulations on the same community. In this case, we re-simulated after removing the most influential turncoats and direct competitors, as determined by the largest indirect positive effects and competition coefficients, respectively. We varied the proportion of the total species removed from 0 to 0.5 by increments of one species, and conducted these simulations on 1000 communities. We ran these analyses for each level of mean resources used per species, $Mu = 15$ and 30.

3. Results

Invasion probability increased as the numbers of resources and species increased, and with increasing levels of relative

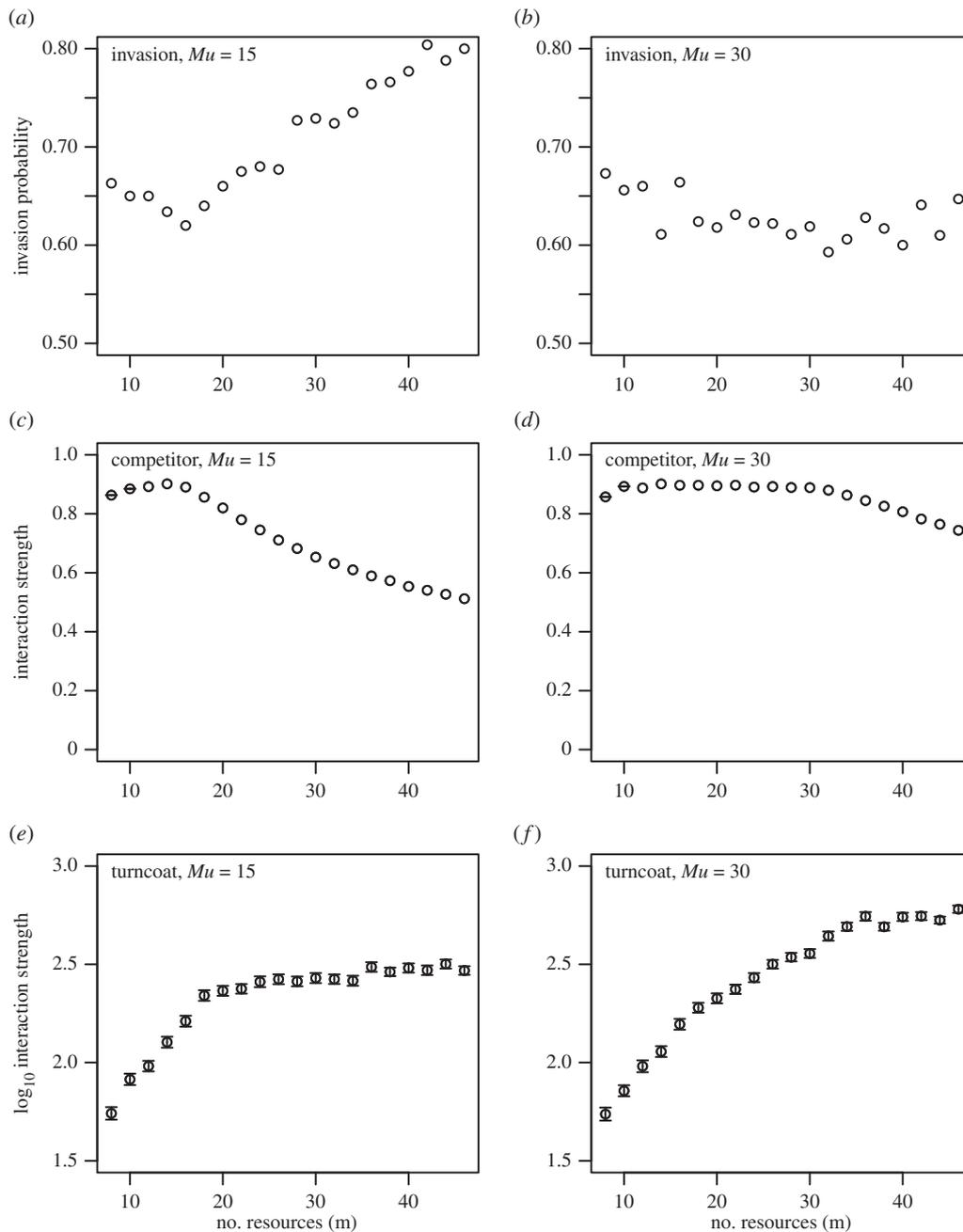


Figure 3. Effects of variation in the number of resources available to a community (m) and number of native species ($n = m - 1$) on the probability of species invasion (*a,b*), the mean of the top five direct, *per capita* competitive interaction strengths on the non-native species (*c,d*), and the mean of the top five indirect, positive *per capita* \log_{10} -transformed interaction strengths from turncoat species on the invasive species (*e,f*). Models represent either species with specialized resource use patterns (mean resources used/species (Mu) = 15; *a,c,e*), or species with generalized resource use patterns (mean resources used/species (Mu) = 30; *b,d,f*). Invasion probabilities and interaction strength means are calculated across 1000 simulations. (Online version in colour.)

