Trophic Interaction Modifications in Food Webs



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A thesis submitted for the degree of

Doctor of Philosophy

Trinity 2018

Abstract

Trophic interaction modifications are an important, but historically neglected, set of relationships between species within ecological communities. They define how the rate of consumption of a resource by a consumer is affected by the population of other species in the ecosystem. These modifications can derive from a wide range of ecological processes, and individual modifications have been shown to have major effects in small systems. Here I develop ecological understanding of interaction modifications at the whole network scale using theoretical analyses of generalised models. First, I examine in detail how interaction modifications can be considered as distinct processes to conventional pairwise interactions, demonstrating that otherwise disparate ecological processes can be united through a common framework that allows systematic and precise analysis. I illustrate this with a discussion of how the strength of an interaction modification can be understood from multiple angles and contexts. Second, I use models of artificial ecological communities to test for the properties that determine the importance of particular interaction modifications for the dynamics of whole communities in terms of directional predictability of responses to perturbations and local stability. I find that, in general, interaction strength-based methods are more effective than topological based metrics of key modifications. Third, I examine the impact that structured distributions of interaction modifications within ecological communities can have on the overall pattern of dynamic interactions and the resultant consequences for the stability of ecosystems. I demonstrate that certain reasonable distributions of interaction modifications can generate significant additional structure. Fourth, I directly test the impact of the multi-species nature of interaction modifications on the robustness of ecological communities to extinctions in response to sustained perturbations using generalised models of ecosystems. I show that interaction modifications shift the relative vulnerability of species and that higher-order models give notable different results to pairwise representations. I conclude with a discussion of approaches to gather network-level empirical data of the distribution of interaction modifications in order to translate the theoretical advances into natural systems.

Format of Chapters

This thesis is based on four free-standing papers. Each main chapter has been formatted to meet requirements of the academic journal to which they have been, or are planned to be, submitted to. As free-standing articles, there is therefore an inevitable degree of overlap and repetition between the chapters. The supplementary material for each chapter is presented in Appendices A-D. Figure references are internal to each chapter and the corresponding supplementary information appendix. These journals are:

Chapter 1: *Ecology Letters* (Ideas and Perspectives)

Chapter 2: *Oikos* (Research Paper)

Chapter 3: *American Naturalist* (Article)

Chapter 4: *Journal of Animal Ecology* (Standard Paper)

Statement of Authorship

The papers that constitute each main chapter are co-authored with my supervisors (Rebecca Morris and Michael Bonsall). In each case I was first and corresponding author, designed the aims and methods, conducted the analyses and lead the writing of the manuscript. The authorship statement included with submissions to journals for all four papers was as follows: '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 first draft of the manuscript, and all authors contributed substantially to revisions.'

Code and Data Availability

All code used to generate results and raw simulation data is available within a publicly available repository on the Open Science Framework https://osf.io/qtrg9/.

Funding

This thesis was funded through a NERC Oxford Environmental Research DTP studentship (NE/L002612/1).

Acknowledgements

Many thanks are due to all the people who have helped me over the last four years. Firstly, my supervisors. Becky Morris and Mike Bonsall. Both have been fantastic throughout, always ready with comments and advice, as well as giving me the space to explore my own ideas and projects.

I have also been incredibly lucky to have been part of two lively research groups (CERO and MERG) who have made all the various offices across Oxford such great places to work. Special mentions to Beth Raine, Harriet Downey, Kristiina Visakorpi and Rob Paton who have been there for most of it.

Finally, my thanks to Sarah McSwiggan for joining me in Oxford, all her support and keeping me grounded in the real world.

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Introduction

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The science of ecology seeks to understand how the properties of individual organisms scale up to the patterns observable in the natural world. At the subject's core are fundamental questions regarding how the large and intricate systems of the natural world endure, how the abundances of species in particular locations are determined and the ultimate drivers of changes to those populations. Improving our understanding of ecosystem dynamics and pushing back ecological forecast horizons (Clark *et al.* 2001, Petchey *et al.* 2015) is crucial to informing how we as humans engage with ecosystems as we seek to harvest resources, conserve species and mitigate global change.

Three broad classes of impacts on populations can be discerned, the interrelationship and relative importance of which has been the focus of sustained debate (Elton 1927, Andrewartha and Birch 1954, Bjørnstad and Grenfell 2001). First, there are processes of direct density-dependence on the growth rate of a population. These include direct effects of resource depletion and toxin accumulation, as well as intraspecific competition mediated through factors such as the availability of suitable nest sites or effects of population age-structure (Ives 2009). Such processes alone can produce complex or even chaotic dynamics (May 1974, Costantino *et al.* 1997). Second, populations can be affected by external abiotic effects, such as annual weather variations (Frederiksen *et al.* 2008) or longer term climate change (McLean *et al.* 2016), but also including anthropogenic pressures (Benítez-López *et*

al. 2017). Last, the influence populations of other species in the community can be felt through a diversity of interspecific interactions, which in turn interact with and modulate the other contributors to population dynamics (Coulson *et al.* 2001).

Direct bi-directional interactions between populations include the consumption of resources by consumers (trophic interactions) or parasites (Crawley 1992), mutualistic relationships including pollination (Bascompte and Jordano 2013) or competitive interactions such as inter-specific territoriality (Minot and Perrins 1986). Other interspecific interactions are unidirectional, with only one species discernibly affected (Frank *et al.* 2018). The analysis of such pairwise interactions has been a cornerstone of ecology for many years, but they are not the only means by which species can interact (Wootton 1994). Chains of direct interactions cascading through ecosystems can lead to significant 'indirect' effects, such as trophic cascades (Pace *et al.* 1999) or apparent competition (Holt and Lawton 1994, Bonsall and Hassell 1997, Morris *et al.* 2004). Moreover, populations can also be affected by the modification to their direct interactions caused by other species in the community. Improving our understanding of the impact of these 'interaction modifications' (Wootton 1993), a distinct category of processes between species in ecological systems, is the focus of this thesis.

The ecological mechanisms through which interaction modifications can act are highly diverse, but are united by their dynamic consequences. Classic examples include the changing foraging behaviour of consumers due to fear of attack by predators (Brown *et al.* 1999), the switching of consumers between multiple food options (Abrams 2010a) or providing defence from predators (Holland *et al.* 2005). Attempts to organise the diversity of processes have categorised modifications by the means of transmission (behavioural, chemical, morphological or environmental, Miller and Kerfoot 1987) or the type of modified process (trophic, non-trophic or migratory, Kéfi *et al.* 2012). Interaction modifications are a distinct process to direct interspecific interactions, acting through the modulation of direct interactions. Despite being in some senses a step removed from direct interactions, there have been many demonstrations that the impact of interaction modifications on populations

can be as large, or larger, than direct interactions (Werner and Peacor 2003, Preisser *et al.* 2005, Ohgushi *et al.* 2012). As such there is increasing interest in their applied use, for example the control of agricultural pests (Heil 2014, van Veen 2015). However, current understanding regarding their role in dynamics of populations lags considerably behind that of the contribution of other mechanisms (Peacor and Cressler 2012, Levine *et al.* 2017).

Interaction modifications within ecological science

Even before current anthropogenic pressures and modern scientific enquiry, there has been interest in the factors determining the populations of animals. For much of history this was couched in the concept of the 'balance of nature', apparent back as far as Herodotus (III, 108), and often explicitly linked to theological arguments (Egerton 1973). The role of species interactions was also appreciated, with simple descriptions of food chains described by Abu 'Uthman 'Amr ibn Bahr (al-Jahiz) in the early 9th century (Egerton 2002). Interaction chains involving non-trophic effects were described by Darwin (1859), who traced a link between local cat populations and the growth of clover through field mice and 'humblebee' populations.

Despite early acknowledgement that species can vary their traits in response to other species (e.g. Smellie (1790), quoted in Egerton (2009)), the concept of interaction modifications as a distinct process is not clearly observable in early work. It was not until the early 20th century that quantitative ecological abstraction at the level of the population by those such as Lotka (1926), Volterra (1926) and Gause (1932) led to rapid developments in population biology (Kingsland 1995). An early model from this period developed by Gause *et al.* (1936) includes the plasticity of a protist predator in response to other species in the community. Despite this, the study of interaction modifications first came into focussed attention around 1970 with a series of papers that sought to determine if a linear, pairwise, approach to species interactions was sufficient or whether 'higher-order' terms were necessary (Hairston *et al.* 1968, Vandermeer 1969, Neill 1974).

Overall, these results were mixed and by the 1980s these efforts had largely slowed, with attacks on the statistical tests used (Case and Bender 1981) and parsimony-based arguments against the invocation of higher-order interactions (Pomerantz 1981). While there was much work on the mechanisms that can lead to interaction modifications, examining topics such as optimal foraging theory (Stephens and Krebs 1986) and the impact of the search for enemy free space (Werner *et al.* 1983), this was at a comparative distance to much population dynamics work. Abrams (1983) was a relatively lone voice arguing for the importance of interaction modifications. An analysis by Karieva (1994) found that over 60% of the papers published by*Ecology* in this decade dealt with at most two species. As a further example, a collection of essays discussing key ecological topics for the 75$^{\text{th}}$ anniversary of the British Ecological Society as identified by a member survey (Cherrett 1989) scarcely mentions higher-order interactions – there is only a passing mention in chapter dedicated to food webs on the need to simultaneously consider predator-prey, mutualistic and competitive networks (Lawton 1989).

This changed at the start of the 1990s, with the highlighting of the importance of non-trophic effects (e.g. Strauss 1991) and the clear exposition of the distinction between interaction chains and interaction modifications (Worthen and Moore 1991, Wootton 1993, 1994). This was followed by a special issue of *Ecology* discussing approaches for measuring interaction modifications (Kareiva 1994). Concurrently, the influence of ecological engineers was highlighted (Jones *et al.* 1994). In turn, this led to an increase in clear manipulative experiments, demonstrating the large impacts interaction modifications could have. For example, Beckerman *et al.* (1997) demonstrated how predatory spiders can reduce the herbivory rate of grasshoppers, even when neutralised by gluing shut their mouthparts.

The proliferation of such studies allowed a number of synthetic reviews that together robustly established the strong role that interaction modifications could play across systems and contexts (Sih *et al.* 1998, Agrawal 2001, Borer *et al.* 2001, Wootton 2002, Bruno *et al.* 2003, Werner and Peacor 2003, Schmitz *et al.* 2004, Ohgushi 2005, Creel and Christianson 2008). These were swiftly followed

by attempts to quantify the strength of resultant non-trophic effects through meta-analysis (Peacor and Werner 2004, Preisser *et al.* 2005) and compare them directly to the strength of trophic effects. The latter goal proved challenging since the standard experimental protocols used to demonstrate the impact of non-trophic effects were poorly suited to direct comparisons (Okuyama and Bolker 2007, Abrams 2007, 2010b, McCoy and Bolker 2008). Nevertheless, the role of non-trophic effects became well established, leading to a re-interpretation of many 'classic' results (Peckarsky *et al.* 2008).

Over this period the theoretical development of interaction modifications was largely focused on model systems with small numbers of species (Peacor and Cressler 2012). In their review, Bolker *et al.* (2003) were able to describe the short term qualitative impacts of interaction modifications as being 'well in hand', but that knowledge was missing regarding the shapes of response functions and the ability to scale up to longer term effects in complex communities (Bolker *et al.* 2003 p. 1102). Since it was demonstrated that essentially any dynamic responses could be generated from a system with particular interaction modifications (Abrams 1995), tight relationships between theory and experiment were understood as being essential. However, work to explicitly incorporate quantified interaction modifications into experimental population dynamics studies has been restricted to a handful of small experiments (Vos *et al.* 2001, van Veen *et al.* 2005). Similarly, theoretical analyses of the impact that generalised interaction modifications can have on large communities have been very rare (Wilson 1992, Arditi *et al.* 2005, Goudard and Loreau 2008, Lin and Sutherland 2014, Bairey *et al.* 2016), often focussing on only particular groups of interaction modifications (e.g. Kondoh 2003). There remains a significant gap in our understanding of the emergent impacts of interaction modifications at the whole community scale.

The development of network ecology

The earliest descriptions of ecological networks (Forbes 1887, Elton 1927) were essentially collections of the known natural history of a community (Egerton 2007).

Since then, especially after the development of analytical network theory, the construction and analysis of ecological networks has become well established as a highly valuable tool within ecology (Memmott 2009, Poisot *et al.* 2016, Harvey *et al.* 2017). Networks, particularly quantified networks, allow a system to be analysed as a whole and routes of indirect effects to be understood. Historically, there was a strong focus on networks of trophic interactions (food webs) since these are the routes of energy flux (Odum 1953, Cohen 1978), although this approach never went unchallenged (Polis 1991, Polis and Strong 1996).

In the last decade, there has been a concerted push towards merging non-trophic interactions, including interaction modifications, into network ecology that had been dominated by the role of trophic interactions within food webs (Ings *et al.* 2009, Olff *et al.* 2009, Beckerman *et al.* 2010, Fontaine *et al.* 2011, Kéfi *et al.* 2012, Ohgushi *et al.* 2012, García-Callejas *et al.* 2018). While ecology is rarely susceptible to true 'paradigm shifts' (Cuddington and Beisner 2005), the move from single interaction type networks to holistic approaches is very marked and in part led by repeated failures of a purely trophic approach in predicting responses to perturbations (Doak *et al.* 2008, Tack *et al.* 2011, Barbosa *et al.* 2017).

A majority of ecological network research has roots in mathematical graph theory (Montoya *et al.* 2006, Dale 2017), describing systems as a set of nodes (vertices) and links (edges) (Newman 2010). However, this essentially 'two-dimensional' approach struggles with the diversity of non-trophic interactions, especially interaction modifications. In order to cope, extensions to conventional network theory have recently been suggested, including the use of 'multilayer' networks to combine multiple networks into one system (Pilosof *et al.* 2017) and 'hypergraphs' allowing the linkage of an arbitrary number of species with a single hyperedge (Golubski *et al.* 2016). However, these approaches struggle to capture the distinctive properties of interaction modifications. There is therefore a need to improve and standardise how interaction modifications are incorporated within mainstream ecology.

Approach and outline of thesis

Despite recent attention, the relative role of interaction modifications in the dynamics of ecological communities in the context of the other processes is not yet confirmed (Levine *et al.* 2017). The long list of examples does not in itself demonstrate their importance relative to other processes, and cannot determine whether these are special cases, or whether at the community level the effects mitigate each other (Golubski and Abrams 2011). Time and funds to study ecological systems are limited, necessitating the determination of when and where a particular ecological process is required to adequately understand a system. Simply because interaction modifications can produce interesting dynamics is not a sufficient argument to include them in predictive ecological theory (Adler and Morris 1994). This empirical gap is to some extent maintained by the lack of a clear framework into which to study interaction modifications – instead, despite their unity as a dynamical process, their study is scattered throughout ecological disciplines.

As the first empirical assessments of interaction modifications at the community level begin (Kéfi *et al.* 2016, Mayfield and Stouffer 2017), this thesis sets out to develop the underlying framework in which to study interaction modifications, particularly trophic interaction modifications, and improve the understanding of their contribution to population dynamics. In particular, by using generalised models of ecosystem structure and dynamics (Williams and Martinez 2000, Allesina and Tang 2012, Delmas *et al.* 2017) to examine the role of additional processes within baseline systems, this thesis aims to take initial steps in breaking the vicious circle of insufficient data. By identifying specific mechanisms and properties that drive dynamics in these systems, theory can assist empirical work to become more targeted and better able to inform our understanding.

