Interaction modifications lead to greater robustness than pairwise non-trophic effects in ecological networks

J. Christopher D. Terry* (james.terry@zoo.ox.ac.uk)[1]
Rebecca J. Morris[1,2]
Michael B. Bonsall[1,3]
[1] Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK.
[2] Biological Sciences, Life Sciences Building 85, University of Southampton, Highfield Campus, Southampton, SO17 1BJ, UK.
[3] St. Peter's College, New Inn Hall Street, Oxford, OX1 2DL UK;

Abstract

1. Considerable emphasis has been placed recently on the importance of incorporating non-trophic effects in to our understanding of ecological networks. Interaction modifications are well established as generating strong non-trophic impacts by modulating the strength of inter-specific interactions.
2. For simplicity and comparison with direct interactions within a network context, the consequences of interaction modifications have often been described as direct pairwise interactions. The consequences of this assumption have not been examined in non-equilibrium settings where unexpected consequences of interaction modifications are most likely.
3. To test the distinct dynamic nature of these 'higher-order' effects we directly compare, using dynamic simulations, the robustness to extinctions under perturbation of systems where interaction modifications are either explicitly modelled or represented by corresponding equivalent pairwise non-trophic interactions.
4. Full, multi-species representations of interaction modifications resulted in a greater robustness to extinctions compared to equivalent pairwise effects. Explanations for this increased stability despite apparent greater dynamic complexity can be found in additional routes for dynamic feedbacks. Furthermore, interaction modifications changed the relative vulnerability of species to extinction from those trophically connected close to the perturbed species towards those receiving a large number of modifications.
5. Future empirical and theoretical research into non-trophic effects should distinguish interaction modifications from direct pairwise effects in order to maximise information about the system dynamics. Interaction modifications have the potential to shift expectations of species vulnerability based exclusively on trophic networks.

Key words

ecological network, food web, higher-order effect, non-trophic effect, robustness, stability, trophic interaction modification

Introduction

There is a building appreciation that to improve our understanding of the population dynamics of ecological communities it is necessary to move beyond studies that focus on a single interaction process at a time (Kéfi et al., 2012; Levine, Bascompte, Adler, & Allesina, 2017). Trophic interaction modifications (Terry, Morris, & Bonsall, 2017; Wootton, 1993) are class of higher-order process where a consumer-resource interaction is modulated by additional species. Examples include associational defences (P. Barbosa et al., 2009), fear effects (Sih, Englund, & Wooster, 1998), certain impacts of ecosystem engineers (Sanders et al., 2014) and foraging choices (Abrams, 2010). It has been empirically demonstrated that many strong non-trophic effects are caused by such processes (Ohgushi, Schmitz, & Holt, 2012; Preisser, Bolnick, & Benard, 2005; Werner & Peacor, 2003) with

large implications for community structure and dynamics (M. Barbosa, Fernandes, Lewis, & Morris, 2017; Donohue et al., 2017; Matassa, Ewanchuk, & Trussell, 2018; van Veen, van Holland, & Godfray, 2005).

Approaches to understanding interaction modifications often try to distil the inherently multi-species process into a pairwise non-trophic effect (or 'trait-mediated indirect effect') from the modifier species onto one or both of the recipient species (Okuyama & Bolker, 2007). This allows the direct comparison of non-trophic and trophic interaction strengths (Preisser et al., 2005) and network structure (Pilosof, Porter, Pascual, & Kéfi, 2017) but is a representation of a different class of dynamic process (Terry et al., 2017). While this simplification is fully justified in studies of communities at equilibrium (Grilli, Barabás, Michalska-Smith, & Allesina, 2017), the consequences of this assumption in a transient, fluctuating or heavily perturbed system has yet to be fully explored. Previous studies introducing interaction modifications to trophic networks (Arditi, Michalski, & Hirzel, 2005; Goudard & Loreau, 2008; Lin & Sutherland, 2014) have demonstrated their potential impact on the dynamics of ecosystems, but not whether this is attributable to the higher-order nature of interaction modifications, or rather shifts in connectance and interaction strength.

One such important case is the dynamics of ecological systems in the face of species removal, where there is the potential for secondary extinctions and eventually the collapse of the ecosystem (Dunne, Williams, & Martinez, 2002). This aspect of stability, often described as 'robustness', is an important question both from the perspective of managing anthropogenic change and in terms of understanding the fundamental stability of ecological communities. Since empirically testing how whole communities respond to extinctions is difficult or impossible (although see Sanders et al. (2018)), a number of studies have attempted to determine the properties that make ecological communities robust through simulation (Dunne & Williams, 2009; Säterberg, Sellman, & Ebenman, 2013). However, incorporating the acknowledged flexibility of ecological networks is a perennial challenge for such studies (Montoya, Pimm, & Solé, 2006).

The impact on robustness in ecological networks of one specific subset of interaction modifications, those caused by the flexible foraging in response to resource availability, has been examined by a number of studies (Valdovinos, Ramos-Jiliberto, Garay-Narváez, Urbani, & Dunne, 2010). Approaches have included topological rewiring (Gilljam, Curtsdotter, & Ebenman, 2015; Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch, 2010; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010; Thierry et al., 2011), multi-species functional responses (Uchida & Drossel, 2007) and adaptive dynamics models (Kondoh, 2003). These models showed that the additional dynamic process impacted robustness, but only addressed a restricted subset of interaction modifications caused by predator switching. However, consumption rates are influenced by more than the just the prey available to them. Interaction modifications can also be caused by the threats to the consumer (Suraci, Clinchy, Dill, Roberts, & Zanette, 2016), facilitation (Bruno, Stachowicz, & Bertness, 2003), associational susceptibility (Underwood, Inouye, & Hambäck, 2014) or mutualistic defence (Holland, Ness, Boyle, & Bronstein, 2005) amongst others (Ohgushi et al., 2012). This introduces considerable additional dynamic connectance to ecological communities, yet studies of generic interaction modifications in large networks are limited (Arditi et al., 2005; Bairey, Kelsic, & Kishony, 2016; Garay-Narváez & Ramos-Jiliberto, 2009; Goudard & Loreau, 2008; Lin & Sutherland, 2014), with most theoretical analyses of interaction modifications focussing on small community units (Abrams, 2010; Bolker, Holyoak, Křivan, Rowe, & Schmitz, 2003; Holt & Barfield, 2013).

Calls to incorporate the full panoply of non-trophic effects into our understanding of ecological networks have built substantially in recent years (Fontaine et al., 2011; Ings et al., 2009; Kéfi et al., 2012; Levine et al., 2017; Ohgushi et al., 2012; Olff et al., 2009) and the first empirical inventories are being established (Kéfi et al., 2015; Kéfi, Miele, Wieters, Navarrete, & Berlow, 2016). Theoretical analyses can play a significant role in guiding the empirical creation of networks, identifying the information necessary to best understand these systems. Here we demonstrate the distinctive

nature of interaction modifications compared to pairwise non-trophic effects through a direct standardised comparison of their impacts on the robustness of large artificial networks. We then examine the role of interaction modifications in determining the consequences of species loss and species level vulnerability to secondary extinction.

Methods

We conducted our analyses using model food webs where system dynamics are derived from metabolic scaling relationships. As detailed below, interaction modifications were introduced to communities at an initial equilibrium before mortality was added to a single species at a time and the resultant extinctions after the model was integrated to a new equilibrium examined.