specialization in species' resource use patterns (figure 3*a*), but declined when resource use patterns were more generalized (figure 3*b*). For more specialist competitors, the magnitude of competition from the top competitors on the non-native species declined as the number of resources increased (figure 3*c*), but for more generalist competitors the mean magnitude of direct competition was high across the spectrum of resource usage (figure 3*d*). In models describing each type of resource use pattern, we found that the positive *per capita* effects of the most influential native turncoat species increased with the number of resources and species (figure 3*e,f*). The increase in the effects of native turncoats on the non-natives stems from increases in species richness more than resource availability *per se* (electronic supplementary material, figures A1 and A2), suggesting that it is the added network size

and/or complexity that contributes to the relationship between indirect influence and spatial scale.

When competitors were relatively specialized in their resource use patterns ($Mu = 15$) we found that native turncoat species indirectly facilitated invasive species by competing with the non-native species' main competitors. Indeed, removal of these native turncoat species reduced the probability of invasion (figure 4*a*), and the final density of the non-native species (figure 4*c*). These effects of species removals were stronger when the number of resources and species was higher ($m = 40$, $n = 39$ versus $m = 10$, $n = 9$) (figure 4*a,c*). By contrast, when competitors exhibited more generalized resource use patterns, we found that removing particularly important species (native turncoat or competitor species) only weakly affected invasion success and final