In Chapter 1 I develop the interaction modification framework and show how it can usefully unite disparate areas of ecology by setting out how the strength of an interaction modification can be conceptualised and measured. In Chapter 2 I seek to identify properties of individual interaction modifications that exert particular influence on network level dynamics. To do this I introduce analogues of

topological metrics from conventional network theory to the higher order concept of interaction modifications. I then use these to examine approaches for identifying interaction modifications that affect local stability and directional determinacy under perturbation. In Chapter 3 I test the network-level consequences of interaction modifications to show that the relationship between trophic and non-trophic effect topology is critical to understand the dynamics of the community as a whole. Lastly, in Chapter 4 I directly test the impact of representing interaction modifications as pairwise non-trophic effects and demonstrate that this leads to dramatically different robustness in dynamic systems when faced with large perturbations.

1

Trophic interaction modifications: an empirical and theoretical framework

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Published in *Ecology Letters* as Terry *et al.* (2017) doi: 10.1111/ele.12824

Abstract

Consumer–resource interactions are often influenced by other species in the community. At present these 'trophic interaction modifications' are rarely included in ecological models despite demonstrations that they can drive system dynamics. Here, we advocate and extend an approach that has the potential to unite and represent this key group of non-trophic interactions by emphasising the change to trophic interactions induced by modifying species. We highlight the opportunities this approach brings in comparison to frameworks that coerce trophic interaction modifications into pairwise relationships. To establish common frames of reference and explore the value of the approach, we set out a range of metrics for the 'strength' of an interaction modification which incorporate increasing levels of contextual information about the system. Through demonstrations in three-species model systems, we establish that these metrics capture complimentary aspects of interaction modifications. We show how the approach can be used in a range of empirical contexts; we identify as specific gaps in current understanding experiments with multiple levels of modifier species and the distributions of modifications in networks. The trophic interaction modification approach we propose can motivate and unite empirical and theoretical studies of system dynamics, providing a route to confront ecological complexity.

Introduction

Trophic interactions between species are often affected by other species within the community (Abrams 1983; Werner and Peacor 2003). There have been growing calls to incorporate these processes into studies of system dynamics (Bolker *et al.* 2003; Ings *et al.* 2009; Fontaine *et al.* 2011; Kéfi *et al.* 2012; Ohgushi *et al.* 2012; Sanders *et al.* 2014) since these trophic interaction modifications, hereafter 'TIMs' (Wootton 1993; Golubski and Abrams 2011), are often identified as the cause of unexpected responses to perturbations (Doak *et al.* 2008; Tack *et al.* 2011; Barbosa *et al.* 2017). Focussed, short-term, studies with small numbers of species have repeatedly demonstrated that TIMs have the capacity to drive population dynamics (Werner and Peacor 2003; Preisser *et al.* 2005) and there is growing impetus to test the potential role of modifications in more complex systems. A greater understanding of how they influence population dynamics will be a key part of improving our ability to forecast how ecosystems will respond to change (Kéfi *et al.* 2012).

A very wide range of ecological processes can cause TIMs and historically these have been studied independently within ecological sub-disciplines. While this breadth highlights the importance of interaction modifications and associated indirect effects, it may result in generalisations being missed and lost opportunities to draw inferences. Consistent and comparable quantification of TIMs that can be broadly applicable will be an essential tool to draw general conclusions regarding their impact (Abrams 1992, 2007; Okuyama and Bolker 2012). Although it can be comparatively clear which species are linked by trophic interactions, interaction modifications must be inferred from their effect upon the consumer and resource species. Furthermore, any species could hypothetically affect almost any interaction in a community to some degree. This potentially overwhelming complexity places great value on the ability to define when interaction modifications are 'large' enough to require consideration in order to understand the dynamics of a given system.

Here, we advocate extending our understanding of interaction modification effects beyond pairwise approaches through the use of an explicitly multi-species TIM approach. To establish common frames of reference and explore the value of

this approach, we develop a set of metrics to show how TIMs can be interpreted, quantified and linked to experimental data. We show that this TIM concept offers a lens to unite a range of important processes that has the potential to greatly enhance our understanding of these effects on both theoretical and empirical system dynamics.

Delineating Trophic Interaction Modifications

Trophic interaction modifications are defined as the modification of a consumer–resource interaction by a third species (Wootton 1993; Golubski and Abrams 2011). This common property can link a wide range of important ecological phenomena as modifications of functional responses and as such form a useful and discrete subset of the wider field of 'non-trophic interactions' (Kéfi *et al.* 2012). Examples of sources of TIMs include foraging choices (Abrams 2010a) and associational defences (Barbosa *et al.* 2009), which act to cause non-trophic interactions such as ecosystem engineering impacts (Sanders *et al.* 2014), fear effects (Brown *et al.* 1999) and mutualistic relationships (Holland *et al.* 2005). By focusing on effects that involve consumption, and not attempting to also include other processes that have been grouped into the category of 'non-trophic effects' (such as reproductive interference, migration effects and mutualistic impacts on survival), we believe this TIM framework strikes a balance between grouping a wide range of ecological effects while still being able to examine common dynamic consequences in depth. Nonetheless many of the concepts discussed in this paper could also apply to non-trophic interaction modifications, such as modulation of competition for space by a third species.

Two alternate concepts for the study of this same set of ecological phenomena have developed (Table 1[1]), which we will refer to here as the TIM approach and the trait-mediated indirect interaction (TMII) approach, where 'trait' is broadly defined to include any property of an organism that affects its functional response or that of its consumer (Bolker *et al.* 2003). The TIM approach conceptualises the modification of the interaction as a distinct entity of study in itself, while the TMII

[1]Since this paper was published, I have come across two other phrases that could be added: 'gratuitous mutualism' (Case and Bender 1981) to the first category, and 'coaction' (Roughgarden and Diamond 1986) to the second.

Process	Terminology	Reference
Pairwise effect		
	trait-mediated indirect interaction	Werner and Peacor (2003); Abrams (2007)
	functional indirect interaction	Janssen *et al.* (1998)
	trait-mediated biotic indirect effect	Goudard and Loreau (2012)
	trait-initiated indirect effect	Abrams (2004)
	trait-transmitted indirect effects	Abrams (1995)
	behavioural indirect effect	Miller and Kerfoot (1987)
	chemical response indirect effect	Miller and Kerfoot (1987)
	non-consumptive predator effect	Preisser and Bolnick (2008)
	non-trophic interaction	Kéfi *et al.* (2015)
	risk effect	Creel and Christianson (2008)
	emergent multi-predator effects	Sih *et al.* (1998)
	higher-order interaction	Vandermeer (1969)
Change to interaction		
	trophic interaction modification	Golubski and Abrams (2011)
	interaction modification	Wootton (1993)
	rheagogy	Arditi *et al.* (2005)
	environment-mediated interaction modification	Wootton (2002)
	associational resistance / susceptibility	Barbosa *et al.* (2009)
	resource choice	Abrams (2010b)
	prey switching	Koen-Alonso (2007)
	higher-order interaction	Billick and Case (1994)

Table 1.1: Terminology used to describe approaches focussing on pairwise effects and changes to interactions. Note that 'higher-order interaction' has been used for both concepts

approach emphasises the pairwise consequences of the modification. The distinction between proximate cause (change in trait), dynamic (change to the interaction) and consequence (resultant effect between species not otherwise linked) can be blurred and the terms conflated since the TIM and TMII approaches attempt to represent the same underlying ecology (Fig. 1).

A pairwise TMII approach brings certain advantages; for example, facilitating direct comparisons with other classes of trophic and non-trophic interactions through established network metrics and extensions into multi-layer networks (Kéfi *et al.* 2016). However, this coercion of a process involving at least three species into an interaction between two species risks obscuring fundamental features and mechanisms that differentiate these trait-mediated processes from other interactions (Golubski *et al.* 2016). As a very direct example, if species B of the system depicted in Fig. 1(a) is no longer present, there should no longer be an A–C interaction, but the dependence on B is not included in the specification of the A–C indirect pairwise link. In contrast, the TIM concept does not allow conventional network analysis (Newman 2010), since that requires a distinct set of nodes and links (edges).

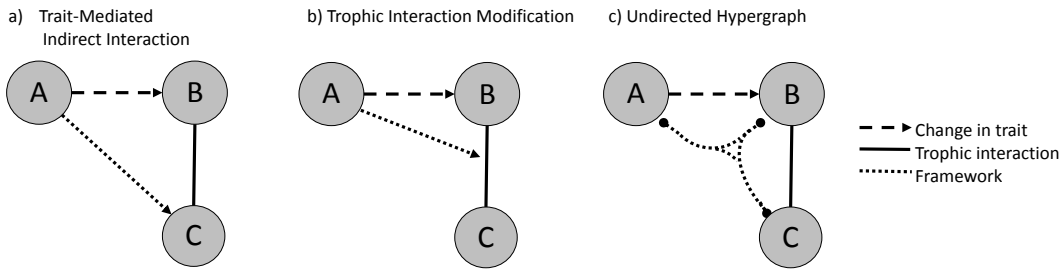


Figure 1.1: Illustration of the distinction between different frameworks that can represent the impact of the influence of third species on trophic interactions. A trait-mediated indirect interaction approach (a) represents the resultant link between A and C, a trophic interaction modification approach (b) represents the change in the interaction strength, while an undirected hypergraph approach (c) represents a relationship between all three species.

However, for this very reason, a TIM framework is a more direct representation of the process from a system dynamics perspective, in particular identifying the distinctive roles of the species involved.

A third approach using the mathematical concept of 'hypergraphs' has recently been proposed by Golubski *et al.* (2016). This framework represents interactions with 'hyperedges' that can link any number of species, in contrast to conventional network links that each represent interactions between exactly two species. This incorporates the multi-species nature of effects caused by interaction modifications and allows the application of hyper-dimensional extensions of network metrics. However, as Golubski *et al.* (2016) discuss, this approach is limited in its ability to represent the underlying dynamics as it does not yet allow the specification of the identity of modifier and interactors, or the directionality of the effect.

Opportunities of TIM Approach

Compared to pairwise TMII analyses, a TIM framework provides a practical approach to consider a greater range of dynamic consequences from the same underlying ecology. TIMs provide a mechanism to translate potentially disparate and

complex underlying processes into an understanding of how they lead to consequences at higher levels of organisation. To examine some of these opportunities, we first consider how the 'strength' of TIM effects can be defined. Here we outline five aspects of interaction modifications that can be considered through metrics of their magnitude to demonstrate the potential utility of the approach.

Firstly, the impact of an interaction modification can depend on the strength of the interaction being modified – a large proportional effect on a weak interaction may be less likely to have a large effect on the system as a whole. However, interaction strength has been specified by a host of different complimentary approaches (Laska and Wootton 1998; Berlow *et al.* 2004), ranging from consumption rate to response ratios. For simplicity, most simulation models seeking to evaluate the impact of TIMs specify them as relative modifiers of interactions (Křivan and Schmitz 2004; Arditi *et al.* 2005; Goudard and Loreau 2008). With the ability to consider explicitly the aspect of interaction strength that is being modified, the dynamic impact of the modification under consideration can become clearer.

Secondly, conceptions of TIM strength can consider the extent to which they incorporate indirect effects of TIMs and resultant feedbacks, with important consequences for the interpretation of experiments. The presence of a modifying species can change an interaction in three distinct ways, which we define as direct, secondary and density-mediated TIMs (Fig. 2). As an example, consider a three-level (plant–herbivore–predator) food chain where higher densities of the predator cause the herbivore to reduce its consumption rate of the plant. The TIM would reduce the herbivore–plant interaction directly, but the interaction would also be affected by the reduced herbivore population due to reduced food intake (secondary TIM) and because of predation losses (density-mediated TIM). There is no guarantee that an indirect TIM would be in the same direction as, or of lesser magnitude than, the direct TIM. Many verbal descriptions of interaction modifications include only direct TIMs and their effects, yet where populations vary secondary and density-mediated mechanisms can play considerable roles in experimentally observed changes

in interactions. A TIM framework allows a more precise description of the scope of processes that are being described.

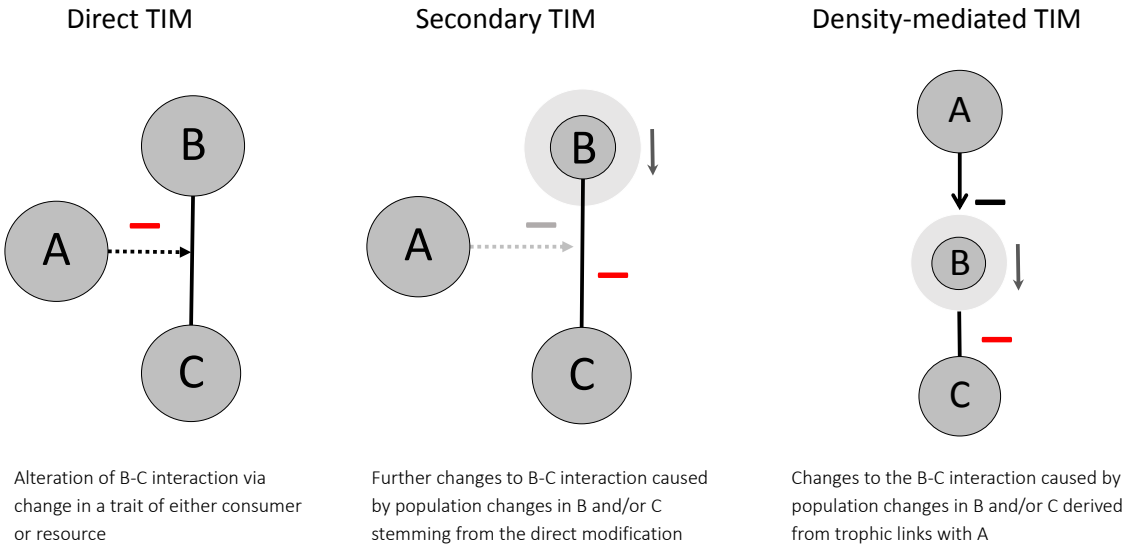


Figure 1.2: Illustration of distinction between direct and indirect trophic interaction modifications (TIM). The dotted arrows show the proximate driver of the change to the interaction. For the indirect cases, the grey arrows depict the process by which the interaction was modified.

Thirdly, TIMs are inherently dynamic concepts and the full range of their impacts often only become visible in non-equilibrial systems or after perturbations (Doak *et al.* 2008). If the modifying species is at low or unvarying density there may be little observable modification effect, despite a large potential to affect an interaction if the modifier's population was perturbed. Modifications can obscure their own impact on dynamics if they lead to the stabilisation of systems (and hence reduce the variation in interaction strength). There is therefore an important bi-directional link between system dynamics and TIM strength, which pairwise approaches are unable to handle as easily.

Fourthly, modifications to interactions may occur only after a considerable time lag to changes in the modifier population (Bolker *et al.* 2003) and such delays can have notable effects (Hastings *et al.* 2007). Delays could stem from the time taken to learn behavioural responses, time for genetic selection to occur, or time taken for environmental changes to the ecosystem to develop. Multi-scale models can incorporate delayed interaction modifications directly with a time lag, or more

commonly with an additional state variable representing an environmental cue or a trait. The trait changes can be determined by adaptive considerations (Kondoh 2003; Valdovinos *et al.* 2010) or as a direct function of the modifier (Garay-Narváez and Ramos-Jiliberto 2009). A dynamic-focused TIM approach is amenable to studying system responses over different timescales. Transient dynamic metrics can also be applied to investigate dynamics distinct to long-term asymptotic behaviour. However, for the remainder of this paper, we will focus on the effect of changes that can be reasonably be modelled as instantaneous.