Bio-energetic Model

The change in biomass density, B_i, of each species in the community was modelled using a simple Lotka-Volterra type model with a linear (Holling Type I) functional response and logistic intrinsic growth rates, parameterised using body-mass relationships:

$$\frac{dB_i}{dt} = B_i\left(r_i - m_i - B_i/K_i - \sum_{j \in consumers\ of\ i}^{j} \mu_{ij}\, a_{ij} B_j + \sum_{l \in resources\ of\ i}^{l} \mu_{li}\, e_{li} a_{li} B_l\right) \quad (1)$$

Each species was assigned a body mass (M_i) drawn from a distribution based on their trophic level (see SI 1) which was then used to calculate further parameters using quarter-power body-mass scaling laws (Yodzis & Innes, 1992). Relative intrinsic growth or metabolic loss rates, r_i, were set at 1 for all producers (trophic level 1) and $r_i = -0.1M_i^{-0.25}$ for each consumer (trophic level ≥2). Consumer-specific consumption rates were set at $a_{ij} = \omega_j M_j^{-0.25}$, where the generality term ω_j was set to $1/n$, the number of resources of each consumer j. Assimilation efficiencies, e_{ij}, for each trophic interaction were drawn from a uniform distribution, $e_{ij} \sim \mathcal{U}(0.05{:}\,0.15)$. Carrying capacities, K_i, were drawn from $K_i \sim \mathcal{U}(1{:}\,10)$ for producers and $K_i \sim 10^{\,\mathcal{U}(2:3)}$ for consumers. Initially, external mortality, m_i, was set to 0 and modification terms, μ_{ij}, set to 1.

Trophic topology and population densities of starting communities were determined as follows. Initial trophic topologies were generated using the niche model (Williams & Martinez, 2000), with 35 species and a connectance of 0.14, removing cannibalistic interactions. Each population density was initially set to 10 and these were then numerically integrated to a stable equilibrium (see SI 4 for criteria). Only connected communities with at least 18 persisting species were retained and used as starting communities for the robustness tests. Properties of the starting communities are described in SI 2.

Specification of TIMs

Trophic interaction modifications were introduced to this community through modification terms, μ_{ijk}, that specify the impact of modifier species k on the consumption of species i by species j, with the constraint that $i \neq j \neq k$. These are positive numbers that multiply the attack rate as a function of the divergence of the biomass density of a modifying species, B_k, from its starting equilibrium value B_k^*. Where there are multiple modifications of the same interaction these were assumed to combine multiplicatively $\mu_{ij} = \prod^k \mu_{ijk}$ (Golubski & Abrams, 2011; Goudard & Loreau, 2008). The TIMs were distributed at a defined rate of occurrence such that each potential modification (combination of trophic interaction and third species) had an equal chance of existing.

When $\mu_{ijk} < 1$, the interaction is weakened and when $\mu_{ijk} > 1$ the interaction is strengthened. In our model μ_{ijk} can not be negative, preventing the reversal of the direction of the trophic interaction. Where an increase in the modifier species leads to an increase in the strength of the

interaction, we describe it as a facilitating TIM. This can be said to be beneficial to the consumer and detrimental to the resource, in the sense of the immediate impact from an increase in the modifier population. We term the reverse situation an interfering TIM. See Figure 1 for diagrammatic explanation of these terms.

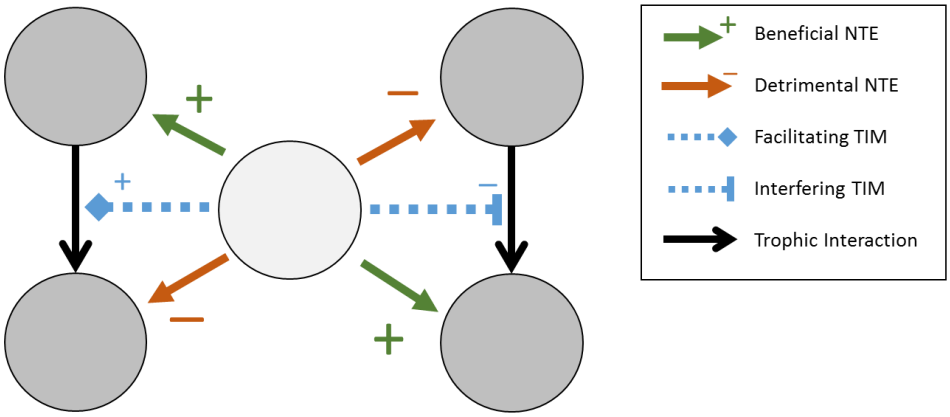

Figure 1. Distinctions between terms used to describe interaction modifications and their impacts in terms of the effect of an increase in the density of the modifier species (centre). 'Facilitating' (α >0) and 'interfering' (α<0) trophic interaction modifications (TIMs, dotted arrows) cause 'beneficial' and 'detrimental' short term non-trophic effects (NTEs, solid arrows), alternately on the consumer and the resource.

Alternative representation of TIMs as Pairwise Non-Trophic Effects

As an alternative to modelling the impact of trophic interaction modifications in full (using 'higher order' terms), equivalent pairwise non-trophic effects (NTEs) can be derived. These match the impact of the full TIM model, the only distinction being the NTE from a modifier k to a trophic interactor is no longer dependent on the biomass of the other member of the trophic pair (Figure 2). To maintain parity with the TIM model, this was done by first partitioning the process into trophic and non-trophic components, then fixing the value of the other trophic interactor to the density at the original equilibrium: $B_{int} = B_{int}^{*}$. Full steps of the derivation are in SI 6. A trophic interaction onto a resource influenced by a modifier can be partitioned from:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots \underbrace{-\mu_{ij}a_{ij}B_j}_{Trophic\ Term\ with\ TIM} \qquad (2)$$

to:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots \underbrace{-a_{ij}B_j}_{Trophic\ Term} + \underbrace{a_{ij}B_j^{*}(1-\mu_{ij})}_{Non-Trophic\ Term} \qquad (3)$$

The corresponding terms for the interactions onto the consumer, j, are:

$$\frac{1}{B_j}\frac{dB_j}{dt} = \cdots + \underbrace{e_{ij}a_{ij}B_i}_{Trophic\ Term} + \underbrace{e_{ij}a_{ij}B_i^{*}(\mu_{ij}-1)}_{Non-Trophic\ Term} \qquad (4)$$

As an example, a facilitating TIM, when B_k increased, would lead to a μ_{ij} greater than 1. This would lead to a negative NTE on the resource i (independent of B_j) and a positive NTE on the consumer j (independent of B_i). This partitioning process is only straightforward when each trophic interaction is modified by at most one modifier species because of the synergistic relationship between multiple modifiers assumed by our model.

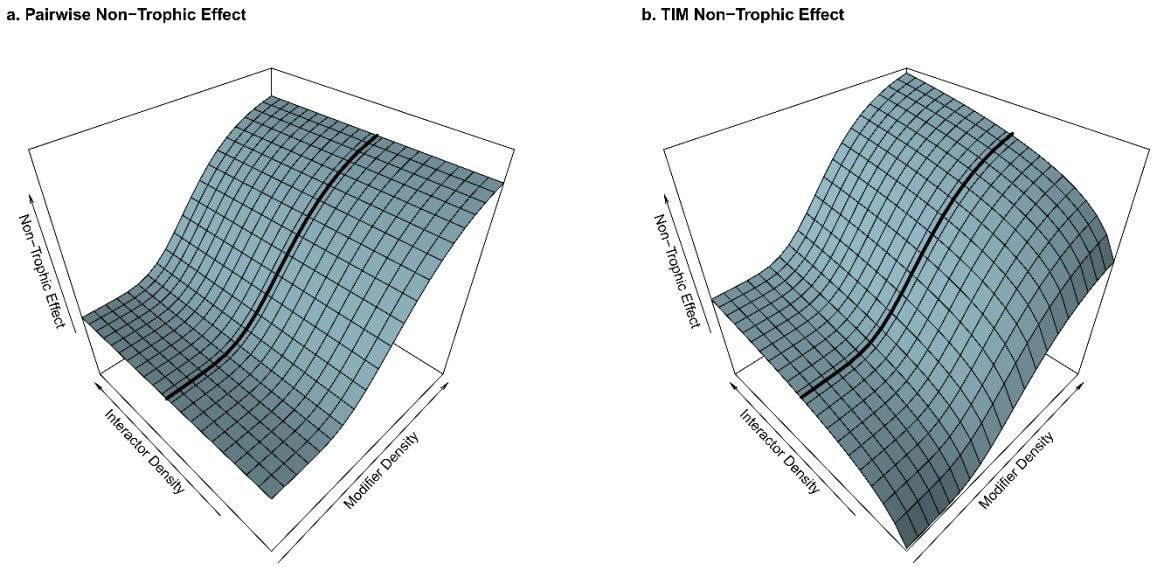

Figure 2. Illustrative response surfaces showing the distinction between non-trophic effects caused by pairwise interactions and those from a higher-order interaction modification process involving three species. Per-capita effects are shown in the vertical axis on a logarithmic scale. In both cases, the response to the modifier is identical at the starting density of the trophic interaction partner of the focal species, shown by the black line. However, the density of the trophic interaction partner of the focal species (left-hand axis) does not affect the non-trophic effect in the pairwise case (a), but does with the full interaction modification model (b). Note also that as the interactor's density becomes small, the strength of the non-trophic effect rapidly declines.