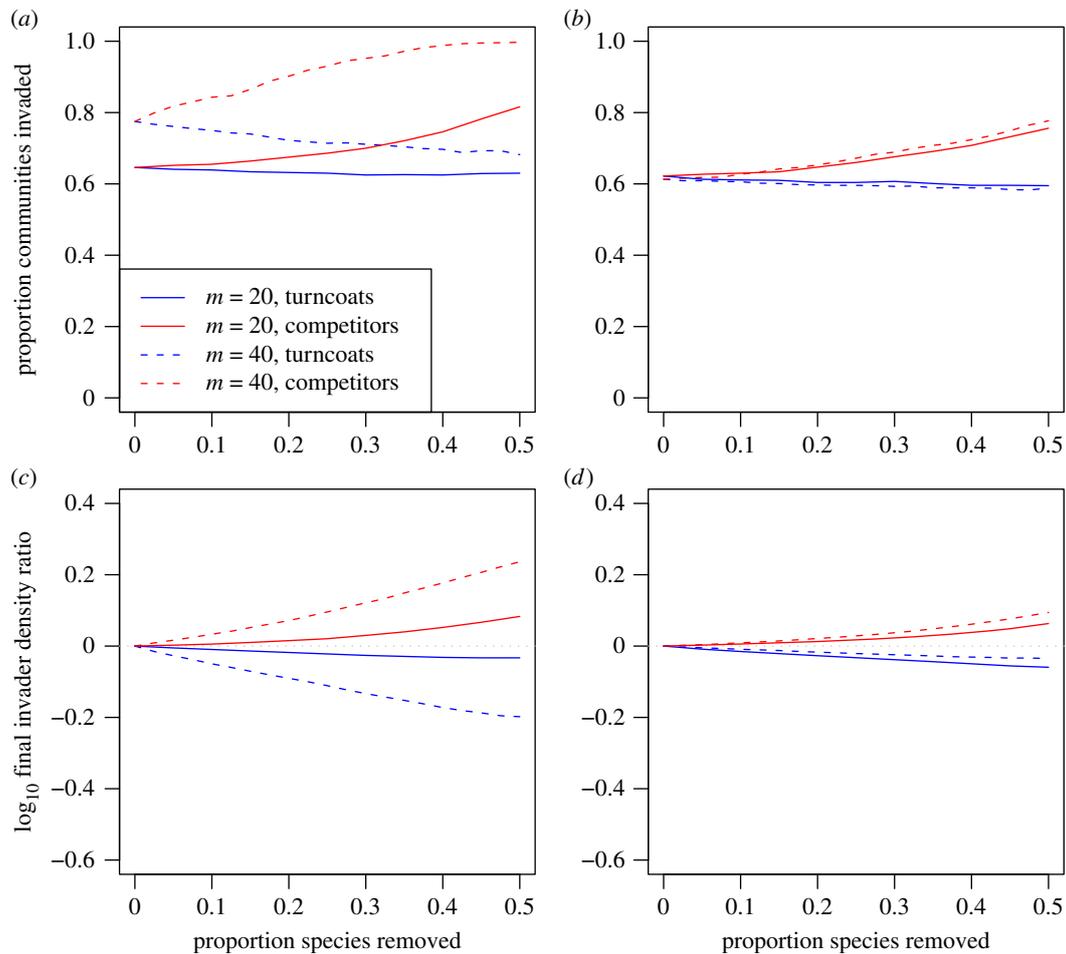


Figure 4. The invasion probability (*a,b*) and the \log_{10} ratio of the final non-native density relative to initial equilibrium conditions (*c,d*), when species are removed according to the rank of their direct competitive effects on non-natives (red lines), or strength of their positive indirect effects on non-natives (blue lines). Solid lines represent communities with 10 resources (m) and 9 native species plus one non-native, and dashed lines represent communities with 40 resources and 39 native species plus one non-native. Panels (*a*) and (*c*) represent the model of more specialized species (mean resources used/species (Mu) = 15), and panels (*b*) and (*d*) represent the model of more generalist species (mean resources used per species (Mu) = 30). The grey dotted line in panels (*c*) and (*d*) represents zero (no difference) for comparison. Outputs are averaged across 1000 simulations. Error bars in panels (*c-f*) represent mean ± 1 s.e.

non-native density (figure 4*b,d*). Furthermore, these effects did not vary much with changes in the number of resources and species in the community (figure 4*b,d*).

4. Discussion

The current invasion literature suggests that native species can directly inhibit species invasions, an effect that is strongest at relatively small scales and when species richness is low [3,13]. However, empirical evidence suggests there is an invasion paradox; that this relationship between species richness and biotic resistance to invasion breaks down or even reverses at larger scales, potentially due to variation in resource availability, or the inclusion of species that directly facilitate non-native species [12,13]. Here, we modelled and simulated these findings, and by applying concepts and approaches taken from the coexistence literature to invasion ecology [46,48], find that positive indirect effects of competitors on potential invaders are more common in communities characterized by higher species richness and resource availability. Niche dimensionality generally increases with scale, and thus we expect increases in scale (from the small scale of experiments to large landscape or geographical scales) to be associated with invasion success mediated by native

turncoats. Indeed, we found that native turncoats can strongly promote the success of a non-native species, suggesting that these indirect effects may contribute to the invasion paradox—that the negative relationship between species richness and biotic resistance breaks down at larger scales [13]. The idea that indirect interactions can strongly influence species coexistence has long been supported by evidence from experimental [18,39] and theoretical [45,54,55] approaches, and here we build on this theory to suggest indirect interactions can also promote species invasions.

We find that the effects of reducing biodiversity by removing particularly strong competitors are strongest when species are specialized in their resource use patterns. Similarly, indirect beneficial interactions are more likely to be common and impactful where there is greater variation in interaction strengths between species [46], as is the case of communities composed of species with specialized resource use patterns. Thus, the effects of indirect interactions on species invasions at larger scales (i.e. greater numbers of resources and species) may be strongest between species that are more specialized in their resource use patterns. These results are consistent with the rich history of theoretical and empirical ecological research on resource use dynamics [47,56], but are an element of the ecological literature rarely discussed and not previously shown to be of importance in an invasion context.

Increasing the number of resources and species can increase the strength of positive indirect interactions in two ways. First, as the number of resources and species increases, the variation among resource use patterns increases, leading to greater variation in direct interaction strength. This increased variance in interaction strength is generally correlated with a greater number of positive indirect interactions in competitive communities [45,46]. In addition, as the number of species in a community increases, the number of indirect species interactions increases at a faster rate than the number of direct interactions (figure 1). Indeed, the number of negative indirect interactions also increases with species richness. However, as direct competitive interactions are always negative, communities influenced strongly by indirect interactions are expected to have more positive interactions than those dominated by direct interactions (or in which only direct interactions are studied). Thus, by random chance alone, strong indirect interactions are more likely to occur in more species-rich communities. Indirect interactions are expected to become more important at larger scales through increased variation in direct species interaction strengths (due to reduced niche overlap), and by the sheer number of indirect interactions.