Finally, multiple modifying species can exert simultaneous modifications upon a focal interaction (Fig. 3a, Relyea 2003; Golubski and Abrams 2011). While it is possible to partition consumption directly to particular species, partitioning effects of modifications poses a fundamentally challenging question since the process is not directly observable. Multiple modifying species can cause changes in the same, opposite or a completely different direction in the trait-space of the interactors-alternatively described as functionally equivalent, functionally inverse or functionally diverse (Herzog and Laforsch 2013). By focussing on the combined changes to interactions, the TIM framework aids the generation of hypotheses for how modification effects combine (Golubski and Abrams 2011) and a route to possible additional model structures, such as introducing cue variables (Fig. 3b, Garay-Narváez and Ramos-Jiliberto 2009). Furthermore, the TIM framework allows a distinction between multiple modifications acting simultaneously and the modulation of modifications where a TIM is itself directly modified by a fourth species (Fig. 3c; for example Liere and Larsen 2010).

Metrics

Concepts of TIM strength are contingent on the extent to which information about the wider system is incorporated. Table 2 outlines a set of TIM metrics, both long-standing and newly proposed, that sequentially increase the amount of information incorporated about the system. TIM effects have been studied in a wide range of theoretical frameworks (Peacor and Cressler 2012) including: network re-wiring

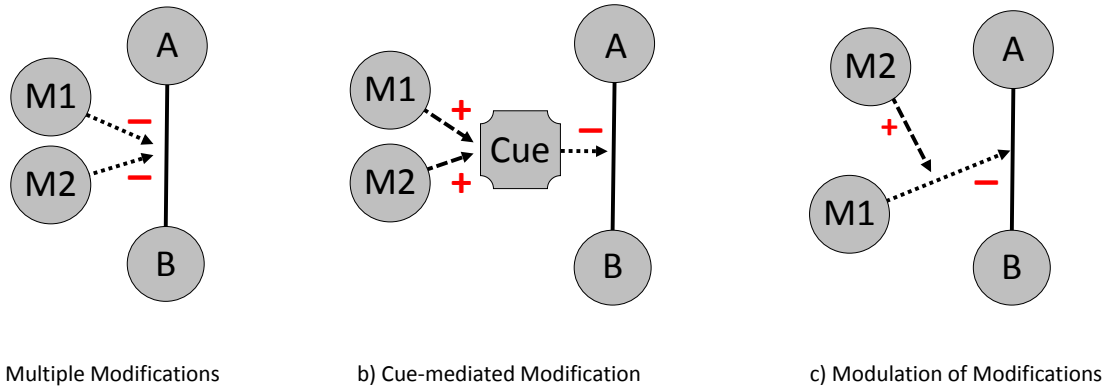


Figure 1.3: Illustration of how multiple modifying species can act on an interaction. Dotted lines indicate interaction modifications; dashed lines indicate other processes related to interaction modifications: increase in 'cue' in (b) and a modification of a modification in (c).

(Staniczenko *et al.* 2010), sign-only matrices (Dambacher and Ramos-Jiliberto 2007), fitness-based models (Valdovinos *et al.* 2010), explicit cue-state variables (Garay-Narváez and Ramos-Jiliberto 2009) and individual-based models (Peacor *et al.* 2007; Railsback and Harvey 2013). Here, we focus on a common framework where sets of differential equations represent the rate of each population's density change and the TIM is represented by additional functional response components (Arditi *et al.* 2005; van Veen *et al.* 2005; Holt and Barfield 2013). This population-level representation abstracts over individual variation and the underlying (often trait-based) causes of interaction modifications to focus on resultant effects at the level of the species. Nevertheless, the distinctions between TIM effects as measured by different metrics are not specific to this modelling approach.

Modification parameter

With a functional response model that includes a TIM it is possible to identify a parameter that specifies the strength and direction of the TIM influence on the interaction. These values can be found by fitting models to experimental data (van Veen *et al.* 2005) and can be specified directly in models (Křivan and Schmitz 2004; Goudard and Loreau 2008; Holt and Barfield 2013), thereby providing a direct link between experiment and theory. A range of symbols have been used for the TIM parameter in the literature, here we use c_{ijk} to represent the effect

Metric	Composition	Explanation
Modification Parameter	c_{ijk}	Parameter in function that links modifier species density to consumption rate in the functional response model (van Veen *et al.* 2005).
Modification Term	$f(c_{ijk}, x_k)$	The term by which a functional response parameter, such as attack rate, is modified. It incorporates modifier density and TIM model structure (Golubski and Abrams 2011).
Flux Change	$\Delta_{rel} = \frac{f(x_i, x_j, x_{k=0})}{f(x_i, x_j, x_k)}$	The difference in the interaction strength (as measured by biomass or energy flux) due to the modifier, as either a raw difference or a ratio (Peacor and Werner 2004).
	$\Delta_{abs} = f(x_i, x_j, x_{k=0}) - f(x_i, x_j, x_k)$	
Change in B_{CR}	$\frac{x_i^*}{x^*_{i,c_{ijk}=0}}$	The relative B_{CR} (biomass potential of the resource consumed, computed from the relative change in equilibrium density of the resource in the presence of the consumer (Gilbert *et al.* 2014)) change due to a TIM as the ratio of the equilibrium value of the prey with and without the TIM.
Modification Coefficient of Variation	$\frac{\sigma_{f(x_k)}}{\mu_{x_f(k)}}$	For non-stationary systems, the ratio of the standard deviation of the interaction strength modification divided by the mean modification over a period of time.
Elements of Jacobian Matrix	$\frac{\partial \dot{x_i}}{\partial x_k}$, $\frac{\partial \dot{x_j}}{\partial x_k}$	TMII-framework metric representing the direct effects of the modifier species on each interactor (Abrams 2008; Okuyama and Bolker 2012).
Partial derivatives of Jacobian Matrix	$\frac{\partial}{\partial x_k}\mathbf{A}_{ij}$, $\frac{\partial}{\partial x_k}\mathbf{A}_{ji}$	The change in direct interaction strengths between the interactors with respect to modifier density.
Partial derivatives of inverse negative Jacobian Matrix	$\frac{\partial}{\partial x_k}(-\mathbf{A}^{-1})_{ij}$, $\frac{\partial}{\partial x_k}(-\mathbf{A}^{-1})_{ji}$	The change in total (indirect and direct) interaction strength between the interactors with respect to modifier density.

Table 1.2: Metrics of trophic interaction modification strength, discussed in the main text. x_i, x_j and x_k represent the density of population of the resource, consumer and modifier populations respectively. Dots indicate the derivative with respect to time.

species k has on the consumption of species i by species j. However, exactly how the resultant modification relates to this parameter is critically dependent on the form of the functional response model used. While some studies have used fully linear representations of TIMs (e.g. Bairey *et al.* 2016), non-linearities in functional responses and the modification effect are likely to be prominent. It is possible for any aspect of a non-linear functional response to be modified (Preisser and Bolnick 2008; Kéfi *et al.* 2012) including consumption rate (Arditi *et al.* 2005; Goudard and Loreau 2008), handling time (Vos *et al.* 2004), sigmoidality (Alexander *et al.* 2013) or additional interference terms (Vos *et al.* 2001; van Veen *et al.* 2005; Larsen 2012).

Given the huge diversity of possible models, it is useful to consider separately the underlying functional response model, the choice of the affected parameter, and the sub-model linking the TIM parameter to changes of the affected functional response parameter. Previous work has used a wide variety of functions to link the density of the modifier to the modification term, outlined in Appendix 1 in Supporting Information, to introduce a variety of thresholds and non-linear relationships. So far, there has been little theoretical comparison of different generic TIM functional responses (although see Holt and Barfield 2013). With the exception of prey switching effects (Koen-Alonso 2007; Abrams 2010b), the only class of TIM that are often implicitly included in population dynamic models, there is little experimental data to inform the choice of TIM functional form. Until a significant body of data develops, the choice of formulation will depend on fit to biologically informed criteria, such as those suggested by Goudard and Loreau (2008).

Modification term

The term representing the effect of the TIM within the functional response model incorporates the density of the modifier species. This gives a measure of the modification at a particular system state. As it is a sub-element of the functional response model, the use of this term as a metric requires contextualisation within the wider model being used. The modification of different aspects of the functional response (such as handling time, attack rate or total consumption rate) can have very

different effects on the change in consumption at different densities of interactors. This metric has had particular use in describing the combined effect of multiple modifications (Golubski and Abrams 2011).

Change in flux

The most direct approach to incorporate the strength of the interaction being modified is to calculate the change in flux rate (biomass or energy) due to the modification. Either a ratio or an absolute flux difference can be considered. Indirect TIM effects (see Fig. 2) can lead to mixed responses to modifiers making it important to consider which effects are included in the measurement of flux change for comparisons to be meaningful.

Change in B_{CR}

The B_{CR} framework (Gilbert *et al.* 2014) proposes a metric of interaction strength that relates the energy flow between a consumer and a resource to static measures of the resource biomass in order to measure the biomass potential of the resource captured by the consumer. It can be calculated from the equilibrium biomass of the resource with and without the consumer being present, as well as directly from model parameters (Gilbert *et al.* 2014). As such it provides a way of linking empirical and theoretical studies and has been shown to be useful in relating interaction strength to stability (Nilsson and McCann 2016). Conveniently, as we show in Appendix 2 in Supporting Information, the relative change in this metric with and without the TIM can simplify to the relative density of the resource with and without the TIM. This is experimentally tractable compared to metrics that need to measure the flux and the metric can also be defined from model parameters (e.g. see Appendix 2 in Supporting Information).

Coefficient of variation in modification parameter or interaction strength metric

Trophic interaction modifications are likely to be particularly critical in systems not at an equilibrium, but assessing the 'strength' of TIMs in such cases poses

challenges. Where a model of the system is available, the coefficient of variation (the ratio of standard deviation to mean) of the modification parameter term can represent the dynamic changes a TIM is exerting. However, a low degree of variation in parameter modification does not necessarily mean the TIM is not having a significant impact since it is readily possible to show TIM effects that lead to the stabilisation of cycling systems (Appendix 3 in Supporting Information). Measures such as coefficient of variation in flux or other interaction strength metrics can also be derived from non-equilibrium systems. These can be considered with reference to the level of environmental stochasticity underlying the system. There is considerable room within the TIM framework for a more sophisticated understanding of how modification effects interact with system variation to determine population dynamics (Peacor and Cressler 2012).

Partial derivatives of Jacobian matrix

The metrics outlined above have represented a given TIM with a single value. An interaction is not necessarily symmetric in its effect on the interactors which can result in a pair of values for each TIM, representing the effect of the interaction modification on each species. Jacobian matrices of community dynamics models are composed of the partial derivatives of each species' population change functions with respect to each species in the community. Within a pairwise TMII framework, the elements from this matrix have been put forward as a metric of modification effect (Abrams 1984). These correspond to the effect of modifier density on the modified species population growth. A development of this metric, taking the proportional change in growth rates with respect to the modifier, has also been put forward (Abrams 2008; Okuyama and Bolker 2012) to compare trait-and density-mediated indirect interactions at a particular community state. We propose here a related metric aligned with the TIM concept that is able to distinguish TIM effects from direct interactions linking the modifier and interactor. This can be computed by taking the partial derivative with respect to the modifying species of the Jacobian matrix elements that specify the modified interaction. This corresponds to the effect

a modifier species has upon the direct interaction. For simple models it is possible to calculate interpretable expressions for how this metric responds to the system parameters. A significant feature of this metric is that it specifies the dynamic relationship of modifier and the interaction for a particular community at a given state, most likely an equilibrium. As with all Jacobian and gradient based metrics, it involves linearisation and hence is only strictly valid for system states very close to that in which it was defined, which could hinder direct experimental assessment.

Partial derivatives of inverse negative Jacobian ('net-effects') matrix

The previous metric can be extended to include indirect interactions between species. The inverse of the negative Jacobian matrix $-\mathbf{A}^{-1}$ represents the combined direct and indirect interactions between species (Levine 1976; Bender *et al.* 1984). Partial derivatives of elements of this 'net-effects' matrix with respect to the modifier species density equate to the effect the modifier has on the total effect of the interactors on each other. Such an approach may lead to a more thorough understanding of the extent of impact that a TIM is having within a given system. However, there are some significant difficulties. Expressions of the value of this metric in terms of model parameters can be uninterpretably complex and numerical analysis can propagate errors due to the multiple differentiation and whole matrix manipulation steps. More fundamentally, because indirect effects are incorporated, values can be non-zero when no explicit TIM effect is included due to density-mediated TIM effects (see Fig. 2 and Case and Bender 1981).

Comparison of metrics

The need to differentiate between the diversity of potential approaches to TIMs is highlighted by a lack of consistency in the concepts of TIM strength. To demonstrate this, we applied the different metrics to three model systems with TIMs (Fig. 4): a tri-trophic food chain with linear functional responses and TIM, a tri-trophic system with non-linear functional responses and TIM and the experimentally parameterised

aphid-parasitoid system described in van Veen *et al.* (2005). In each case, the strength of the model's TIM parameter was varied and the metric in question recalculated at the resultant equilibrium densities. Full model details are given in Appendix 4 in Supporting Information.

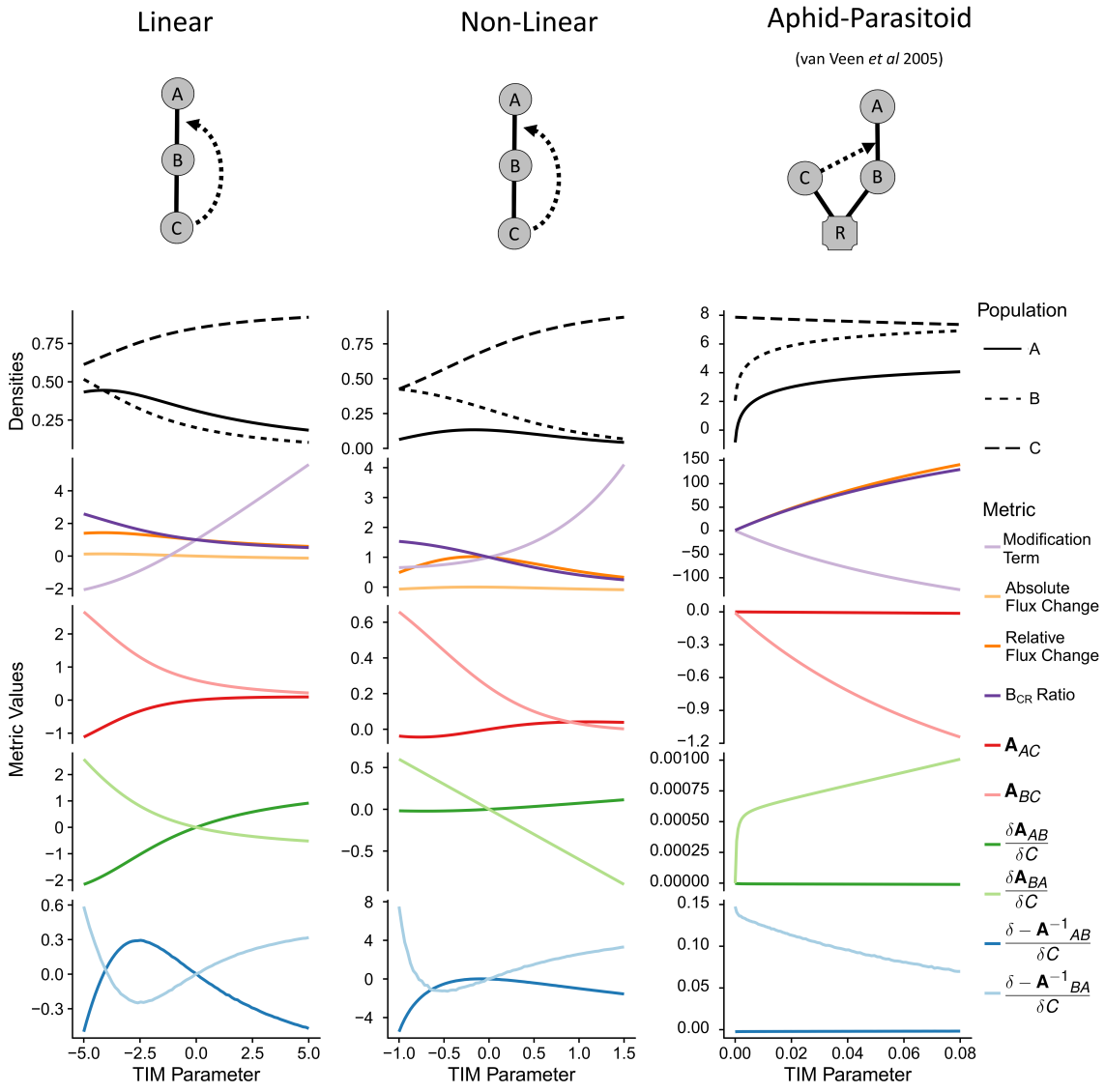


Figure 1.4: Demonstration that trophic interaction modifications (TIM) metrics display different qualitative and quantitative responses to changing the underlying parameter representing the TIM strength. Full model structures and parameters are given in supporting information. Note that the aphid-parasitoid system population densities are on a log-scale.