Functional Form of TIM

To represent the relationship between the density of the modifier species and the modification of the interaction we used a Gompertz sigmoidal curve parameterised to control features of ecological relevance, detailed in full in SI 3. This function links the divergence of B_k from its start point, $\log_{10}(B_k/B_k^*)$, and three control parameters, τ (the proportional change on a logarithmic scale from the equilibrium to a threshold where the interaction is most greatly impacted by the change in modifier), α (the direction and maximum rate of change in the modified interaction as the modifier density increases) and σ (the range of magnitudes over which μ_{ijk} spans), depicted in Figure 3. A positive α denotes a facilitatory modification and a negative α an interference modification. A key attribute of our parameterisation is that when $B_k = B_k^*, \mu_{ijk} = 1$. This maintains the original trophic interaction strength when the modifier is at its starting equilibrium point - in effect these strengths are assumed to already incorporate changes to the interaction at the equilibrium.

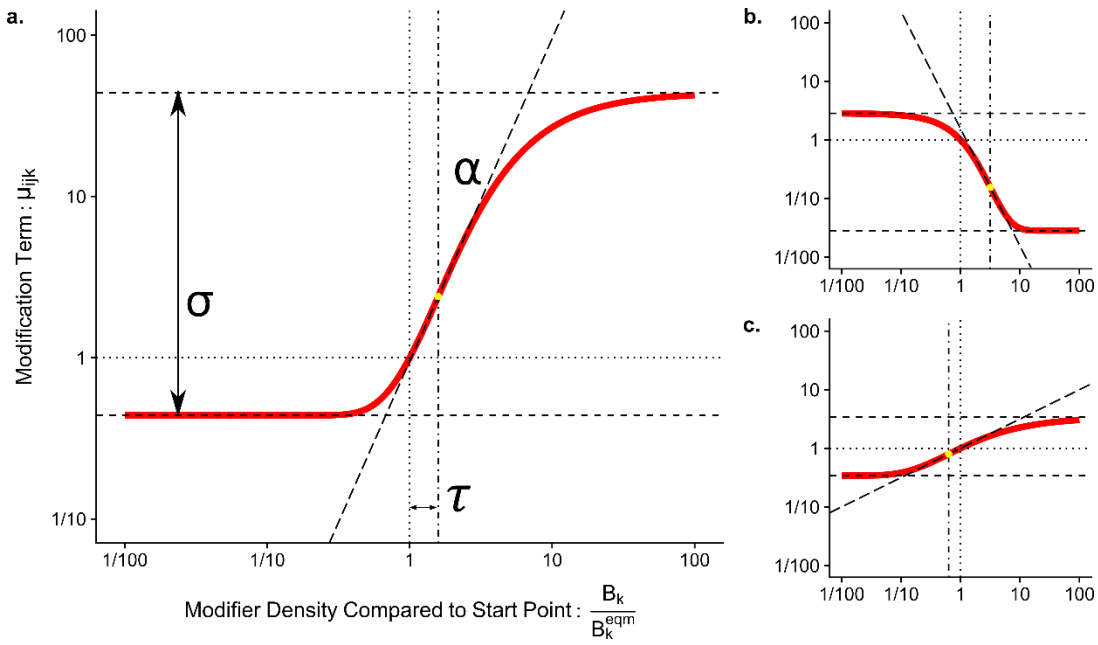

Figure 3: Graphical representation of the relationship between the control parameters and the response of the sigmoidal function used to determine the modification term μ_{ijk} from the density of the modifier B_k. Panel a) uses a maximum slope (α) of 2, a distance to threshold (τ) of 0.2 and a range of effects (σ) to 2. Note that the function is calculated on a base 10 logarithmic scale. Parameters for panel b): α = -2, τ = 0.5, σ = 2 and panel c): α=0.5, τ = -0.2, σ =1.

Test 1. Comparison of robustness between pairwise NTE and higher-order TIMs

For each of 200 initial communities we added TIMs at an occurrence rate of 0.05 such that each interaction was modified by at most one other species. Shape parameters for each TIM were drawn from uniform distributions: slope $\alpha \sim \mathcal{U}(-4{:}\,4)$, range $\sigma \sim \mathcal{U}(0.1{:}\,4)$ and threshold $\tau \sim \mathcal{U}(-1{:}\,1)$.

For each robustness test, the external mortality rate (m_i) of a single species (to which we will refer for convenience as the 'targeted' species, although the mortality could be attributable to a range of non-directed processes) was then set to 1, the system numerically integrated to a new steady state and the status of each species in the resultant community assessed. Species were considered 'extinct' if their biomass fell permanently below 10^{-4} (several orders of magnitude below the starting values of most of the populations, SI 2), 'functionally extinct' if their biomass fell to below 1/10th of their starting value and considered to have 'exploded' if the final density was over 10 times the starting value. This was repeated targeting each species in turn, for each community, to give a total of 3736 completed robustness tests (93.8% successful integrations, SI 4). All analyses were carried out in R v.3.5.0 (R Core Team, 2018) using the *deSolve* numerical integration package (Soetaert, Petzoldt, & Setzer, 2010).

We then repeated the robustness tests after conversion of the TIMs into pairwise NTE form, and in a third case without any TIMs. In each case the underlying trophic interactions and distribution of TIMs was identical.

Test 2. TIMs and distribution of extinctions

To examine the relationship between the distribution of TIMs and consequent secondary extinctions, the robustness tests of the full TIM case as described above was repeated with a higher occurrence rate of TIMs (0.08) and a relaxation of the assumption that only one modification can affect each trophic interaction. Results are reported for parameters drawn from $\alpha \sim \mathcal{U}(-3{:}\,3)$, $\sigma \sim \mathcal{U}(0.1{:}\,3)$, $\tau \sim \mathcal{U}(-1{:}\,1)$. Further tests, with different TIM occurrence rates and distributions of

shape parameters, reached qualitatively similar results. Properties of the community and the relationship between the 'targeted' species and the extinct species were then calculated.

The trophic distance was calculated as the shortest route, in terms of the number of trophic links, between the targeted species and each secondarily extinct species. This was compared to the distribution of trophic distances between targeted and secondarily extinct species in the tests without TIMs and to the baseline distribution of trophic distances between all species in the networks. The number and class (whether they are initially beneficial or detrimental for the focal species) of the NTEs affecting each extinct species, both just from the targeted species and from all species, was compared to the expected number of NTEs upon each species given its trophic connectance.