In sum, our theoretical results and the empirical literature suggest that native species, termed native turncoats here, may commonly promote invasions by indirectly benefiting non-native species. Indirect interactions in competitive communities are strongest when the species involved are relatively specialized in their resource use patterns. We have identified a number of other types of indirect species interactions that have not been documented in the invasion literature. Although we have not evaluated the impacts of these other interaction types on invasions, the strong effects of indirect interactions within our model communities, paired with their absence in the literature, suggest that the absence of the other interaction types on invasion processes is likely to be due to a lack of studies looking for them, rather than reflecting a genuine ecological absence. In competitive communities, all direct interactions are negative, so any native species that is advantageous in a community context to the non-native species is a native turncoat. However, when evaluating interaction webs that contain positive and negative direct effects, it may be useful to compare the sign and magnitude of indirect and direct effects of each native species on the non-native species. This approach will aid in

the identification of species changing their stripes and help identify native turncoats that encourage species invasion.

In reviewing the literature for this paper, many studies were found to be well designed to capture the full spectrum of indirect interactions even though they were rarely examined. In the future, our results suggest that taking the relatively simple step of looking for indirect interactions in studies of non-native species interactions with a native community would require little more than assessing the impacts on both native and non-native species rather than one or the other alone. Based on the results from our literature exploration and modelling exercise, it is clear that more empirical studies are needed that assess a wider range of interactions likely to be occurring among native residents and non-native species. While these studies are sometimes logistically difficult, when possible it would allow us to gain a full understanding of the mechanisms involved in invasion success. Furthermore, our results suggest that altering interactions within native communities to reduce the influence of native turncoats may represent a novel methodology for controlling invasion spread in the future. For example, it has been suggested that excluding native herbivores may enhance competitive resistance to invasive plants (e.g. [28]). Identifying native turncoats in other ecological communities may provide similar paths to limiting species invasions. For such techniques to be fully developed, however, we need more studies documenting these types of interactions in natural systems. Finally, identifying the role of native turncoats may contribute to our understanding of the breakdown of the relationship between species richness and biotic resistance, and help fully explain the invasion paradox [13].

Data accessibility. No empirical data were generated as part of this study. Code for developing a vector of carrying capacities that allows coexistence of the native community is available in the electronic supplementary material.

Authors' contribution. The study was conceived through a workshop attended by all authors. T.D.N. conducted the analyses with significant input from D.B.S. T.D.N. and L.L. wrote the first draft, and the remaining authors contributed to subsequent drafts and provided critical feedback.

Competing interests. We have no competing interests.

Funding. Financial support was provided by a James Cook University mid career researcher grant to L.L.

Acknowledgements. We thank Erik Noonburg for providing C code for linear programming.

References

- Catford JA, Jansson R, Nilsson C. 2009 Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* **15**, 22–40. (doi:10.1111/j.1472-4642.2008.00521.x)
- Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J. 2013 Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecol. Evol.* **3**, 182–196. (doi:10.1002/ece3.431)
- Elton CS. 1958 *The ecology of invasions by animals and plants*. London, UK: Methuen.
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P. 2002 Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–638. (doi:10.1038/nature00776)
- Keane RM, Crawley MJ. 2002 Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170. (doi:10.1016/S0169-5347(02)02499-0)
- Case TJ. 1990 Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl Acad. Sci. USA* **87**, 9610–9614. (doi:10.1073/Pnas.87.24.9610)
- MacArthur R. 1970 Species packing and competitive equilibrium for many species. *Theor. Popul. Biol.* **1**, 1–11. (doi:10.1016/0040-5809(70)90039-0)
- Tilman D. 2004 Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci. USA* **101**, 10 854–10 861. (doi:10.1073/Pnas.0403458101)
- Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T, Gale S. 2000 Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**, 97–108. (doi:10.1034/j.1600-0706.2000.910108.x)
- Fargione JE, Tilman D. 2005 Diversity decreases invasion via both sampling and complementarity effects. *Ecol. Lett.* **8**, 604–611. (doi:10.1111/j.1461-0248.2005.00753.x)
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ. 2005 Spatial heterogeneity