There are notable quantitative and qualitative differences in how the strength of the TIM, as measured by different metrics, responds to the changing underlying

TIM parameter (Fig. 4). Since they measure different properties, it is not possible to propose one metric as universally superior. Successfully applying TIM strength metrics to specific questions will require measures of 'strength' that have tangible links to the theoretical concepts being considered, requiring a repertoire of diverse approaches. Furthermore, many approaches require specific conditions (such as the system being at equilibrium) that reduce their universality. Improving our understanding of how different aspects of interaction modifications relate to each other will be an important area for further research. While 'lower-level' metrics are likely to be simpler to quantify, 'higher-level' metrics place the modification in context and can provide more information on their role and impact in a dynamic system.

With the exception of the modification parameter, the metrics represent the strength of the TIM at a particular community state. These can provide considerable detail and insight about the process occurring in the system, but extending conclusions to consider larger perturbations may be challenging. This trade-off reflects the highly dynamic nature of interaction modifications where taking a snapshot is essential to describe a system property concisely. For this reason, quantifying model parameters has particular advantages for understanding the system dynamics. Combined with a model specification they can describe the underlying process in a way that is not specific to a given system state and can allow the derivation of other measures.

Many of the apparently idiosyncratic relationships between the TIM parameter and the TIM strength observable in Fig. 4 are caused by interactions via changing equilibrium densities, with significant consequences for the interpretation of experimental data. Cascading effects of the changing link strength can counter the naïve expectation that increasing the magnitude of the TIM parameter should lead to greater recorded 'strength' of the TIM. The capacity to explore the multi-facetted nature of TIM effects is a significant advantage of this approach.

Linking Theory and Experimental Systems

There is a significant gap between the concepts of interaction modifications that are used in theoretical or simulation studies and the objectives of the majority of experimental work. Despite repeated calls to try and close this gap (Bolker *et al.* 2003), a focussed programme of work has yet to emerge (Kéfi *et al.* 2012; Peacor and Cressler 2012). Key questions regarding the distribution, functional form and impact of TIMs in natural systems are only starting to be addressed (Perfecto *et al.* 2014; Kéfi *et al.* 2015; Suraci *et al.* 2016). The focus of a considerable number of experiments has been to identify the relative roles of trait-mediated and density-mediated effect pathways in tri-trophic systems (Peacor and Werner 2004; Bolnick and Preisser 2005; Preisser *et al.* 2005). These studies have played a significant role in demonstrating that such effects can have major impacts, despite issues with the interpretation and duration dependence of such experiments (Abrams 2001, 2008; Okuyama and Bolker 2007). However, other experimental approaches will become necessary to deepen our understanding of these processes both to understand the causal mechanisms underlying TIMs and to quantify the modification.

A model-fitting approach is able to overcome some of the challenges involved in quantifying modifications and their effects. Ideally, experiments seeking to investigate the effect a presumed TIM is having on a system would use an experimental treatment where the putative modifying species is present and trophically connected to the web, but the modifying effect is blocked. However, there are few systems where this is feasible. Consequently, many studies have conducted the reverse experiment, introducing a modification without the modifier being trophically connected to the system. A common experimental protocol has been to observe the effect of a single level of disabled, fear-inducing, predator on the consumptive behaviour of another species (Werner and Peacor 2003). The extent to which these studies can inform our understanding of system dynamics is limited by the lack of information about the shape of the response and the lack of feedbacks to the modifier species (Bolker *et al.* 2003; Abrams 2008; McCoy *et al.* 2012; Okuyama and Bolker 2012). A shift in emphasis towards a TIM-centred approach based on functional responses, as we

outline here, rather than attempting to straightjacket such processes into an indirect-interaction framework, will provide a profitable route of analysis. This would apply equally to modelling approaches at either individual or population levels.

Short-term experiments

Ideally, experimental studies seeking to quantify TIMs would seek to parameterise a functional response model by fitting a response surface of the strength of the interaction across multiple levels of the modifier (Fig. 5; Denny and Benedetti-Cecchi 2012; Okuyama and Bolker 2012). While such studies are inevitably more labour intensive than single-level studies, Okuyama and Bolker (2012) present simulations that suggest even a low level of replication would provide useful results. Experimental functional responses have been fitted at different levels of modifier (e.g. Kehoe *et al.* 2016; Wasserman *et al.* 2016) and it would be a relatively small step for similar studies to define a single functional response model. TIMs themselves can be context dependent, for example, depending on prey hunger levels (Gravem and Morgan 2016) or temperature (Sentis *et al.* 2017). As it is well established that TIM effects have the potential to be large (Werner and Peacor 2003), future studies would be most valuable if they are as representative of natural conditions as possible rather than being designed with the aim of demonstrating an effect.

Long-term experiments

Model selection and parameter fitting with time series can give powerful insights into system dynamics (Mueller and Joshi 2000). Studying populations displaying natural dynamics can avoid the problems of contextualisation with short-term experiments. Several studies have experimentally introduced a modification to a system, such as a predator cue, and studied the resulting dynamics (Peacor *et al.* 2012; Frago and Godfray 2014; Suraci *et al.* 2016). However, to the best of our knowledge, as yet only one study has included the modifier species treatment as a dynamic part of the system and gathered time series data to fit a mechanistic model (van Veen *et al.* 2005). Where the modifier is not a dynamic part of the system, cue-based

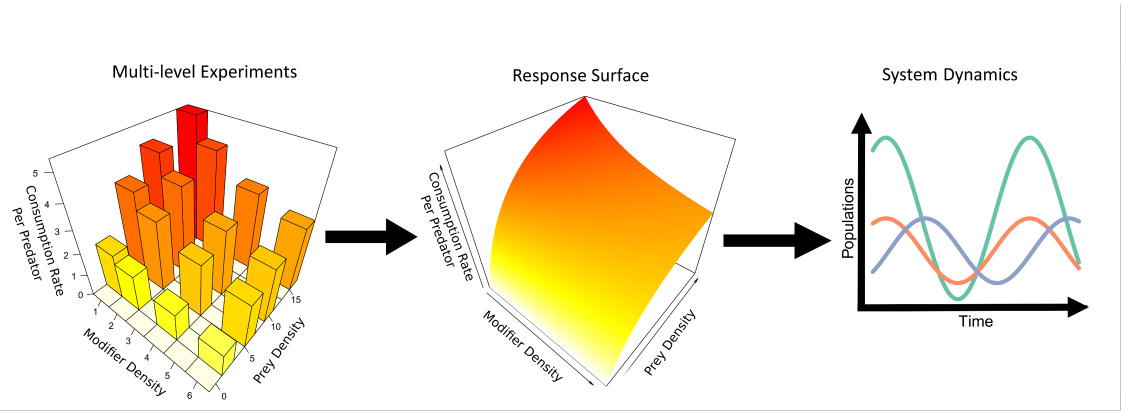


Figure 1.5: Illustration of how the results of multi-level experiments can be used to specify a response surface that is of value for understanding system dynamics. Short-term functional response experiments that include multiple levels of both prey and modifier can be used to define a function corresponding to a response surface, either by fitting parameters of a mechanistic model or with a regression based spline model. Such a function can then be used as part of models of the population dynamics of the system.

studies risk making an assessment of the effect of an altered parameter, rather than the effect of the dynamic nature of the TIM, as discussed further below.

Unfortunately, the difficulties commonly encountered when fitting models to time series could be exacerbated when studying interaction modifications. In order to detect changes to interactions the unmodified pairwise relationships must be well characterised. Furthermore, for robust model selection it is necessary for the populations to vary sufficiently for the system to traverse a significant part of the multi-dimensional space specified by the modifiers and the interactors. In many systems, experimental perturbations would be necessary for this to occur in a reasonable period of time. Tight correlations between the modifier and either of the species involved in the interaction may hinder accurate parameterisation. Characterisation of the model structure is likely to have to remain the domain of short-term studies since model selection in addition to model-fitting is likely to require data beyond most available or feasible datasets. Because of the high level of experimental effort necessary, preliminary analysis using detailed models would be of value to examine the potential impacts of TIMs and aid the design of appropriate experiments.

Using time series methods to detect TIMs *de novo* is challenging because of the large potential number of modifications and hence a high risk of identifying artefacts. Nonetheless, it may be possible to calculate Jacobian-based metrics directly from reconstructed manifolds based on long time series (Deyle *et al.* 2016). Well-studied systems with existing time series also offer a wide scope to investigate TIM effects (Peckarsky *et al.* 2008) and would reduce the need to conduct new TIM-specific time series experiments.

Outlook

The stronger conception of interaction modifications we suggest here will allow new analyses and perspectives. One such area is highlighting TIMs that exert dynamic influences, compared to those emanating from species with comparatively fixed densities that may exert a strong, but unvarying influence. While stable equilibria may be a consequence of TIMs, modifications within systems at equilibrium introduce a constant change and the risk of examining the effect of a changed trait, not an additional dynamic property. For example, the stabilising effect of a TIM in three-species model food chains (Křivan and Schmitz 2004; Holt and Barfield 2013) can be almost completely replicated by directly changing the model parameters to represent the modification without introducing a dynamic TIM (Appendix 5 in Supporting Information). It is important to consider the situations for which specifically introducing the added complexity of TIMs is valuable. For example, many plants have been shown to release volatiles to attract enemies of their herbivores (van Veen 2015). Where the trait modification is unrelated to the plant population density this could be represented by a statically changed functional response. This would be a more parsimonious representation of the process than introducing a dynamic TIM from the plant population to the herbivore-enemy interaction. However, where the attractant effect is dependent on other herbivores (e.g. Vos *et al.* 2001) the TIM framework has much to offer by representing the relationship between the other herbivore and the enemy-herbivore interaction.

This paper has largely discussed modelling at a population level, making the simplifying assumption that populations are homogenous and that their dynamics are tightly coupled. There is a body of evidence that intraspecies behavioural syndromes can exert a strong impact on ecological processes (Sih *et al.* 2012) and it has been demonstrated that some individuals consistently exhibit bolder behaviours in response to predation threat (Griffen *et al.* 2012). Even without a diversity of behavioural syndromes, environmental heterogeneities can create differences in how interactions of individuals are modified. For example, it has been shown that hunger level can determine whether individuals respond to predator cues by reducing their foraging (Gravem and Morgan 2016). One route to address the effects of intraspecific diversity (Bolnick *et al.* 2011) would be individual-based modelling approaches (Peacor *et al.* 2007; Railsback and Harvey 2013). In principle, it would be possible to build up from individual measurements of response to modifiers to create individual-based models (DeAngelis and Mooij 2005), although the demands on data would be high. Additionally, relatively abstract population-level models cannot easily provide a causal explanation for the modification to interactions. 'Bottom-up' approaches would supplement the population dynamic approach that has been principally discussed in this paper, in particular for their potential to show how individual behavioural optimisation in response to the trade-offs involved in foraging choices leads to interaction modifications (Werner 1992).

While their ubiquity has been well established (Werner and Peacor 2003), the distribution of TIMs in empirical networks is a major unknown that will need to be addressed. There is every reason to expect that non-random distributions will impact how TIMs influence community dynamics. Nonetheless, simulation studies using random networks of TIMs can still provide useful insights – much useful work was done with random trophic networks (May 1973; Allesina and Tang 2015) before and since detailed experimental data on trophic webs was developed. However, theoretical simulation studies must carefully consider the consequences of their choices of inter-TIM relationships. If TIMs combine non-additively, introducing a balanced distribution of positive and negative TIM

parameters can shift average interaction strength, a key determinant of food-web properties (Berlow *et al.* 2004). Goudard and Loreau (2008, 2012) suggest that such shifts in interaction strength may have contributed to the relationship between TIM connectance and ecosystem functioning they found in their simulation study. Calibrating modifications to maintain the average interaction strength may be challenging for complex communities. A profitable route may be to compare results to matched simulations that vary average interaction strength to identify where results can be attributed specifically to dynamic effects of TIMs.

There is currently only one study that attempts to represent the distribution of non-trophic interactions in a whole natural community (Kéfi *et al.* 2015). It is highly unlikely that TIMs will be distributed randomly as current models (Arditi *et al.* 2005; Goudard and Loreau 2008; Lin and Sutherland 2014; Bairey *et al.* 2016) have assumed (Golubski and Abrams 2011). In particular, there is likely to be a tight relationship between the TIM topology and the underlying trophic network. For instance, it would be reasonable to expect that TIMs are more prevalent between species that are closely trophically connected. Despite the large challenges, there are reasons to be optimistic that significant progress can be made in empirically determining the distributions of TIMs in more systems. Mayfield and Stouffer (2017) demonstrate a model selection framework to identify TIM effects in a community of plants. There is also the opportunity to make use of allometric scaling relationships to make pattern-based models for the distribution of modifications in a system (Krenek and Rudolf 2014).

Conclusion

The field of non-trophic interactions is poised to build upon demonstrations of possible effects towards an understanding of their role in the dynamics of natural systems. Trophic interaction modifications are a key set of processes where there is particular potential for progress. Theoretical work demonstrates that almost any set of dynamics can be generated from a model incorporating TIMs, necessitating communication between theory, laboratory experiment and field work to constrain

possibilities (Bolker *et al.* 2003). Here we have put forward specific examples of the additional perspectives and depth that a TIM framework can bring and hope this encourages those planning experiments to take advantage of the opportunities. As with estimates of interaction strength (Laska and Wootton 1998), there is a benefit to identifying diverse perspectives for the strength of interaction modifications to understand and improve the links between theory and experiment. With a shift towards a focus on the modification itself as a discrete entity, we believe there are many exciting prospects to improve our understanding of ecosystem dynamics.

Data Accessibility Statement

R code to run the models and generate Figure 4 is available on the OpenScience Framework. DOI: 10.17605/OSF.IO/QTRG9

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Identifying important interaction modifications in ecological systems.

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Pre-print: https://doi.org/10.1101/228874

Abstract

Trophic interaction modifications, where a consumer-resource link is affected by additional species, are widespread and significant causes of indirect effects in ecological networks. The sheer number of potential interaction modifications in ecological systems poses a considerable challenge, making prioritisation for empirical study essential. Here, we introduce measures to quantify the topological relationship of individual interaction modifications relative to the underlying network. We use these, together with measures for the strength of trophic interaction modifications to identify modifications that are most likely to exert significant effects on the dynamics of whole systems. Using a set of simulated food webs and randomly distributed interaction modifications, we test whether a subset of interaction modifications important for the local stability and directional determinacy of complex networks can be identified. We show that trophic interaction modifications from low-density species, those affecting high-flux interactions, those that connect species otherwise distantly linked, and those that act from high trophic level modifiers to interactions lower in the web have particular importance for dynamics. In contrast, the centrality of modifications provided little information. This work demonstrates that analysis of interaction modifications can be tractable at the network scale and highlights the importance of understanding the relationship between trophic and non-trophic effect distributions.