Results

The introduction of TIMs greatly increased the number of extinctions (Figure 4), but almost half the number of extinctions were found when the interaction modifications were modelled directly compared to when they were modelled as pairwise effects (mean difference = 5.4, t-test paired by community and targeted species ID: $p<0.0001$, $t = 61.5$, $df = 3941$). The number of functional extinctions was very similar to full extinctions (means: No-TIM: 1.98, Pairwise: 11.33, Full-TIM: 5.85). Population explosions were rare in all scenarios. Without NTEs there was a mean of 0.09 explosions per robustness test, with nearly twice as many under pairwise NTE (0.189). The TIM case had the fewest, only 0.05 explosions per robustness test.

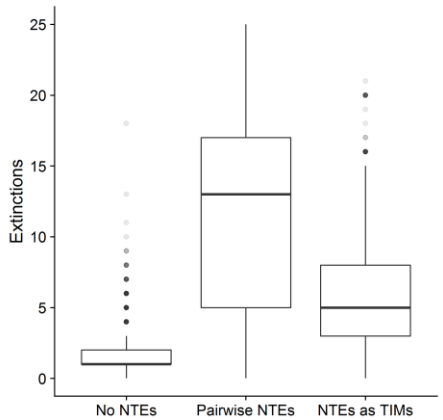

Figure 4. Boxplot showing that robustness was significantly lower when TIMs were modelled as pairwise interactions rather than directly as interaction modifications. Both cases produced significantly more extinctions than the no-TIM case.

In robustness tests without TIMs nearly 60% of secondary extinctions were species directly trophically linked to the targeted species (Figure 5). The introduction of TIMs shifted the trophic distance (the number of trophic links between species by the shortest route) much closer to the underlying distribution of trophic path lengths (Figure 5).

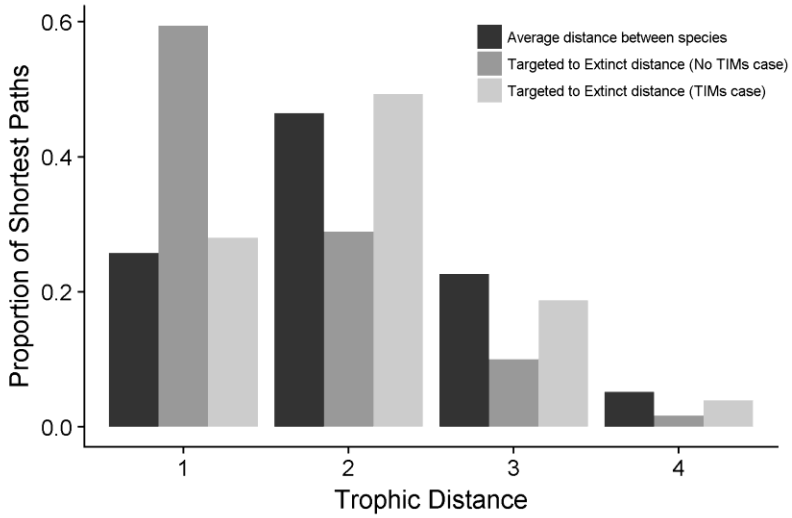

Figure 5. Distribution of trophic distances between all species in the communities (black) and between targeted species and secondarily extinct species in communities without TIMs (dark grey) and communities with TIMs (light grey). The distance from the targeted species to the secondarily extinct species in the TIM case was intermediate between the two baseline cases. Trophic distances above 4 were very rare in our model and not shown.

Compared to the expected number of NTEs from TIMs of a particular sign for each species with a given connectance (mean = 3.79), secondarily extinct species tended to be recipients of both more beneficial (mean = 4.53) and more detrimental (mean = 4.02) NTEs. When counting just TIMs from the targeted species, secondarily extinct species tended to have more beneficial (0.289) and fewer detrimental (0.178) NTEs than the expected number (0.207) (t-tests paired by species ID, all $p<0.0001$, n =3576).

The targeting of species that caused more TIMs induced more extinctions (Figure 6a, Poisson glm, $p<0.0001$, n= 3825), with each additional TIM leading an average of 7% more secondary extinctions. Model fits splitting the sign of the TIMs (Figure 6b) indicated that each additional interference TIM caused a greater increase in the number of extinctions (+10.4%), compared to each additional facilitatory TIM (+4.1%). Including the trophic connectance of the web as an additional predictor variable did not give a significant improvement in the model fit (χ^2 comparison of models, p=0.113).

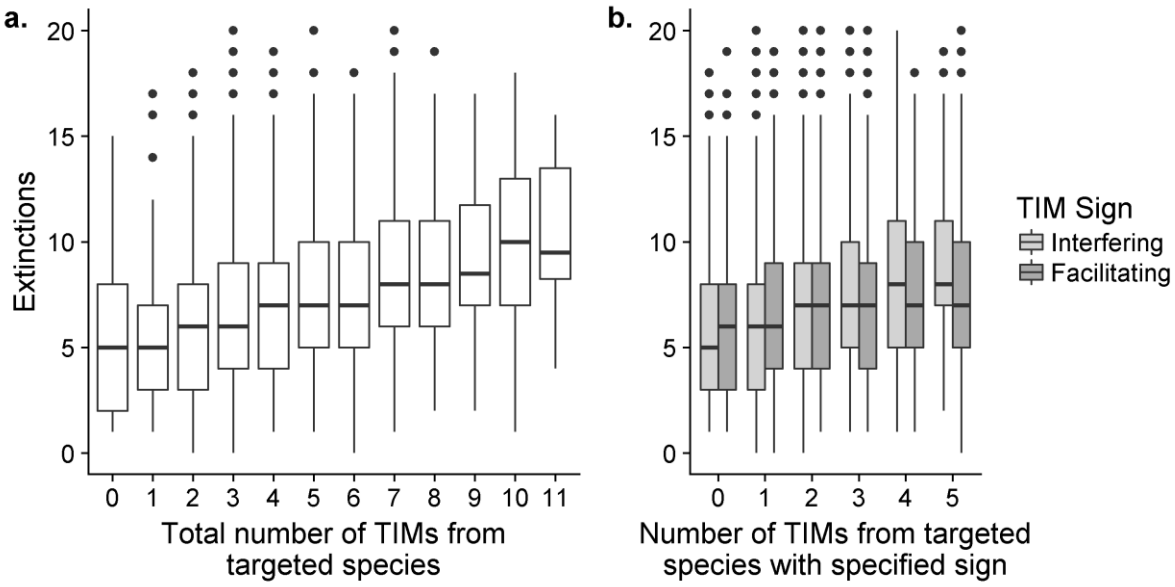

Figure 6. Boxplots showing the increase in the resultant number of extinctions as the number of TIMs caused by the targeted species increased. Panel a) shows the response to the total number of TIMs, panel b) shows the distinct responses to the number of each sign of TIM.

Discussion

Here we have examined the ecological robustness of networks to demonstrate that interaction modifications have distinct dynamic effects. In ecological systems, efforts to include non-trophic effects into food webs (Fontaine et al., 2011; Pilosof et al., 2017) should take into account the higher-order nature of interaction modifications. Without quantitative information of the topological and strength distribution of TIMs it is not yet possible to precisely calculate their impacts relative to trophic interactions. Nevertheless, it is clear that they have the potential to change our expectation of both the relative vulnerability of species to extinction and the impact the loss of certain species will have (Donohue et al., 2017).

We found that despite an increase in the number of 'moving parts' the full TIM model was more robust than the exclusively pairwise model. Generally, unstructured dynamic models of community stability suggest that a higher connectivity is destabilising (May, 1972; Uchida & Drossel, 2007) making our result somewhat surprising, but there are a number of explanations. The overall level of dynamic connectance (fraction of realised pairwise links) between our two representations of TIMs is the same. In part, our result can be attributed to the tendency for an overall decline in population densities under the perturbation. When the strength (and disruptive influence) of the resultant NTE is dependent on the product of two species, in general the overall strength of NTEs will decline faster than when the strength is dependent on just one species. Furthermore, if the density of the other interactor falls to zero, the NTE under the full TIM model will also fall to zero, but with the pairwise model the NTE is maintained (even though the mechanism is no longer extant). Hence, as species become extinct the effective dynamic connectance of the full TIM model declines faster than in the pairwise case.