- explains the scale dependence of the native–exotic diversity relationship. *Ecology* **86**, 1602–1610. (doi:10.1890/04-1196)
12. Levine JM. 2000 Species diversity and biological invasions: relating local process to community pattern. *Science* **288**, 852–854. (doi:10.1126/science.288.5467.852)
 13. Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle, B. 2007 The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88**, 3–17. (doi:10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2)
 14. Shea K, Chesson P. 2002 Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* **17**, 170–176. (doi:10.1016/S0169-5347(02)02495-3)
 15. Stohlgren TJ, Barnett DT, Kartesz J. 2003 The rich get richer: patterns of plant invasions in the United States. *Front. Ecol. Environ.* **1**, 11–14. (doi:10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2)
 16. Bruno JF, Stachowicz JJ, Bertness, MD. 2003 Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* **18**, 119–125. (doi:10.1016/s0169-5347(02)00045-9)
 17. Abrams PA. 1987 Indirect interactions between species that share a predator: varieties of indirect effects. In *Predation: direct and indirect impactson aquatic communities* (eds WC Kerfoot, A Sih), pp. 38–54. Hanover, NH: University Press of New England.
 18. Connell JH. 1983 Interpreting the results of field experiments—effects of indirect interactions. *Oikos* **41**, 290–291. (doi:10.2307/3544279)
 19. TerHorst CP, Lau JA, Cooper IA, Keller KR, La Rosa RJ, Royer AM, Schultheis EH, Suwa T, Conner JK. 2015 Quantifying nonadditive selection caused by indirect ecological effects. *Ecology* **96**, 2360–2369. (doi:10.1890/14-0619.1)
 20. Estes JA *et al.* 2011 Trophic downgrading of planet earth. *Science* **333**, 301–306. (doi:10.1126/science.1205106)
 21. Hairston NG, Smith FE, Slobodkin LB. 1960 Community structure, population control, and competition. *Am. Nat.* **94**, 421–425. (doi:10.1086/282146)
 22. Schmitz OJ, Hamback PA, Beckerman AP. 2000 Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* **155**, 141–153. (doi:10.1086/303311)
 23. Bascompte J, Jordano P. 2007 Plant–animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. S.* **38**, 567–593. (doi:10.1146/annurev.ecolsys.38.091206.095818)
 24. Memmott J, Waser NM, Price MV. 2004 Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* **271**, 2605–2611. (doi:10.1098/rspb.2004.2909)
 25. Knight TM, McCoy MW, Chase JM, McCoy KA, Holt RD. 2005 Trophic cascades across ecosystems. *Nature* **437**, 880–883. (doi:10.1038/nature03962)
 26. White EM, Wilson JC, Clarke AR. 2006 Biotic indirect effects: a neglected concept in invasion biology. *Divers. Distrib.* **12**, 443–455. (doi:10.1111/j.1366-9516.2006.00265.x)
 27. Castillo DM, Kula AAR, Dotterl S, Dudash MR, Fenster CB. 2014 Invasive *Silene latifolia* may benefit from a native pollinating seed predator, *Hadena ectypa*, in North America. *Int. J. Plant Sci.* **175**, 80–91. (doi:10.1086/673536)
 28. Seabloom EW, Borer ET, Martin BA, Orrock JL. 2009 Effects of long-term consumer manipulations on invasion in oak savanna communities. *Ecology* **90**, 1356–1365. (doi:10.1890/08-0671.1)
 29. Siddon CE, Witman JD. 2004 Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. *Ecology* **85**, 2938–2945. (doi:10.1890/03-0519)
 30. Aschehoug ET, Callaway RM. 2015 Diversity increases indirect interactions, attenuates the intensity of competition, and promotes coexistence. *Am. Nat.* **186**, 452–459. (doi:10.1086/682901)
 31. Dormann CF, Roxburgh SH. 2005 Experimental evidence rejects pairwise modelling approach to coexistence in plant communities. *Proc. R. Soc. B* **272**, 1279–1285. (doi:10.1098/rspb.2005.3066)
 32. Palmer TM, Stanton ML, Young TP, Lemboi JS, Goheen JR, Pringle RM. 2013 A role for indirect facilitation in maintaining diversity in a guild of African acacia ants. *Ecology* **94**, 1531–1539. (doi:10.1890/12-1873.1)
 33. Kempel A, Nater P, Fischer M, van Kleunen M. 2013 Plant–microbe–herbivore interactions in invasive and non-invasive alien plant species. *Funct. Ecol.* **27**, 498–508. (doi:10.1111/1365-2435.12056)