Introduction

The study of the network dynamics of whole ecological communities is dominated by trophic interactions (Dunne and Pascual 2006). However, it is increasingly recognised that non-trophic effects must be considered to improve our understanding of the dynamics of ecosystems (Kéfi *et al.* 2012). Interaction modifications (Wootton 1993), where third-party species influence the strength of interactions, are a significant cause of non-trophic effects and are known to be widespread in ecological communities (Werner and Peacor 2003, Kéfi *et al.* 2015). By grouping the diverse processes that can be represented as modifications of functional responses, the trophic interaction modification (TIM) approach (Golubski and Abrams 2011, Terry *et al.* 2017) provides a route to investigate a significant portion of non-trophic effects.

Studies in small empirical model systems have demonstrated that the impact of TIMs can be considerable, comparable with trophic interactions (Schmitz *et al.* 2004), and capable of driving community dynamics (van Veen *et al.* 2005). Interaction modifications have often been identified as the cause of unexpected ecosystem responses to perturbation (Doak *et al.* 2008, Peckarsky *et al.* 2008, Tack *et al.* 2011). However, despite growing interest (Ohgushi *et al.* 2012, Levine *et al.* 2017), applications to complex natural systems have been slower to develop (Kéfi *et al.* 2012). The number of possible interaction modifications rises rapidly with increasing community size. Identification and prioritisation of the most important processes (Aufderheide *et al.* 2013) is therefore necessary to accelerate the improvement of our understanding of ecological networks.

Interaction modifications do not fit directly within conventional network theory (Newman 2010) as they cannot be depicted as a set of nodes linked by edges. Instead, the nodes directly affect edges. Approaches to deal with this discontinuity within conventional network theory have generally taken two approaches. Most commonly, studies focus on resultant pairwise effects, drawing conventional 'non-trophic interaction' links between the modifier and both interactors (Kéfi *et al.* 2012) which can be analysed as multi-layer networks (Pilosof *et al.* 2017) while keeping non-trophic and trophic networks distinct. Alternatively, hyper-graph approaches

can be used where edges can link any number of nodes (Golubski *et al.* 2016). Both these approaches have significant drawbacks in terms of maintaining the distinct features of interaction modifications (Terry *et al.* 2017).

Here we introduce analogues of conventional network metrics that can describe how individual interaction modifications are situated within the wider trophic network. Using simulated food webs with random distributions of trophic interaction modifications, we show that it is possible to detect a valuable subset of interaction modifications, the identification of which can offer significant gains in directional determinacy and the estimation of community stability.

Methods

Generating communities

We generated a set of *in silico* communities, using empirically derived allometries, to which we added a random set of TIMs and conducted our dynamic analyses. We describe these systems at an equilibrium by modelling the interactions between each population with a community matrix (Novak *et al.* 2016). All analyses were carried out using R v.3.4.3 (R Core Team 2017) and all code is available.

Initial trophic network topologies were generated using the niche model algorithm (Williams and Martinez 2000) with species number and trophic connectance set at 25 and 0.1, respectively. This simple algorithm has been generally validated as a useful approach to generate networks that have similar structural properties to natural systems (Williams and Martinez 2008). Cannibalistic interactions were removed and trophic levels were assigned from the network structure following the unweighted pathway method of Levine (1980). Species body-masses, m_i, were assigned based on trophic level following empirical distributions of consumer-resource ratios (Brose *et al.* 2006a, detailed in SI 1).

The biomass density of each species, B_i, was drawn from a distribution based on the individual body mass as $B_i = 10^{-2.36+g+\epsilon} m_i^g$ following the approach of Tang *et al.* (2014), where $\epsilon \sim \mathcal{N}(0, \sigma = 0.2)$. The scaling factor between body mass and biomass-density, g, can vary considerably between communities (Reuman *et al.*

2009). We therefore repeat our analyses with three values of g within the range of empirical estimates (0.25, 0.1 and -0.1). To ease comparison between different scaling terms, the mean population density across each community was standardised to 1.

Trophic interactions

To define the effect of trophic interactions between populations, we used body-mass allometries (Yodzis and Innes 1992, Woodward *et al.* 2005) to parameterise a Type I functional response model:

$$\frac{dB_i}{dt} = \sum_{l \in \text{ prey of } i}^{l} e_{li} a_{li} B_l B_i - \sum_{j \in \text{ predators of } i}^{j} a_{ij} B_i B_j. \tag{2.1}$$

This allows us to specify a community matrix $\mathbf{A}$, where each element $\mathbf{A}_{ij} = \frac{\partial}{\partial B_j}\frac{dB_i}{dt}$, detailing the change in the growth rate of the population of i in response to a small change in the population of j.

Each element of the community matrix representing the trophic effect of the population of predator j on a population of prey i is specified as $\mathbf{A}_{ij} = -a_{ij}B_i$ while the reverse effect, $\mathbf{A}_{ji} = e_{ij}a_{ij}B_j$. Conversion efficiencies, e_{ij}, were drawn from a uniform distribution $\mathcal{U}(0.1, 0.2)$. Biomass-density specific attack rates, a_{ij}, were defined based on the documented relationship between consumer-resource size ratios and per-capita attack rates (Pawar *et al.* (2012) , detailed in SI 1) and incorporating a penalty for predator generality.

Self-regulation terms

The diagonal elements of the community matrix $\mathbf{A}_{ii}$ represent the self-regulation of each species. We tested two approaches to specify these terms. First, each species was assigned a negative self-regulation term equal to twice the mean of the absolute size of interactions exerted upon it. In a second approach, producers were assumed to be more strongly self-regulating than consumers. Each producer was assigned terms equal to twice the strongest trophic interaction in the network while each consumer was assigned a term 100 times smaller.

Interaction modifications

We model interaction modifications as a multiplicative term, where the resultant attack rate is dependent on the relative divergence of the modifier species density, B_k, from their equilibrium:

$$a'_{ij} = a_{ij}\left(1 + \sum_{k \in \text{modifers}}^{k} c_{ijk} \log\left(\frac{B_k}{B_k^*}\right)\right) \tag{2.2}$$

Species are assumed to not modify their own trophic interactions ($k \neq j$), or rather any effect is considered subsumed into the self-regulatory terms. A positive slope parameter, c_{ijk}, causes an increased level of the modifier to strengthen the underlying trophic interaction. A negative value would weaken the interaction. Each TIM results in two additional non-trophic effect terms to be added to the community matrix:

$$\frac{\partial \dot{B}_i}{\partial B_k} = \ldots - a_{ij} B_i B_j c_{ijk} \frac{1}{B_k^*}, \quad \frac{\partial \dot{B}_j}{\partial B_k} = \ldots + e_{ij} a_{ij} B_i B_j c_{ijk} \frac{1}{B_k^*} \tag{2.3}$$

We assume that the trophic interaction specified by the allometries incorporates the influence of the modifier at the equilibrium density, i.e. it is already at 'post-modification' strength. This allows the effect of interaction modifications to be clearly distinguished from disruption of the trophic network, something that has not been possible in previous dynamic analyses of the effect of interaction modifications on system dynamics (e.g. Arditi *et al.* 2005, Goudard and Loreau 2008, Lin and Sutherland 2013) where the introduction of interaction modification shifts the underlying trophic interaction distribution. Each potential TIM (combination of consumer, resource, and third-party species) had an equal and independent probability (0.05) of being present. This resulted in an expectation of 69 TIMs per community of 25 species and trophic connectance 0.1. Slope parameters (c_{ijk}) for each extant TIM were drawn from a uniform distribution $\mathcal{U}(-0.5, 0.5)$. The resultant log-normal distribution of non-trophic effect components largely overlapped that of the trophic interactions but tended to be weaker (SI. 2).

Quantifying TIMs

Topology

We quantify the location of a TIM within a trophic network in seven aspects of topology, illustrated in Fig. 1. The simplest method records the *trophic height* of the modifier species and of the interaction (the mean trophic level of the two interactor species). Here, we calculate trophic level using the unweighted trophic network and the pathway method of Levine (1980). These can then be compared to measure what we term the '*trophic direction*' of the modification. We define this as the trophic height of the interaction minus the trophic level of the modifier. Therefore, positive values imply modifications to interactions higher in the web than the modifier and negative values imply the opposite. The '*trophic span*' of a modification constitutes the mean number of trophic links from the modifying species to each interactor by the shortest route and measures the extent to which a TIM links otherwise disconnected species.

	Modification:	
Metric	·····●	– – –●
Trophic Height of Modifier	3	2
Trophic Height of Interaction	2.5	3.5
Trophic Span	1	2
Trophic Direction	-0.5	+1.5
Modifier Betweenness	0	24.5
Interactor Betweenness	19.5	3.75
Interaction Betweenness	17.5	7.5

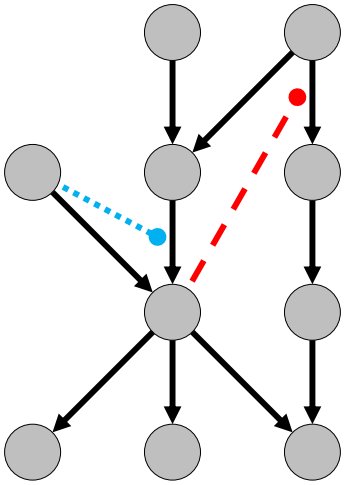


Figure 2.1: Example values of topological metrics for interaction modifications (dashed lines) within a simple trophic network (solid lines).

The *centrality* of the species involved in a TIM can be used to determine the connectivity of the TIM to the wider trophic network. The centrality of a node within a network can be measured by a diversity of algorithms (Newman 2010).

Here we use '*betweenness*', the number of shortest paths between all nodes that pass through a given node. We only consider unweighted trophic links (excluding TIM connectance) when calculating centrality as this information is more widely available. We measure the '*interactor betweenness*' as the mean of the centrality of the two interactors. Lastly, the centrality of the interaction being modified was measured as the '*interaction betweenness*', the number of shortest paths that pass through a given interaction.

Strength of TIMs

Interaction strengths can be simultaneously considered with multiple useful approaches (Laska and Wootton 1998, Berlow *et al.* 2004). This extends to TIMs which can be meaningfully considered from a range of perspectives (Terry *et al.* 2017). We measure the strength of a modification in our linearised equilibrium systems in four distinct ways (Table 1). Here we solely measure strength with respect to the prey species since in our simple model the impact on the predator is very closely related to the impact of prey. In addition, we test the information contained in the density of the modifier species and the size of the underlying trophic interaction as a proxy for interaction modification strength, as measured by the attack rate, a_{ij}, and the biomass flux rate, $a_{ij}B_iB_j$.

Assessment of metrics

The ability of metrics to identify influential TIMs was assessed by testing how well a system containing only a subset of interaction modifications that had been selected using a metric under examination was able to capture the dynamics of the complete system (Figure 2). We assess dynamics in two ways: 1) accuracy in estimating local stability and 2) the ability to determine the direction of response to sustained perturbations.

Metric	Description	General Specification	Calculation
TIM Function Slope	The strength of the relationship between the modifier species density B_k and the interaction rate.	$\frac{\delta}{\delta B_k} a_{ij}$	c_{ijk}
Direct Non-Trophic Effect of TIM	The contribution of an individual TIM to the effect from the modifier to an interactor. Also described as the trait-mediated indirect effect (Abrams 2008, Okuyama and Bolker 2012).	$\mid \mathbf{A}_{ik}^{Full} - \mathbf{A}_{ik}^{c_{ijk}} \mid$	$a_{ij} B_i B_j \lvert c_{ijk} \rvert \frac{1}{B_k^*}$
Impact on Interaction	The change in the direct interaction strength caused by the TIM. This is a measure of instantaneous effect of a TIM.	$\mid \frac{\delta}{\delta B_k} \mathbf{A}_{ij} \mid$	$a_{ij} B_i \lvert c_{ijk} \rvert \frac{1}{B_k^*}$
Impact on Net-Effects between Interactors.	The change in the 'net-effect' between species as the modifier species density changes. Contextualises the role the trophic interaction plays in the overall interaction between species.	$\mid \frac{\delta}{\delta B_k^{\text{mod}}} [\mathbf{A}^{-1}]_{ij} \mid$	Calculated numerically. (Only the density of the modifier term in the TIM function is varied to isolate from those mediated through direct interaction chains)

Table 2.1: Description of the TIM strength metrics used to rank TIMs in the model systems. In each case i,j and k indices denote the prey, predator and modifier species respectively.

Stability

Local asymptotic stability, whether a system will eventually return to its previous equilibrium after a small perturbation, is a widely used dynamic system property and can be determined from the sign of the real part of the largest eigenvalue of a system's community matrix, $\mathfrak{R}\left(\lambda_1^{\mathbf{A}}\right)$. Where this is negative the system can be considered locally stable. With sufficient self-regulation any system can be stabilised. To focus our analysis on the impact of the interaction modifications, rather than the distribution of self-regulation terms (van Altena *et al.* 2016, Barabás *et al.*

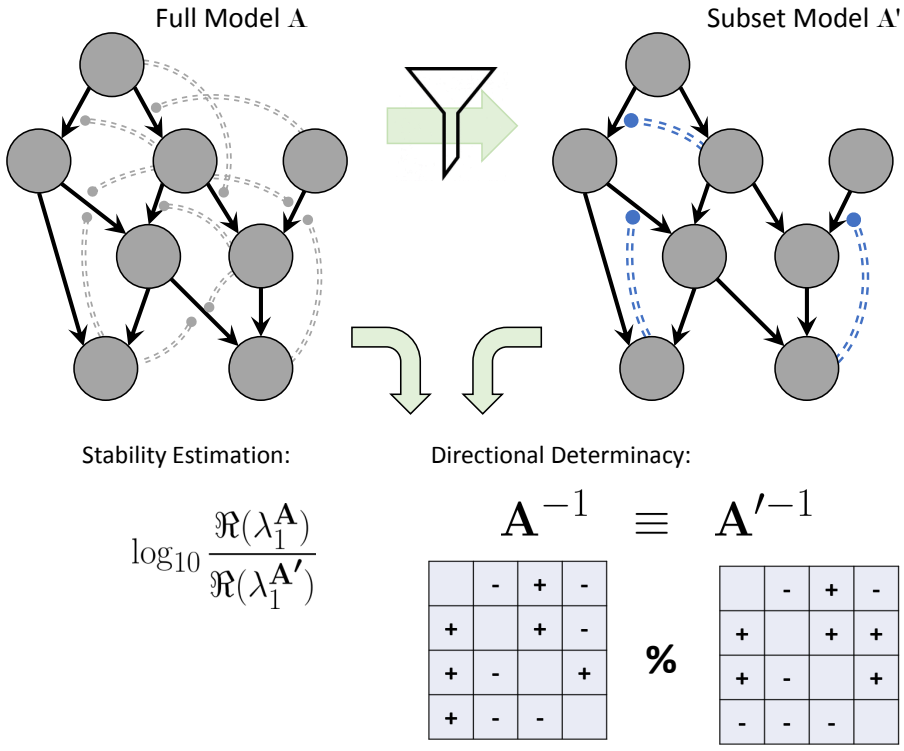


Figure 2.2: Schematic showing overall approach to test methods for identifying interaction modifications that are influential in the dynamics of model ecological communities. The trophic interaction modifications in the full community model are quantified and 20% retained using a particular metric. The capacity for the subset model to represent the dynamics of the null model system are then assessed stability estimation and directional determinacy.