There are also differences in the prevalence and rapidity of more specific feedback loops, although despite our relatively simple model this factor is challenging to trace in these complex systems (Dambacher & Ramos-Jiliberto, 2007). Feedbacks modulating the strength of the NTEs are heavily dependent on the relative speed and strength of multiple feedback loops, which are derived from individual species properties. Nonetheless, as the impact of the more complex full TIM model

293 derived NTEs are dependent on more species, in general, it appears that mitigating feedback loops
294 are more immediate in the full TIM case. The effects caused by an interaction modification (however
295 modelled) will cause an immediate increase in one affected species and decrease in the other. In the
296 full TIM model, where the strength of the interaction modification is dependent on $B_i \times B_j$, the
297 change to the NTE will be mitigated since B_i and B_j move in opposite directions. In the pairwise case
298 the strength of the NTE on each species will rapidly diverge. That said, algebraic solutions of the
299 consumer-resource module show that in the longer term an increase in an attack rate can lead to a
300 reduction in both of the interacting species equilibrium values (Morin, 2011), highlighting the
301 multiple timescales over which these processes operate.

302 At least in this simple model, it appears that TIMs determine extinction risk in a somewhat
303 predictable way. The extinction risk is shifted from those species that are closely trophically
304 connected to perturbed species, to be more evenly distributed throughout the network. Overall, the
305 species that went extinct tended to be those that were affected by more TIMs. When considering
306 NTEs from all species, this was true of both 'beneficial' and 'detrimental' NTEs. Those species that
307 directly benefit from the presence of other species are clearly affected by extinction cascades.
308 However, those species receiving an above-expectation number of detrimental NTEs were also at
309 higher risk of extinction. It would be expected that these species would benefit from the reduction
310 or removal of their inhibitors. Note that the correlation between the increased species level
311 connectance and the number of modifications received was taken into account by comparing
312 expected number of TIMs on a per-species basis.

313 There are two complementary explanations for this impact of detrimental NTEs. Firstly, in a complex
314 model certain species do increase their density, at least for a period of time, which would have
315 negative effect on the focal species. Initial responses of the populations to a small reduction in the
316 population of a single species were as commonly positive as negative (51.1% of non-neutral growth-
317 rate responses to a 1% density reduction in a random species were positive in the TIM models, SI 5).
318 The low number of species maintaining large increases at the end of the process (what we defined
319 as population explosions) shows that such increases were relatively transient. When considering
320 only TIMs from the targeted species, which always decrease in density, extinct species received
321 fewer than expected detrimental NTEs, supporting this direct mechanism. Secondly, in the simple
322 model of population dynamics we used, an increase in the attack rate of a consumer (which would
323 be classed as 'beneficial') eventually leads to a reduction in the equilibrium density of the consumer
324 since the population of resource is pushed down to a level that cannot sustain as high a consumer
325 population.

326 Much previous work has shown that complex networks are stabilised by consistent patterns in key
327 parameters, which can be derived from body-mass scaling rules (Brose, Williams, & Martinez, 2006;
328 Otto, Rall, & Brose, 2007). In our model this source of stability declines, as these patterns are
329 disrupted by interaction modifications that effectively push each a_{ij} value out of the allometrically
330 specified range in both directions. However, attack rates in real systems do take place in the context
331 of other species and significant disruptions to pairwise interaction strengths derived from laboratory
332 experiments caused by interaction modifications have been empirically observed (Jonsson,
333 Kaartinen, Jonsson, & Bommarco, 2018). Our results suggest that although species that rely on
334 others are indeed more sensitive, the overall level of dynamic linkage is as important and that both
335 potential 'beneficial' and 'detrimental' processes should be considered.

336 Our choice of function to represent interaction modifications, although mathematically complex in
337 form, offers certain advantages compared to previous linear (Arditi et al., 2005; Bairey et al., 2016),
338 exponential (Goudard & Loreau, 2008; Lin & Sutherland, 2014) or rational function (Sanders et al.,
339 2014) models. In particular, it has ability to directly and independently control salient features of the
340 function with clear ecological relevance (distance to threshold, maximum rate of change, range
341 between maximum and minimum). The dependence on the relative divergence from an equilibrial

starting point rather than the absolute value of the density of the modifier is also likely to be more representative of ecological processes and considerably more straightforward to parameterise in an ecologically meaningful manner.

Nevertheless, this is still a highly simplistic model. The interaction modifications included in this study were introduced at random, in the sense that each potential modification had an equal chance of existing. Considerable stabilising structuring has been observed within non-trophic effects networks (Kéfi et al., 2015; Kéfi, Miele, et al., 2016) but there is not yet sufficient data to be able to determine whether there are consistent features across ecosystems. Analyses of the stability of systems at equilibrium demonstrate the key role of the distribution of interaction modifications (Terry, Bonsall, & Morris, 2018) and the potential for emergent structure from the combination of trophic and non-trophic interaction networks. The distribution of interaction modifications will have important consequences for structural network properties such as trophic coherence, modularity and nestedness that have been demonstrated to affect stability (Johnson, Domínguez-García, Donetti, & Muñoz, 2014; Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010).

Interaction modifications do not solely affect consumption rates and there is considerable scope to develop and test theoretical models of additional processes, such as non-trophic interaction modifications and modification of other aspects of consumer functional responses (Kéfi et al., 2012). The assumption of multiplicative combination of multiple TIMs in a synergistic manner in our second analysis is also questionable. While empirical patterns have not been quantified, it is a reasonable estimate that many modification effects act antagonistically to each other (Golubski & Abrams, 2011). For instance, the presence of a second fear-inducing predator may well have less effect than the first, dampening the impact of a change in either modifier population.

Further opportunities are also open to introduce specific accounting for the timescale of changes and the size of perturbations. It is possible that higher-order interactions are stabilising against small perturbations, which may make the system as a whole more susceptible to large impacts, such as the extinction of certain species (Levine et al., 2017). TIMs also have the potential to create the necessary positive feedback structures to maintain alterative stable states (Holt & Barfield, 2013; Kéfi, Holmgren, & Scheffer, 2016). As yet, the prevalence of these features is largely unknown. The speed of interaction modifications themselves can also vary. While many TIMs are behaviourally mediated and occur essentially instantaneously, others are due to accumulated environmental changes (Sanders et al., 2014) or evolutionary processes (Benkman, Siepielski, & Smith, 2012) and operate at somewhat slower timescales.

Conclusion

In summary, interaction modifications are potent forces that introduce distinct dynamics to ecological networks. This distinctive nature of interaction modifications is of relevance for dynamic systems in many fields that make use of networks (Strogatz, 2001). The complexity of networks is more than the product of connectance and the number of interacting units and our work highlights the importance of transient dynamics in the collapse of communities (Hastings, 2001).

Despite long-standing calls for the inclusion of non-trophic effects into the mainstream of ecological network science that has been long dominated by food webs (Ings et al., 2009), and the publication of the first empirical community level non-trophic network (Kéfi et al., 2015), there remains a great number of significant unknowns about the role of non-trophic effects at the network scale. Our work shows that maintaining interaction modifications as distinct processes within empirical and theoretical networks, rather than as pairwise non-trophic effects (Grilli et al., 2017), will enable us to have a more complete understanding of the system dynamics and allow better predictions of community responses to perturbations. This need not require significant additional effort on the part of the original investigator, but would be challenging for others to retroactively discern from

published pairwise interaction networks. Analyses of network robustness are used extensively to understand anthropogenic impacts on natural communities (Evans, Pocock, & Memmott, 2013; Kaiser-Bunbury et al., 2017; Säterberg et al., 2013); as the development and analysis of comprehensive interaction networks expands (Kéfi, Miele, et al., 2016), we must incorporate interaction modifications appropriately.