 34. Levine JM. 1999 Indirect facilitation: evidence and predictions from a riparian community. *Ecology* **80**, 1762–1769. (doi:10.1890/0012-9658(1999)080[1762:lfeapf]2.0.Co;2)
 35. Allesina S, Levine JM. 2011 A competitive network theory of species diversity. *Proc. Natl Acad. Sci. USA* **108**, 5638–5642. (doi:10.1073/pnas.1014428108)
 36. Beggs J. 2001 The ecological consequences of social wasps (*Vespa* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biol. Conserv.* **99**, 17–28. (doi:10.1016/S0006-3207(00)00185-3)
 37. McKinney ST, Fiedler CE, Tomback DF. 2009 Invasive pathogen threatens bird–pine mutualism: implications for sustaining a high-elevation ecosystem. *Ecol. Appl.* **19**, 597–607. (doi:10.1890/08-0151.1)
 38. Ezenwa VO, Etienne RS, Luikart G, Beja-Pereira, A, Jolles AE. 2010 Hidden consequences of living in a wormy world: nematode-induced immune suppression facilitates tuberculosis invasion in African buffalo. *Am. Nat.* **176**, 613–624. (doi:10.1086/656496)
 39. Mayfield MM, Stouffer DB. 2017 Higher-order interactions capture unexplained complexity in diverse communities. *Nat. Ecol. Evol.* **1**, 062. (doi:10.1038/s41559-016-0062)
 40. Grilli J, Barabás G, Michalska-Smith MJ, Allesina S. 2017 Higher-order interactions stabilize dynamics in competitive network models. *Nature* **548**, 210–213. (doi:10.1038/nature23273)
 41. Levine JM, Bascompte J, Adler PB, Allesina, S. 2017 Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64. (doi:10.1038/nature22898)
 42. Kerr B, Riley MA, Feldman MW, Bohannan BJM. 2002 Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* **418**, 171–174. (doi:10.1038/nature00823)
 43. Godoy O, Stouffer DB, Kraft NJB, Levine JM. 2017 Intransitivity is infrequent and fails to promote annual plant coexistence without pairwise niche differences. *Ecology* **98**, 1193–1200. (doi:10.1002/ecy.1782/supinfo)
 44. Soliveres S *et al.* 2015 Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett.* **18**, 790–798. (doi:10.1111/ele.12456)
 45. Stone L, Roberts A. 1991 Conditions for a species to gain advantage from the presence of competitors. *Ecology* **72**, 1964–1972. (doi:10.2307/1941551)
 46. Roberts A, Stone L. 2004 Advantageous indirect interactions in systems of competition. *J. Theor. Biol.* **228**, 367–375. (doi:10.1016/j.jtbi.2004.01.013)
 47. Byers JE, Noonburg EG. 2003 Scale dependent effects of biotic resistance to biological invasion. *Ecology* **84**, 1428–1433. (doi:10.1890/02-3131)
 48. Laska MS, Wootton JT. 1998 Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* **79**, 461–476. (doi:10.1890/0012-9658(1998)079[0461:Tcaeat]2.0.Co;2)
 49. Lawlor LR. 1979 Direct and indirect effects of n-species competition. *Oecologia* **43**, 355–364. (doi:10.1007/Bf00344961)
 50. Levins R. 1974 Qualitative analysis of partially specified systems. *Ann. N. Y. Acad. Sci.* **231**, 123–138. (doi:10.1111/j.1749-6632.1974.tb20562.x)
 51. MacArthur R, Levins R. 1967 Limiting similarity convergence and divergence of coexisting species. *Am. Nat.* **101**, 377–385. (doi:10.1086/282505)
 52. Case TJ. 1991 Invasion resistance, species buildup and community collapse in metapopulation models with interspecies competition. *Biol. J. Linn. Soc.* **42**, 239–266. (doi:10.1111/J.1095-8312.1991.Tb00562.X)
 53. Soetaert K, Petzoldt T, Setzer RW. 2010 Solving differential equations in R: package deSolve. *J. Stat. Softw.* **33**, 1–25.
 54. Vandermeer J. 1990 Indirect and diffuse interactions: complicated cycles in a population embedded in a large community. *J. Theor. Biol.* **142**, 429–442. (doi:10.1016/s0022-5193(05)80099-2)
 55. Abrams PA, Matsuda H. 1996 Positive indirect effects between prey species that share predators. *Ecology* **77**, 610–616. (doi:10.2307/2265634)
 56. HilleRisLambers J, Adler PB, Harpole, WS, Levine JM, Mayfield MM. 2012 Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.* **43**, 227–248. (doi:10.1146/annurev-ecolsys-110411-160411)