2017), we set each $\mathbf{A}_{ii}$ to 0. In this case, $\Re\left(\lambda_1^{\mathbf{A}}\right)$ is always positive but can be interpreted as a degree of the self-regulation that would be necessary to stabilise the community. For simplicity we will refer to this quantity as 'stability'.

We generated 2000 communities with interaction modifications for each value of biomass density scaling factor g. For each web, the TIM metrics described in the previous section were calculated for each TIM and the 'top' 20% of TIMs were identified. Where there was no obvious expectation about which extreme would be more important, for example 'centrality', both the highest and lowest values were tested independently. A random subset of 20% of TIMs was also generated for each web to establish a baseline to test metrics against. For each web and

each subset of TIMs, the community matrix was recalculated including the trophic interactions and the selected TIMs. We then calculated the absolute difference in $\log(\mathfrak{R}\left(\lambda_1^{\mathbf{A}}\right))$ between the full model and the subset model. The statistical significance of a metric's ability to identify a subset of TIMs that estimate stability differently to a random subset of TIMs was tested with a Wilcoxon signed rank test, paired by the underlying web topology.

Direction of response to perturbation

The negative inverse of a community matrix ($-\mathbf{A}^{-1}$) encapsulates the responses (via all pathways, interaction chains and interaction modifications) of each species to a sustained, small, perturbation to each other species (Bender *et al.* 1984) to generate a 'net-effects matrix'. This relies on the assumption that the perturbation is sufficiently small that any non-linearities in the response are well represented by the linear approximation of the underlying community matrix. While estimates of the exact values of responses would be empirically unfeasible, the sign of the net-effects between species, i.e. whether a change in a particular population will lead to an increase or a decrease in another population is a reasonable objective (Yodzis 1988, Novak *et al.* 2011, Aufderheide *et al.* 2013).

We tested the proportion of pairwise net-effect relationships between species where the sign of the net-effects matrix of the full model matches that of the model containing only a subset of the TIMs. This directional determinacy, also termed 'predictability' (Novak *et al.* 2011, Iles and Novak 2016) therefore ranges from a minimum of approximately 0.5, where the subset model is no better than chance at correctly identifying species responses, to 1 where the subset model is able to perfectly predict the 'true' response. Analytic expressions of the impact on directional determinacy due to the misspecification of $\mathbf{A}$ have recently been derived (Koslicki and Novak 2018). However, since for multiple error terms the expressions become very complex, we directly calculate the effect numerically.

Because local asymptotic stability is a prerequisite for calculating directional determinacy, additional communities were generated and unstable communities

excluded to create 2000 locally stable communities for each of the three values of g and the two approaches to including self-regulation terms. We then followed the same procedure as for local stability to test each metric's ability to identify valuable TIMs. For each web we compared the directional determinacy of a model including the selected subset of interaction modifications to a model including just the trophic interactions.

Results

It was possible to identify the trophic interaction modifications that influenced the system dynamics. In general, those TIMs affecting directional determinacy also affected the local stability of the system. Results for the case of g=0.1 and stronger self-regulation terms on producers are shown in Figure 3. Results for other values of body mass-biomass density scaling and different self-regulation terms (SI 3) were broadly similar except in specific cases discussed below. The variability in changes to directional determinacy was related to the median improvement – where a metric tended to give a larger improvement, there was also a greater chance that including those TIMs would result in a reduced model that was considerably worse than not including any TIMs at all (SI 3).

The strength properties of TIMs were correlated with each other but topological features considerably less so (Figure 4). Interaction flux was still negatively correlated with interaction trophic level when g=0.1. The positive body-mass - density relationship was counteracted by reduced attack rates from higher consumer resource body-mass ratios at higher trophic levels.

In general, those metrics that addressed aspects of the strength of the interaction modification were the most valuable (shown in green in Figure 3) and the very best allowed a near perfect estimation of stability. Metrics based on the centrality of the interaction modifications were the least effective at identifying TIMs, with many not being significantly different to a random draw. Modifications caused by species with a lower biomass density were more valuable than those with high density.

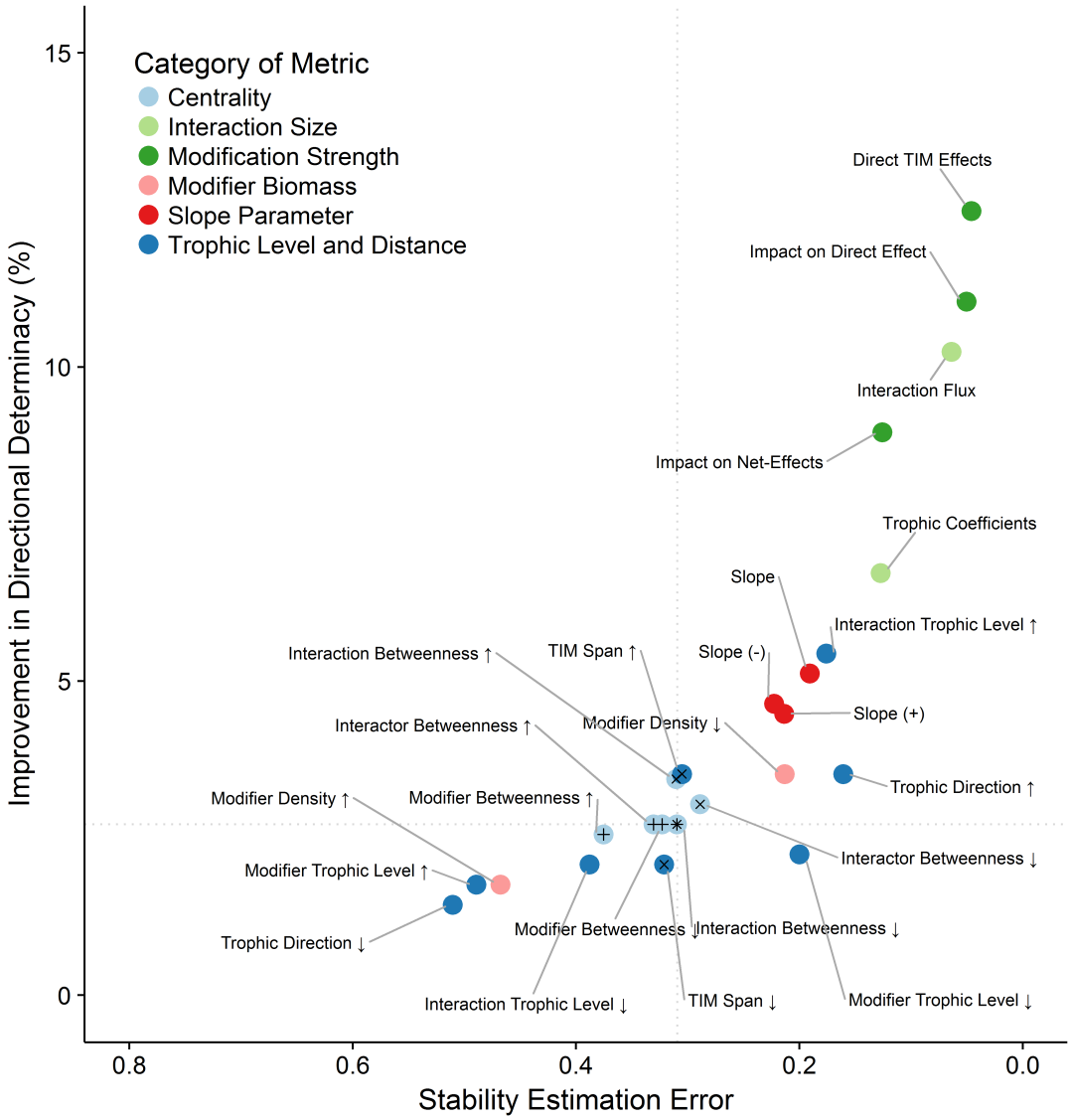


Figure 2.3: Comparison of the capacity of different metrics to identify TIMs that contribute to the dynamics of whole systems. Arrows indicate whether TIMs were selected for inclusion based on high or low values of the given property. Median error in the estimation of the logarithm of the system stability is plotted on the x-axis, median improvement in the percentage of direction of inter-specific net effects correctly estimated on the y-axes. Grey dotted lines show a baseline when TIMs are chosen at random. Those metrics in the top-right quadrant are therefore better than average at identifying TIMs valuable for both types of dynamics, while those in the lower-left quadrant are worse for both. Points marked with symbols were not significantly different to a random draw for the stability (+), the directional determinacy (x) or both (*). Wilcoxon test (n=2000, α = 0.05), paired by underlying network.

Interaction modifications with large slope parameters of either sign were valuable. However, including just the large strengthening (+ c_{ijk}) interaction modifications

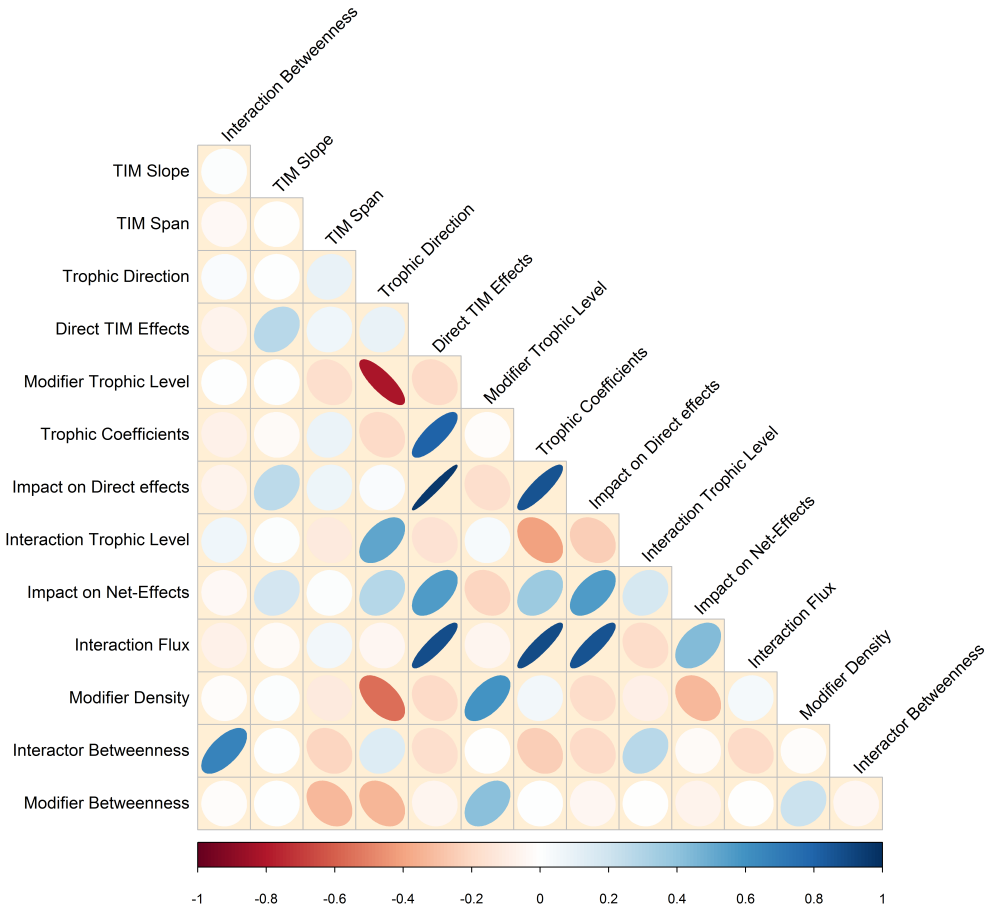


Figure 2.4: Correlation plot showing relationships between the properties of the TIMs in a model food web community ($g = 0.1$, producers higher self-regulation than consumers). Ellipses depict Spearman's rank correlations, blue shapes indicating positive correlations and red negative. Corresponding plots for the other model structures are shown in SI 6.

gave a better estimate of the local stability than the strongly negative interaction modifications. This difference was particularly notable for the g=0.25 case (SI 3). Conversely, selecting interaction modifications for directional determinacy but not for stability.

The influence of trophic height depended on the relationship between trophic level and biomass density (controlled by the g parameter) with modifications of high-trophic level interactions becoming comparatively more important when the webs were more top-heavy. The impact of trophic direction was highly dependent on the distribution of self-regulation terms. Where producers are more

strongly self-regulated than consumers, 'upwards' TIMs are less influential for directional determinacy.

Discussion

We have presented methods to quantify the structure of interaction modifications within a trophic network and shown that it is possible to identify properties of trophic interaction modifications that are particularly influential in the dynamics of model ecosystems. This is informative both on a theoretical level in helping to discern how TIMs affect dynamics, but also is useful from a practical perspective in highlighting which TIMs might be most valuable to study empirically. Our work also highlights areas where empirical information is lacking, in particular the need to understand empirical relationships between trophic and non-trophic interaction strengths.

TIMs introduce a high level of complexity to ecosystem dynamics. It is therefore reassuring to note that relatively simple and easily observable measures, for example trophic interaction biomass flux, are able to identify the TIMs that drive the system dynamics. Similar sets of TIMs were identified as being important in two distinct types of dynamics – response to press perturbations (directional determinacy) and response to pulse perturbations (local stability). By identifying comparatively high-impact TIMs we can make progress despite the present dearth of empirical distributional data. Below we focus our discussion on specific results and their implications, before looking forward to developing this approach in future work.

This study required assumptions regarding the appropriate strength and distribution of TIM values to use. In particular, our results regarding interaction strength are necessarily dependent on the range of the distribution from which the various properties the model are chosen from. If for instance the range of slope parameters was larger compared to the range of biomass densities, the c_{ijk} parameter in our model would have been a more valuable in comparison to the other TIM strength parameters. Empirical distributions of interaction modification strength in a network do not (to our knowledge) yet exist. Meta-analyses of non-trophic effect strength (Bolnick and Preisser 2005, Preisser *et al.* 2005) suggest an approximate

correspondence with trophic interactions. The occasional very strong non-trophic effect at the upper tail of the distribution we used (SI 2) is not necessarily unrealistic as the impact of behavioural effects can in certain circumstances be much faster and stronger than consumptive interactions (Abrams 2001). At the other end of the spectrum, it is necessary to set a threshold where a species' influence on an interaction is considered too weak to include. This decision trades-off the mean strength and the overall connectance of the modification distribution. An additional complication is how interaction modifications combine to influence an interaction (Golubski and Abrams 2011). For example, interaction modifications may act antagonistically to each other, with combined modifications exerting less effect than would be expected from the individual effects. Although in our study this effect is mitigated by our assumption that the trophic interactions are at the post-modification strength this could be significant in more dynamic, non-equilibrium, systems.

The increased impact of low-density modifier species via interaction modifications runs contrary to usual expectations for interaction strength distributions. In our study this results from our assumption of the dependence on relative change in modifier populations (Eq. 2). Hence, a change in the density of a low-density modifier will result in a greater modification than the same absolute change in a more abundant modifier. Whether this is a reasonable assumption is to return to the question of how the strength of TIMs is distributed in natural communities. This effect is opposed by trophic interactions being stronger between high-density populations, leading to opposing effects in mixed-process interaction chains. Consider a case where A consumes B which then modifies an interaction involving C. In our model, if B had a lower density, the A-B trophic interaction would be weaker, but this would be more than outweighed by an increase in the B-C non-trophic effect. Further work will be needed to discern how these processes act in nature, but this result highlights that TIMs can greatly increase the importance of species that might otherwise be neglected or dismissed and may

disrupt assumptions of the structural patterns of interaction strengths in webs based on trophic interactions only.