Acknowledgements

JCDT was funded by the Natural Environmental Research Council through the Oxford Environmental Research Doctoral Training Program (NE/L002612/1).

Data and Code Availability

All R code used in this study and the generated simulation results are available on the Open Science Framework: DOI: 10.17605/OSF.IO/W83BR

Author Contributions

JCDT initiated the research, and JCDT, MBB and RJM contributed to the ideas presented in the manuscript. JCDT conducted the research, facilitated by discussions with RJM and MBB. JCDT wrote the manuscript, and all authors contributed to revisions and approved the final version.

References

Abrams, P. A. (2010). Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology*, *24*(1), 7–17. doi:10.1111/j.1365-2435.2009.01621.x

Arditi, R., Michalski, J., & Hirzel, A. H. (2005). Rheagogies: Modelling non-trophic effects in food webs. *Ecological Complexity*, *2*, 249–258. doi:10.1016/j.ecocom.2005.04.003

Bairey, E., Kelsic, E. D., & Kishony, R. (2016). High-order species interactions shape ecosystem diversity. *Nature Communications*, *7*, 12285. doi:10.1038/ncomms12285

Barbosa, M., Fernandes, G. W., Lewis, O. T., & Morris, R. J. (2017). Experimentally reducing species abundance indirectly affects food web structure and robustness. *Journal of Animal Ecology*, *86*(2), 327–336. doi:10.1111/1365-2656.12626

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 1–20. doi:10.1146/annurev.ecolsys.110308.120242

Benkman, C. W., Siepielski, A. M., & Smith, J. W. (2012). Consequences of trait evolution in a multispecies system. In T. Ohgushi, O. J. . Schmitz, & R. D. Holt (Eds.), *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives* (pp. 278–292). Cambridge University Press.

Bolker, B., Holyoak, M., Křivan, V., Rowe, L., & Schmitz, O. (2003). Connecting Theoretical and Empirical Studies of Trait-Mediated Interactions. *Ecology*, *84*(5), 1101–1114.

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, *9*(11), 1228–1236. doi:10.1111/j.1461-0248.2006.00978.x

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, *18*(3), 119–125. doi:10.1016/S0169-5347(02)00045-9

Dambacher, J. M., & Ramos-Jiliberto, R. (2007). Understanding and Predicting Effects of Modified Interactions Through a Qualitative Analysis of Community Structure. *The Quarterly Review of Biology*, *82*(3), 227–250. doi:10.1086/519966

Donohue, I., Petchey, O. L., Kéfi, S., Génin, A., Jackson, A. L., Yang, Q., & O'Connor, N. E. (2017). Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. *Global Change Biology*, *23*(8), 2962–2972. doi:10.1111/gcb.13703

Dunne, J. A., & Williams, R. J. (2009). Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1524), 1711–1723. doi:10.1098/rstb.2008.0219

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. doi:10.1046/j.1461-0248.2002.00354.x

Evans, D. M., Pocock, M. J. O., & Memmott, J. (2013). The robustness of a network of ecological networks to habitat loss. *Ecology Letters*, *16*(7), 844–852. doi:10.1111/ele.12117

Fontaine, C., Guimarães, P. R., Kéfi, S., Loeuille, N., Memmott, J., van der Putten, W. H., … Thébault, E. (2011). The ecological and evolutionary implications of merging different types of networks. *Ecology Letters*, *14*(11), 1170–1181. doi:10.1111/j.1461-0248.2011.01688.x

Garay-Narváez, L., & Ramos-Jiliberto, R. (2009). Induced defenses within food webs: The role of community trade-offs, delayed responses, and defense specificity. *Ecological Complexity*, *6*(3), 383–391. doi:10.1016/j.ecocom.2009.03.001

Gilljam, D., Curtsdotter, A., & Ebenman, B. (2015). Adaptive rewiring aggravates the effects of species loss in ecosystems. *Nature Communications*, *6*, 8412. doi:10.1038/ncomms9412

Golubski, A. J., & Abrams, P. A. (2011). Modifying modifiers: what happens when interspecific interactions interact? *Journal of Animal Ecology*, *80*(5), 1097–1108. doi:10.1111/j.1365-2656.2011.01852.x

Goudard, A., & Loreau, M. (2008). Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model. *The American Naturalist*, *171*(1), 91–106. doi:10.1086/523945

Grilli, J., Barabás, G., Michalska-Smith, M. J., & Allesina, S. (2017). Higher-order interactions stabilize dynamics in competitive network models. *Nature*, *548*, 210–213. doi:10.1038/nature23273

Hastings, A. (2001). Transient dynamics and persistence of ecological systems. *Ecology Letters*, *4*(3), 215–220. doi:10.1046/j.1461-0248.2001.00220.x

Holland, J. N., Ness, J. H., Boyle, A., & Bronstein, J. L. (2005). Mutualisms as Consumer-Resource Interactions. In P. Barbosa & I. Castellanos (Eds.), *Ecology of Predator-Prey Interactions* (pp. 17–33). Oxford: Oxford University Press.

Holt, R. D., & Barfield, M. (2013). Direct plant–predator interactions as determinants of food chain dynamics. *Journal of Theoretical Biology*, *339*, 47–57. doi:10.1016/j.jtbi.2013.04.034

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., … Woodward, G. (2009). Ecological networks - beyond food webs. *Journal of Animal Ecology*, *78*(1), 253–269. doi:10.1111/j.1365-2656.2008.01460.x

Johnson, S., Domínguez-García, V., Donetti, L., & Muñoz, M. A. (2014). Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences*, *111*(50), 17923–17928. doi:10.1073/pnas.1409077111

Jonsson, T., Kaartinen, R., Jonsson, M., & Bommarco, R. (2018). Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters*, *21*(5), 702–712. doi:10.1111/ele.12938

Kaiser-Bunbury, C. N., Mougal, J., Whittington, A. E., Valentin, T., Gabriel, R., Olesen, J. M., & Blüthgen, N. (2017). Ecosystem restoration strengthens pollination network resilience and function. *Nature*, *542*(7640), 223–227. doi:10.1038/nature21071

Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B., & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecology Letters*, *13*(4), 442–452. doi:10.1111/j.1461-0248.2009.01437.x

Kéfi, S., Berlow, E. L., Wieters, E. A., Joppa, L. N., Wood, S. A., Brose, U., & Navarrete, S. A. (2015). Network structure beyond food webs : mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, *96*(1), 291–303. doi:10.1890/13-1424.1

Kéfi, S., Berlow, E. L., Wieters, E. A., Navarrete, S. A., Petchey, O. L., Wood, S. A., … Brose, U. (2012). More than a meal… integrating non-feeding interactions into food webs. *Ecology Letters*, *15*(4), 291–300. doi:10.1111/j.1461-0248.2011.01732.x

Kéfi, S., Holmgren, M., & Scheffer, M. (2016). When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology*, *30*(1), 88–97. doi:10.1111/1365-2435.12601

Kéfi, S., Miele, V., Wieters, E. A., Navarrete, S. A., & Berlow, E. L. (2016). How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. *PLOS Biology*, *14*(8), e1002527. doi:10.1371/journal.pbio.1002527

Kondoh, M. (2003). Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. *Science*, *299*(5611), 1388–1391. doi:10.1126/science.1079154

Levine, J. M., Bascompte, J., Adler, P. B., & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, *546*(7656), 56–64. doi:10.1038/nature22898

Lin, Y., & Sutherland, W. J. (2014). Interaction modification effects on ecological networks are affected by ratio dependence and network topology. *Journal of Theoretical Biology*, *363*, 151–157. doi:10.1016/j.jtbi.2014.08.025

Matassa, C. M., Ewanchuk, P. J., & Trussell, G. C. (2018). Cascading effects of a top predator on intraspecific competition at intermediate and basal trophic levels. *Functional Ecology*, (April), 1–12. doi:10.1111/1365-2435.13131

May, R. M. (1972). Will a large complex system be stable? *Nature*, *238*, 413–414. doi:10.1038/238413a0

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*(7100), 259–64. doi:10.1038/nature04927

Morin, P. J. (2011). *Community Ecology* (2nd ed.). Wiley-Blackwell.

Ohgushi, T., Schmitz, O., & Holt, R. D. (2012). *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives*. Cambridge: Cambridge University Press.

Okuyama, T., & Bolker, B. M. (2007). On quantitative measures of indirect interactions. *Ecology Letters*, *10*(4), 264–71. doi:10.1111/j.1461-0248.2007.01019.x

Olff, H., Alonso, D., Berg, M. P., Eriksson, B. K., Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1524), 1755–1779. doi:10.1098/rstb.2008.0222

Otto, S. B., Rall, B. C., & Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, *450*(7173), 1226–9. doi:10.1038/nature06359

Pilosof, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, *1*(4), 0101. doi:10.1038/s41559-017-0101

Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, *86*(2), 501–509. doi:10.1890/04-0719

R Core Team. (2018). R: A Language and Environment for Statistical Computing. https://www.r-project.org/

Sanders, D., Jones, C. G., Thébault, E., Bouma, T. J., Heide, T. Van Der, Belzen, J. Van, & Barot, S. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*, 513–524. doi:10.1111/j.1600-0706.2013.01011.x

Sanders, D., Thébault, E., Kehoe, R., & Frank van Veen, F. J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences*, *115*(10), 2419–2424. doi:10.1073/pnas.1716825115

Säterberg, T., Sellman, S., & Ebenman, B. (2013). High frequency of functional extinctions in ecological networks. *Nature*, *499*(7459), 468–470. doi:10.1038/nature12277

Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, *13*(9), 350–355. doi:10.1016/S0169-5347(98)01437-2

Soetaert, K., Petzoldt, T., & Setzer, R. W. (2010). Package deSolve : Solving Initial Value Differential Equations in R. *Journal Of Statistical Software*, *33*(9), 1–25. doi:10.18637/jss.v033.i09

Staniczenko, P. P. A., Lewis, O. T., Jones, N. S., & Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, *13*(7), 891–899. doi:10.1111/j.1461-0248.2010.01485.x

Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(9), 3648–52. doi:10.1073/pnas.1014353108

Strogatz, S. H. (2001). Exploring complex networks. *Nature*, *410*(6825), 268–276. doi:10.1038/35065725

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*, 10698. doi:10.1038/ncomms10698

Terry, J. C. D., Bonsall, M. B., & Morris, R. J. (2018). Interaction Modifications Disrupt The Structure And Stability Of Ecological Communities. *BioRxiv Preprint*, 1–24. doi:10.1101/345280

Terry, J. C. D., Morris, R. J., & Bonsall, M. B. (2017). Trophic interaction modifications: an empirical and theoretical framework. *Ecology Letters*, *20*(10), 1219–1230. doi:10.1111/ele.12824

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*(5993), 853–856. doi:10.1126/science.1188321

Thierry, A., Beckerman, A. P., Warren, P. H., Williams, R. J., Cole, A. J., & Petchey, O. L. (2011). Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic and Applied Ecology*, *12*(7), 562–570. doi:10.1016/j.baae.2011.09.005

Uchida, S., & Drossel, B. (2007). Relation between complexity and stability in food webs with adaptive behavior. *Journal of Theoretical Biology*, *247*(4), 713–722.

doi:10.1016/j.jtbi.2007.04.019

Underwood, N., Inouye, B. D., & Hambäck, P. A. (2014). A Conceptual Framework for Associational Effects: When Do Neighbors Matter and How Would We Know? *The Quarterly Review of Biology*, *89*(1), 1–19. doi:10.1086/674991

Valdovinos, F. S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P., & Dunne, J. A. (2010). Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*, *13*(12), 1546–1559. doi:10.1111/j.1461-0248.2010.01535.x

van Veen, F. J. F., van Holland, P. D., & Godfray, H. C. J. (2005). Stable Coexistence in Insect Communities Due to Density- and Trait-Mediated Indirect Effects. *Ecology*, *86*(12), 3182–3189.

Werner, E. E., & Peacor, S. D. (2003). A Review of Trait-Mediated Indirect Interactions in Ecological Communities. *Ecology*, *84*(5), 1083–1100.

Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs. *Nature*, *404*(6774), 180–183. doi:10.1038/35004572

Wootton, J. T. (1993). Indirect Effects and Habitat Use in an Intertidal Community: Interaction Chains and Interaction Modifications. *The American Naturalist*, *141*(1), 71–89.

Yodzis, P., & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, *139*(6), 1151–1175.

Supplementary Information

Code and simulation data are available on the Open Science Framework repository. https://osf.io/w83br/ DOI: 10.17605/OSF.IO/W83BR

1. Method for determining body masses from trophic level

Body masses are assigned based on trophic level in the original, pre-integration to equilibrium, communities. First, trophic levels calculated on using the pathway method of Levine (1980), rounded into integer trophic levels. These trophic levels were then used to assign relative body masses specified on a logarithmic scale (base 10). We used distributions with a lower variance than empirical distributions to aid the stability of our systems by distributing body-masses in a relatively hierarchical manner with trophic level.

i. Producers were assigned a body mass of 0.

ii. Primary consumer (Trophic level 2)) body-masses were drawn from a normal distribution: $\mathcal{N}(0.65, \sigma = 0.5)$, truncated at 0 to remove the possibility that consumers are smaller than herbivores.

iii. Higher-level consumer (Tropic level 3+) body masses were specified based on the sum of repeated draws from a normal distribution for each trophic level above 2 (h = TL-2), standardising the variance

$$0.65 + \sum_{1,\ldots,h} \mathcal{N}\left(2.73, \sigma = \frac{0.5}{\sqrt{h}}\right)$$

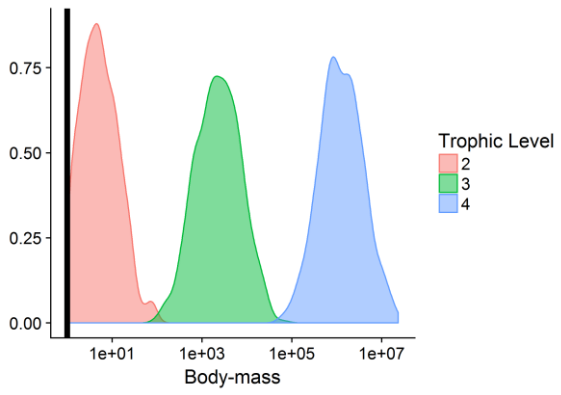

Figure S1. Density plot showing distribution of body masses across integer trophic levels. Black line shows producer body mass. Note the relatively small overlap in body masses and logarithmic scale.

2. Information about starting populations

The baseline communities are available in R list format as part of the online supplementary material. Summary statistics are shown in the Figure S2.