Interpretation of the value of topological measures is more challenging as a significant part of their effect can be attributed to correlations with strength-based metrics. In this study we considered topology based on trophic interactions only, as these are currently more widely available and better understood. However, interaction modifications themselves are part of the dynamic topology of TIMs and ideally should be considered in relation to each other.

The most valuable topological metric was the 'direction' of the TIM. Those TIMs acting 'up' the network were generally more valuable, although the reduced signal with more negative body mass – density relationships suggests this is due to the relationship between trophic height and density rather than pure topological effects. Nonetheless, strongly self-regulated producers may be more resistant to change and hence modifications deriving from them may well be less influential. This highlights that the variability or sensitivity of a species is of equal importance as the magnitude of the modification when considering likely impact.

Trophic net-effects tend to rapidly decline with the number of trophic links between the interactors (Neutel *et al.* 2002). Where the trophic net-effect is weak, there is a greater potential for a TIM to 'short-circuit' the system and dominate the pairwise net-effect between those species. This can be seen in the value of the TIM span metric for directional determinacy, however the comparatively poor potential suggests that other significant features of TIMs may be able to override this expectation. Although TIMs have the potential to reduce the dynamic breadth (the number of interactions between the most distant species) of food webs, given that it is estimated that the majority of species are no more than two trophic links apart (Williams *et al.* 2002) the extent of this effect may be limited in practice.

The poor indicative potential of TIM span for local stability, shows that the increased connectance that long-range TIMs introduce has little impact on local stability, as simple models may predict (May 1973). The powerful strengthening TIMs (that benefit the consumer to the detriment of the resource) influence the

stability more than weakening TIMs. This is a distinct effect to that caused by mutualism or competitive direct interactions (e.g. Mougi and Kondoh 2012, Coyte *et al.* 2015) since every TIM exerts both a negative and a positive influence. This effect could be driven by at least two mechanisms. Firstly, in our model the assumption of top-down dominated interaction strength imbalance caused by the assimilation term e causes non-trophic effects on prey to be larger than on predators (Eq. 3). This has the result that strengthening TIMs ($c_{ijk}>0$) exert larger negative effects (on prey) than positive effects (on predators). Secondly, there will be a topological effect – strengthening TIMs will lead to consistently positive non-trophic effects on high trophic level species and consistently negative impacts on basal species, which will interact with the underlying tropic interaction distribution.

Outlook

For this study we made a number of assumptions about the form, topology and strength of TIMs to construct a plausible distribution. The lack of empirical data at a community level is a particular challenge, although identifying non-trophic effects at the network level is possible (Pocock *et al.* 2012, Kéfi *et al.* 2015) and shows that networks of pairwise non-trophic interactions have considerable structure (Kéfi *et al.* 2016). Our study emphasises the tight relationship between the underlying trophic network and the consequences of interaction modifications. Isolating an interaction modification from its context, for example in a lab study, will result in the loss of valuable information. The properties of TIMs identified here (Fig. 5) are a first step in building a profile that could be used to identify processes that are more likely to have a considerable influence. Without empirical estimates for the distribution of TIMs it is not yet possible to quantify the potential impact in the manner of Novak *et al.* (2011).

The instances where directional determinacy actually reduced on the inclusion of TIMs (SI 3) shows the challenges in attempting to improve ecological understanding. Our results suggest that there are no easy shortcuts, but that the problem is not intractable. One avenue that will need particular work is the degree of accuracy to

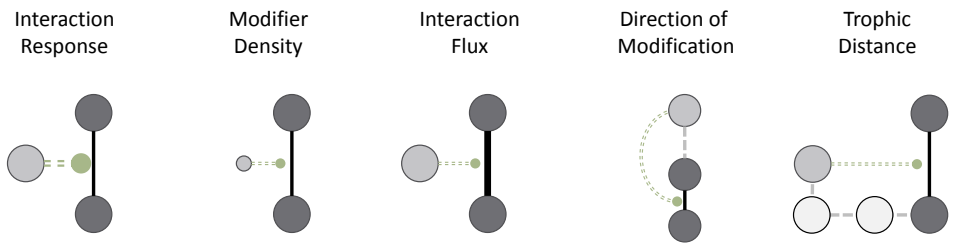


Figure 2.5: Properties of interaction modifications of relevance to determining their impact.

which interaction modifications must be known in order to contribute meaningfully to improving ecological forecasts (Petchey *et al.* 2015). Our assumption that all pairwise interaction strengths are known, and that included TIMs are perfectly quantified, constitutes rather wishful thinking for any system of realistic size. Although for small systems, qualitative analyses (Dambacher *et al.* 2003, Dambacher and Ramos-Jiliberto 2007) can be useful for mapping out the potential responses of systems, for larger systems they can rapidly become indeterminate. Exploratory analyses (SI 7) testing the importance in correctly identifying the slope of the TIM function show that as long as the sign of the modification is correct, choosing either random slopes or a single fixed value for the slope can give improvements of mean directional determinacy of 9.8% and 15%, respectively. Future work should more robustly test alternative approximation approaches, such as 'binning' effects into broad categories, that have been shown to give good results for estimating trophic interaction strengths (Barabás and Allesina 2015).

Equilibrium studies such as ours allow a precise analysis of particular processes in isolation from other sources of variation. However, this approach does not incorporate the full spectrum of impacts TIMs can have in dynamic systems and future work should seek to address this gap. Furthermore, trophic interaction strengths are not purely determined by biotic factors – there is also extensive dependence on the abiotic environment (Wootton and Emmerson 2005, Poisot *et al.* 2015). The balance of the impact of exogenous and endogenous sources of interaction strength variation is unknown. The two processes can interact, with TIMs varying

depending on abiotic conditions (Sentis *et al.* 2017) and interaction modifications allowing species to resist abiotic variability (Bruno *et al.* 2003). The extent to which interaction strength variation will frustrate ecological prediction is unclear. However, at least some of this variation can be accounted for by dependence on other species in the community which, in principle, is quantifiable (Terry *et al.* 2017).

Conclusion

To improve our understanding of ecosystems it will be necessary to incorporate important dynamic processes whether they are consumer-resource links, direct non-trophic effects or interaction modifications (Fontaine *et al.* 2011). This potential complexity poses a daunting challenge but not all interaction modifications are equal. We have shown that considering interaction modifications as distinct entities opens up a range of analyses and that although the underlying mechanisms may be complex, relatively simple heuristics may be useful in identifying significant processes in food webs. Where interaction modifications are suspected, but unquantified, our work provides guidance to determine where further research could bring the greatest improvement in understanding. Fully incorporating interaction modifications into the fold of ecosystem ecology will be a long, but rewarding, endeavour. We hope that our work will encourage further studies, both experimental and theoretical, to understand these critical components of ecosystem dynamics.

Data Statement

All code and raw simulation outputs are available on the Open Science Framework: https://osf.io/49jgr/

3

Trophic interaction modifications disrupt the structure and stability of ecological communities

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Pre-print: https://doi.org/10.1101/345280

Abstract

Understanding the complexity of ecological communities is a long-standing challenge. Resolutions to this problem have largely focussed on trophic interactions, despite the acknowledged importance of non-trophic effects. Trophic interaction modifications, where a consumer-resource interaction is influenced by an additional species, are a major cause of non-trophic effects that have been demonstrated to exert strong influences on the dynamics of natural systems. They offer the potential to use information about trophic interactions to understand the structure and topology of non-trophic effects. Here we examine the impact of interaction modifications, introduced under a range of distributional assumptions, on artificial and empirical trophic networks. We show that local stability and reactivity is critically dependent on the inter-relationship between the trophic and non-trophic interactions. Depending on their distribution, interaction modifications can generate significant additional structure to community interactions making analyses of the stability of ecological systems based solely on trophic interactions unreliable.

Introduction

Understanding how large and diverse ecosystems persist is a core challenge in ecology. Theoretical expectations that large random complex systems are unlikely to be locally stable (May 1972), indicate that the interactions within ecological communities are structured in important ways (Montoya *et al.* 2006). While network analyses need not be inherently specific to a particular class of interaction (May 1972, Allesina and Tang 2012), trophic interactions are commonly focussed upon because of their role in determining energy flux and the comparatively high level of empirical understanding. A growing body of work has demonstrated features of trophic networks that can stabilise communities - including the distribution of weak links (McCann *et al.* 1998, Neutel *et al.* 2002), pairwise correlations (Tang *et al.* 2014), modularity (Grilli *et al.* 2016), row structure (Jacquet *et al.* 2016) and trophic level coherence (Johnson and Jones 2017). However, ecological communities contain complex networks of interactions beyond trophic relationships (Ings *et al.* 2009), and there is an emerging appreciation of the value in studying the full spectrum of interaction types (Olff *et al.* 2009, Fontaine *et al.* 2011, Kéfi *et al.* 2012, Mougi and Kondoh 2012, Coyte *et al.* 2015, Pilosof *et al.* 2017, García-Callejas *et al.* 2018).

The ubiquity and diversity of non-trophic interactions poses a considerable problem for ecologists as organising features appear few and far between. However, networks of non-trophic effects do show considerable non-random structure (Kéfi *et al.* 2016). A notable fraction of non-trophic effects are caused by interaction modifications (Kéfi *et al.* 2012), where a pairwise interaction is dependent on a third species (Wootton 1994). These are pervasive within ecological networks (Werner and Peacor 2003) and capable of exerting impacts as strong as direct trophic interactions (Preisser *et al.* 2005).

Classic examples of interaction modifications include shifts in foraging patterns in response to the threat of predators (Suraci *et al.* 2016) and species providing associational resistance to predation (Barbosa *et al.* 2009), but the concept also encompasses any biotic influences on foraging patterns such as the availability of alternative prey (Abrams 2010a) and many ecosystem engineering effects (Sanders

et al. 2014). This additional source of interactions and dynamic connectance introduces emergent relationships between species that may not otherwise directly interact, potentially greatly increasing the dynamic connectance of the system (Yodzis 2000). The incorporation of interaction modification effects has been empirically demonstrated to be key to understanding the dynamics of ecological systems (van Veen *et al.* 2005, Mayfield and Stouffer 2017, Donohue *et al.* 2017).

Although the distribution of interaction modifications at the network level is essentially unknown, it is reasonable to expect that they will be structured, both internally and with respect to the underlying interactions being modified (Golubski *et al.* 2016). This relationship offers an opportunity to build upon the understanding of the structure of trophic networks (Dunne and Pascual 2006) to inform the likely distribution and consequences of non-trophic effects caused by trophic interaction modifications. While both trophic and non-trophic interactions can be subject to modifications (Kéfi *et al.* 2012), here we focus on trophic interaction modifications to start to move beyond random distributions of non-trophic effects (Mougi and Kondoh 2012, Coyte *et al.* 2015) and higher-order interactions (Wilson 1992, Bairey *et al.* 2016).

Here, we examine the impact non-trophic effects induced by trophic interaction modifications can have on the equilibrium dynamics of simple models of the interactions between species in artificial and empirical networks. We combine interaction matrices representing trophic networks with non-trophic effects generated with a variety of distinct interaction modification distribution models. We examine the properties of the resultant interaction matrices and test the impact on local stability and reactivity to show that the impact of interaction modifications depends crucially on their distribution and relationship with the underlying trophic network.

Methods

Interaction modifications (Wootton 1994) are higher-order processes that induce non-trophic effects from the modifier species onto a pair of interactors. In this paper we distinguish between the underlying trophic interaction modification (TIM) process

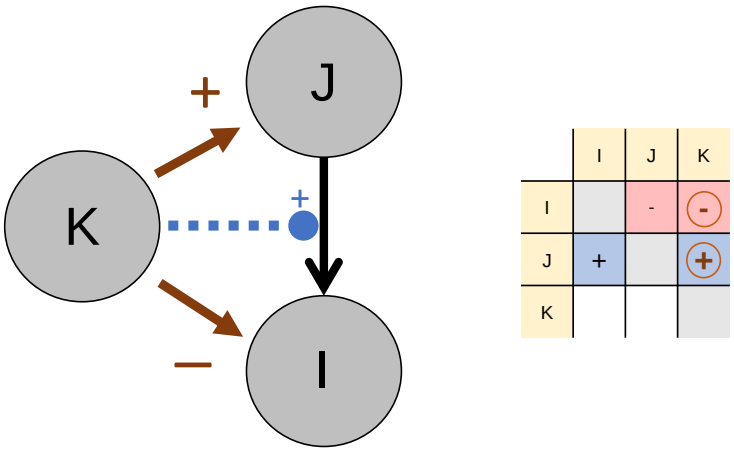


Figure 3.1: Schematic representation of the relationship between a trophic interaction modification (TIM, blue dashed line), consequent non-trophic effects (NTE, brown solid lines) and resultant community matrix where the NTEs have been circled. An interaction modification results in two non-trophic effects from the modifier. Here a modifier species (K) acts to strengthen a trophic interaction between consumer J on resource I. This results in a positive NTE on J and a negative NTE on I. Each column of the community matrix shows the effect of that species on the species in each row.

and the resultant (pairwise) non-trophic trophic effects (NTEs), also termed trait-mediated indirect interactions (Ohgushi *et al.* 2012). This distinction (Figure 1) between process and consequence aids the analysis of these complex processes (Terry *et al.* 2017).

Communities as interaction matrices

We represent the complete set of interactions in a system as a Jacobian matrix **A**, also termed a community matrix (Novak *et al.* 2016), which is assumed to be derived from a set of populations each at a feasible equilibrium. Each element of **A**, a_{ij}, represents the instantaneous effect of a change in the population of species j on the population of species i. The community matrix is considered to be based on a linearisation of more complex processes that govern the relationships between the species and as such the description of the interactions is only strictly applicable close to the original non-trivial equilibrium. We determine **A** to be constructed from the combination of two matrices specifying the trophic (**B**) and

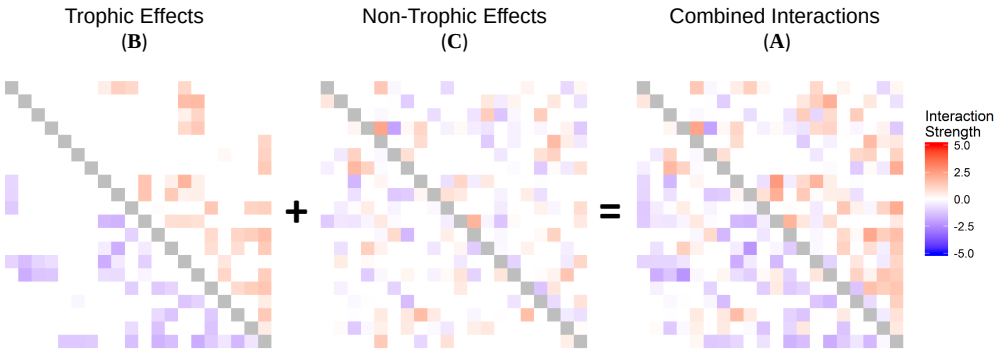


Figure 3.2: Illustration of construction of interaction matrices. At an assumed equilibrium, a combined interaction matrix (**A**) can be split into the impact of trophic (**B**) and non-trophic effects (**C**). The species are arranged approximately in trophic height order, with basal species top/left and top predators at the bottom/right. The underlying trophic network depicted was generated with the niche model (S =20, C=0.2), parameterised with a bivariate normal distribution $\mathcal{N}(\mu_x = -1, \mu_y = 1, sd_x = 0.5, sd_y = 0.5, \rho = -0.8)$. Intra-specific interactions were fixed at zero and shown in grey.

non-trophic (**C**) interactions present in the community (Figure 2). For all matrices, we only consider inter-specific interactions, all intra-specific diagonal terms (a_{ii}) were set to zero (see below).