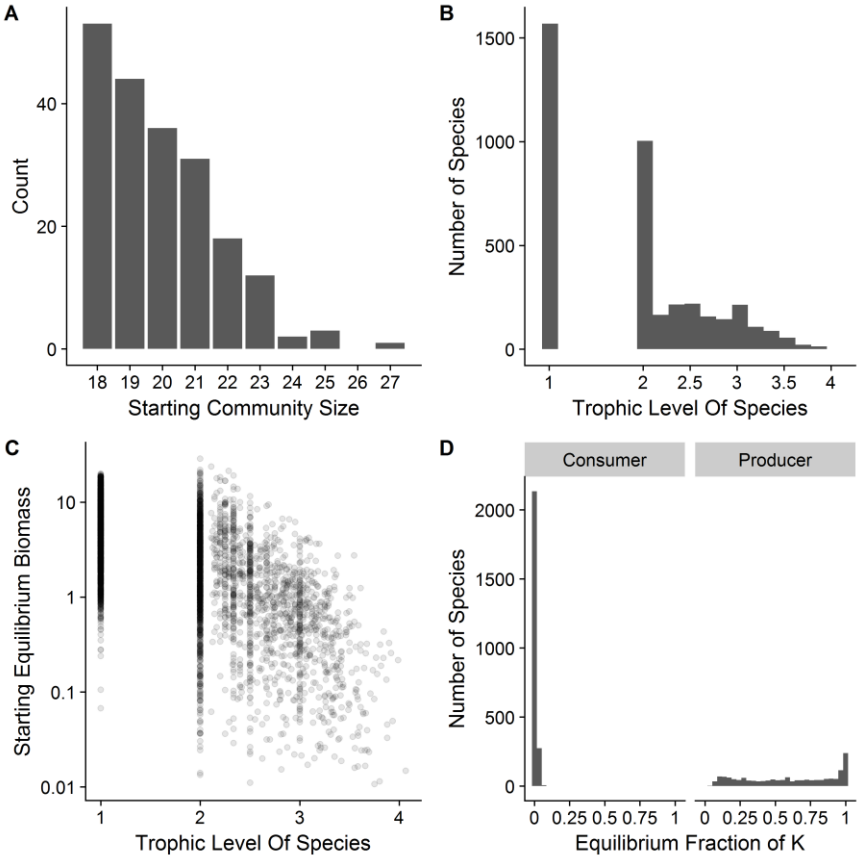

Figure S2. Further details about the properties of the 200 equilibrium communities used in robustness analysis. A: Histogram showing distribution of number of species in each community. Eighteen species was chosen as a lower cut off-point. B: Distribution of 3983 species across trophic levels, as calculated using the unweighted-pathway method. 8 species that had a calculated trophic level above 4 are not shown. C: Relationship between trophic level of a species and its initial equilibrium biomass, showing a general negative relationship. 67 populations has an initial biomass below 0.01 and are not shown for clarity. D: Initial Equilibrium biomass as a fraction of each species carrying capacity. Consumer equilibrium biomass was considerable below carrying capacity in all cases, while producer biomass varied from near capacity to well below.

3. Derivation of Gompertz Control Parameters

The basic form of the Gompertz equation is:

$$f(\theta_{ijk}, x) = g\left(a\, e^{-be^{-cx}} - d\right)$$

In order to maintain the sign of μ_{ijk}, we define it based on the logarthim of the Gompertz function which can be negative

$$\log_{10}(\mu_{ijk}) = f(\theta_{ijk}, x)$$

The core results that we wish to achieve are:

i. $f(\theta_{ijk}, 0) = 0$, When the modifier biomass is at equilibrium, the re is no modification effect

ii. $f'(\theta_{ijk}, \tau) = \alpha$, the slope at the point of inflection is α

iii. $f''(\theta_{ijk}, \tau) = 0$, The point of inflection occurs at x-τ

iv. $\left|f(\theta_{ijk}, \infty) - f(\theta_{ijk}, -\infty)\right| = \sigma$, The range of the equation is σ

v. The function should not, on average, be biased towards increasing or decreasing the strength of the interaction.

The core Gompertz equation ($e^{-be^{-cx}}$) ranges from 0-1, therefore the criterion iv) can be achieved by setting a= σ.

Criterion ii) can be simply met as $\max(\frac{df}{dx}) = \frac{gac}{e}$, which can be rearranged to give $c = \frac{g\alpha e}{\sigma}$.

Criterion iii) can met from solving $f''(x) = 0$ for x, which is $x = ln(b)/c$. This can then be rearranged to give $b = e^{c\tau}$, where c is given by the previous result.

Criterion i) can be simply met, since when $x = 0$, $e^{-cx} = 1$, we can find $d = a\, e^{-b}$, where b and a are set from previous results.

Finally to address v) and fix the intrinsic bias of the core equation towards either positive or negative modifications depending on the sign of the modification, we randomly rotate half of the functions around the point (0,0) by setting $g = \begin{cases} -1 \\ +1 \end{cases}$ with equal probability.

4. Criteria for establishing Equilibriums

Finding of Initial Equilibria.

Each model generated as described in the main text was initiated with a biomass density of 10. All models are available as R functions in the online code appendix. Models were integrated using the deSolve library within R (Soetaert *et al.* 2010), using the default 'lsoda' solver which switches automatically between stiff and non-stiff methods as necessary for the problem. Integration was continued with regular checks whether finishing conditions were met. If the biomass density of a species fell below a density of 10^-10 it was removed (its density was set to zero). After each extinction those consumers left without any remaining resources were also set as extinct. If extinctions resulted in the splitting of the community into multiple sub-webs the largest was kept and all the species in the smaller web were set as being extinct.

Models were run for a minimum of 400 time steps, continued until the community was considered to have reached an equilibrium. This was determined by the mean absolute ratio between the mean population of each species over the previous 200 time unit period and the next was less than 1%. The density of surviving at the last time point was then used as starting values with a multiple root-finding algorithm from the R package *rootSolve* (Soetaert 2009) using the Newton-Raphson method, with the requirement for positive roots. This approach allowed a faster and accurate identification of true equilibria for slow to converge populations. In a handful of cases this root finding process determined the population biomass equilibrium to be below 10^-10. In these cases the model integration was declared a failure.

Robustness Analysis

The community models including external mortality and potentially TIMs were generated as described in the main text, with starting values as determined above. Models were integrated as above, in blocks of 200 time units. If the mean absolute ratio between the mean population of each species over the previous 200 time unit period and the next was less than 1%, the community was considered to have sufficiently stabilised. Consumers without any resources were immediately removed but trophically disconnected subunits were retained. If no acceptable equilibrium point had been reached after 100'000 time units or the integrator tolerances were exceeded the run was declared a failure. For statistical tests only complete pairwise comparisons were used. Failures were dominated by integrator tolerance issues, and were more common with the TIM model:

Test	Successes	%
No TIM Model	3975	99.8
Pairwise NTEs	3897	97.8
Full TIMs	3736	93.8

5. Response of populations to drop in population being as likely positive as negative.

To test the initial direction of response to perturbation we examined the direction of movement of populations when the biomasses were set the starting value with the exception of the 'targeted species' which was set to 99% of its initial value. This was done across all 200 tested communities, for each species. Of 75960 responses, 61.8% were neutral, 18.6 per negative and 19.5% were positive.

6. Partition of Modified Trophic Interaction into Trophic and Non-Trophic Components

For case where i is the focus, j's are the predators of i, l's are the prey of i and k's are the modifier, the original impact term is:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots \underbrace{-\mu_{ij}a_{ij}B_j}_{Trophic\ Term\ with\ TIM}$$

First expand μ_{ij}as:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots - \ (1\ + (\mu_{ij} - 1)\ )\ a_{ij}B_j$$

Then partition into a direct trophic effect and a non-trophic effect:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots \underbrace{-a_{ij}B_j}_{Trophic\ Term} + \underbrace{a_{ij}B_j(1-\mu_{ij})}_{Non-Trophic\ Term}$$

Make the assumption that the B_j in the non-trophic term is fixed at B_j^*:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \cdots \underbrace{-a_{ij}B_j}_{Trophic\ Term} + \underbrace{a_{ij}B_j^*(1-\mu_{ij})}_{Non-Trophic\ Term}$$

This approach is only valid where there is only a single TIM per interaction. Multiple TIMs would require considerable further complex terms to account for synergistic effects of TIMs. A similar process, fixing B_i can then be followed to find the impact on the other species.

References For Supplementary Material

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. Journal of Theoretical Biology 83:195–207.

Soetaert, K. 2009. rootSolve: Nonlinear root finding, equilibrium and steady-state analysis of ordinary differential equations.

Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Package deSolve : Solving Initial Value Differential Equations in R. Journal Of Statistical Software 33:1–25.