Generating trophic networks

We determined the trophic topology of the artificial communities using the niche model (Williams and Martinez 2000), a network generating algorithm that has been shown to reproduce many of the features of real food webs (Williams and Martinez 2008). We generated 100 networks each with 60 species and target connectance of 0.2. We parameterised these interactions with draws from a bivariate normal distribution $\mathcal{N}(\mu_x = -1, \mu_y = 1, sd_x = 0.5, sd_y = 0.5, \rho = -0.8)$ to create each trophic interaction matrix **B**, following Allesina *et al.* (2015). This specification maintains a mean interaction value of 0 and an overall symmetry in impacts between consumer and resource. This simplifies analysis but is known to be unrealistic (Wootton and Emmerson 2005). We therefore repeated the analysis with increased consumer effects on resources (μ_x = -5 & -10, SI 3). Since the draws are unbounded

a small fraction of interactions had the 'wrong' sign combination for an exploitative interaction. As exploitative interactions still made up the overwhelming bulk of interactions, we did not remove these and for convenience we will refer to these underlying networks as trophic networks.

Incorporating interaction modifications

Trophic interaction modifications are 'higher-order interactions' that act through at least three species (Terry *et al.* 2017). However, the short-term consequences of the interaction modification can be linearised to identify the effect of the modifier on the consumer and the resource (Wilson 1992, Bairey *et al.* 2016) at the system state under consideration (Figure 1). These non-trophic effects (NTEs) can be used to construct a matrix, $\mathbf{C}$, of pairwise effects caused by the TIMs. In our representation the value of the original pairwise trophic interaction is left unchanged, i.e. it is assumed that the trophic interaction strengths in $\mathbf{B}$ already incorporate the consequence of the equilibrium level of the modifier species.

Based upon the trophic networks, NTE matrices were generated using a set of 16 models. These varied in topology, strength distribution and translation from TIM to NTEs, discussed below. As a baseline TIM model, each possible interaction modification (combination of consumer-resource pair and third modifier species) was equally likely to be present. Each TIM was assigned an effect parameter, c_{ijk}, representing the size and direction of the modification by species k of the consumption of resource i by consumer j. These were specified such that the mean magnitude of individual NTEs (α) incorporated into a community is 0.5, by setting the standard deviation of the normal distribution to $\alpha\sqrt{\pi}/\sqrt{2}$, in line with results from meta-analysis that suggest an approximate correspondence between the strength of trophic and non-trophic interactions (Preisser *et al.* 2005). A positive c_{ijk} indicates a facilitating modification where an increase in the modifying species would increase the strength of the interaction. It follows that this would lead to a positive effect of the modifier on the consumer and a negative effect of the modifier on the resource. A negative c_{ijk} would cause the reverse, an interfering modification.

The c_{ijk} values determined the NTEs of the modifier on the two interactors ($\mathbf{C}_{jk} = c_{ijk}$, $\mathbf{C}_{ik} = -c_{ijk}$) and were used to construct a TIM effect matrix $\mathbf{C}$.

We only considered TIMs where species modified the interaction between two other species - we did not allow species to modify their own interactions. Multiple NTE from one species to another were combined additively. TIMs were introduced at a TIM density (defined as the expected number of TIMs in the network per species, ω) of either 0, 1, 5, 10, 20, 30, 40 and 50. For a given trophic network, we identified each potential TIM that could exist following a particular distribution model, and assigned each potential TIM a probability of existing equal to $\frac{\omega\ S}{\kappa}$, where κ is the total number of potential TIMs (i.e. combinations of consumer-resource and third species) and S the number of species. Note that TIM density as defined here is distinct to both 'TIM connectance' (the fraction of possible TIMs that are observed, which is dependent on the trophic connectance) and to non-trophic connectance (the resultant fraction of non-zero elements of the consequent TIM effect matrix $\mathbf{C}$, which is dependent on the distribution and overlap of the TIMs).

Different TIM models

Fourteen variations of the baseline TIM distributional model were examined, illustrated in Figure 3 with an example NTE matrix and a cartoon of the model's distinguishing features. In addition, we also tested an NTE distribution model where there was no underlying interaction modification structure. There, NTEs were independently randomly distributed with their strengths drawn from a normal distribution. The mean magnitude of individual NTEs was kept constant across all models. In the results and discussion the key distinguishing feature is used to identify each model rather than a letter for clarity. The properties of empirical distributions of interaction modifications are unknown, and likely to significantly differ between communities. This set of models is therefore an attempt to examine the range of properties that such networks may have in order to identify how interaction modifications may introduce additional significant structure to ecological networks.

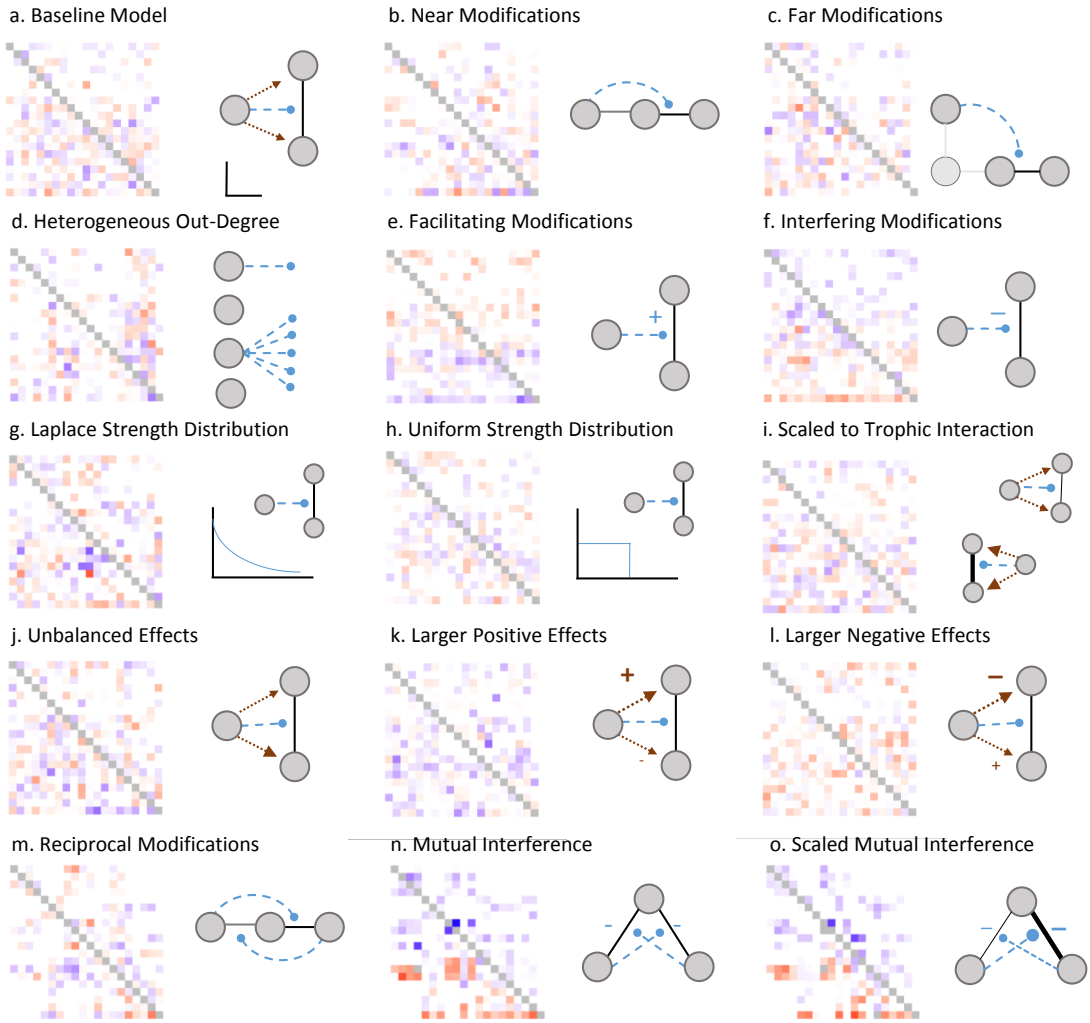


Figure 3.3: Illustration of the TIMs distribution models used in this study with representative non-trophic effect matrices. Cartoons illustrate the distinctive properties of each model compared to the baseline model (a) that used introduced interaction modifications such that each potential modification was equally and independently likely to occur, where the strength of the resultant non-trophic effects were normally distributed and equal on both interactors. See main text and Table S1 for a description of each model.

All TIM models included a dependence on the underlying trophic network, but this interaction modification topology was varied in several of the models. Two models introduced a simple dependence on the trophic distance between the modifier species and the trophic interactors models, testing the effect of interaction localisation within networks. Model b) required that the modifier was trophically connected to at least one of the interactors, while model c) excluded such cases. Model d) tested the effect of certain species exerting a disproportionate number of

modifications, representing topologically the impact of certain 'ecological engineer' species exerting a dominant effect on the interaction within a network. This was carried out by assigning each species an individual probability drawn from a beta-distribution of being the modifier of each generated interaction modification, thereby generating a more greatly heterogeneous TIM out-degree distribution.

The distribution of TIM strength (the c_{ijk} parameter in our framework) were varied in two distinct ways. Firstly, the sign of the modification was varied, introducing either exclusively facilitating (model e) or interfering (model f) TIMs. Note that the balance between individual resultant positive and negative NTEs remained constant. Secondly, distributions with different variance of TIM strength were tested. Model g) used a leptokurtic ('fat-tailed') Laplace distribution such that there was a greater number of high strength modifications, while maintaining the same mean magnitude. By contrast, model h) used a uniform distribution for c_{ijk}.

Modifications of stronger trophic interactions are likely to have a greater overall impact. To examine this effect, model i) scaled the strength of the NTEs to the mean strength of the trophic interaction being modified. For this, each c_{ijk} parameter was drawn from a uniform distribution determined by the relevant elements of the trophic interaction matrix, $\mathcal{U}(-\gamma, \gamma)$, where $\gamma = \frac{2\alpha\,(|a_{ij}|+|a_{ji}|)}{2\mathbb{E}(a_{ij\ \in\ Predation})}$. Here the denominator term maintains the overall mean value of the non-trophic effects as half that of the trophic interactions.

The baseline model assumes that each interaction modification induces equally strong positive and negative NTEs, but the balance is unlikely to be equal. In model k) resultant positive NTEs were set at three times the strength of negative NTEs, while in model l) the negative NTEs were three times larger. In model j) whether the positive or negative NTE was larger was randomised to separately test for unbalanced effects on species pairs.

A final set of three models introduced internal structure to interaction modifications. Model m) introduced TIMs only in tightly reciprocal pairs to represent tight clustering of interaction modifications within particular subgroups of species. In this model, sets of three trophically linked species include two reciprocal modifications

- a species that modifies an interaction between species x and species y, would in turn have its interaction with x modified by y.

Model n) represents the specific but widespread case of interaction modifications caused by foraging choices between two resources, where each resource reduces the consumption of the other by the shared consumer. This 'mutual interference' model therefore includes properties of trophic topology (only trophically nearby modifications are included), sign (only interfering modifications), and internal structure (TIMs are distributed in pairs). Model o) introduces an additional constraint that the size of the NTEs are limited by the size of the trophic interaction being modified, preventing the presence of the additional resource causing a net negative effect on the consumer. This was modelled by drawing c_{ijk} values from a uniform distribution bounded by the corresponding positive trophic term: $\mathcal{U}(-a_{jk},\ 0)$.

Properties of interaction matrices

We applied each of the 16 distribution models (including the unstructured NTE model) at each TIM density across each of the 100 underlying trophic networks for a total set of 11 200 communities. For each community we calculated the following structural properties of the resultant interaction matrices: 1) mean interaction strength (μ) of $\mathbf{A}$, 2) connectance (fraction non-zero entries) of $\mathbf{A}$ and $\mathbf{C}$, 3) variance (V) of the off-diagonal elements of $\mathbf{A}$ and of $\mathbf{C}$, 4) degree heterogeneity of $\mathbf{A}$ as the variance of the normalised in and out-degree distribution, 5) correlation (ρ) of the pairwise elements of $\mathbf{A}$:, $\frac{\mathbb{E}(a_{ij}a_{ji})-\mu^2}{V}$, $(a_{ij}, a_{ji})_{i\neq j}$, 6) covariance between $\mathbf{B}$ and $\mathbf{C}$, 7) row structure ζ_{row} as the variance in mean interaction magnitude across rows $Var(\frac{\sum_j|a_{ij}|}{S})$ and likewise: 8) column structure ζ_{col}, $Var(\frac{\sum_i|a_{ij}|}{S})$. We compared the mean value of each of the above structural properties across the 100 trophic networks for each of the TIM distribution models to the baseline TIM model at a representative TIM density of 10 using a linear model.

We calculated the local asymptotic stability and the reactivity for each community. Local asymptotic stability is determined by the sign of the real part of the leading (dominant) eigenvalue of $\mathbf{A}$, $\mathfrak{R}\left(\lambda_1^{\mathbf{A}}\right)$, under the assumption that the

community is at an equilibrium. If negative, the system will eventually return to the original equilibrium after a small perturbation and is considered locally stable. The diagonal elements of $\mathbf{A}$ specify the self-regulation of each species. With sufficient self-regulation any community can be stabilised. Although the distribution of self-regulation effects can have important consequences (Barabás *et al.* 2017) we follow previous work (Allesina *et al.* 2015, Jacquet *et al.* 2016) and set all diagonal elements of $\mathbf{A}$ to zero to focus on the impact of the inter-specific interactions. Without self-regulation, $\mathfrak{R}\left(\lambda_1^{\mathbf{A}}\right)$ will always be positive but can be interpreted as how far a system is from stability, i.e. how much self-regulation would be necessary to stabilise the system. Hence, although local stability is a binary property, we use 'less stable' to refer to a system farther from stability (a larger $\mathfrak{R}\left(\lambda_1^{\mathbf{A}}\right)$).

The immediate response of a system to perturbation is described by its reactivity, the maximum instantaneous amplification of a small perturbation (Neubert and Caswell 1997, Tang and Allesina 2014). This is computed as the leading eigenvalue of the Hermitian part of the community matrix: $\lambda_1^{\mathbf{H}}$, $\mathbf{H} = \frac{\mathbf{A}+\mathbf{A}^\intercal}{2}$. Since $\mathbf{H}$ is symmetric, its eigenvalues are real.

To assess the extent to which the communities were non-randomly structured we tested the performance of two analytic criteria for local stability derived from generalisations of the circular law of random matrix theory (May 1972, Tang *et al.* 2014, Allesina and Tang 2015). We refer to these as the May criterion: $max((S-1)\,\mu, \sqrt{SV}\,-\mu)$ and the Tang *et al.* criterion: $max((S-1)\,\mu, \sqrt{SV}(1-\rho)\,-\mu)$. Here, S is the number of species (the size of the matrix), V is the variance in interaction strength, μ is the mean interaction strength and ρ is the pairwise correlation between interaction terms, $\frac{\mathbb{E}(a_{ij}a_{ji})-\mu^2}{V}$. The first term of each criteria specifies the eigenvalue derived from the expected row-sum (Allesina and Tang 2012). In most trophic networks (where $\mu \ll 0$), this term is usually the smaller and can be safely ignored, but this is not necessarily true with the addition of non-trophic effects. The second term estimates the radius of the ellipse containing the eigenvalues along the real axis, and hence the likely position of the right-most (dominant) eigenvalue, under

the assumptions of random matrix theory: that the matrix is large and the entries are independent and identically distributed (Tao 2012, Allesina and Tang 2015).

Empirical trophic networks

The stability analysis was repeated for the five largest empirical trophic networks in the set compiled by Jacquet *et al.* (2016). These are models of the trophic interactions in marine fisheries that had been parameterised by the EcoPath modelling approach (Christensen and Pauly 1992) and converted to Jacobian matrices following the method of de Ruiter *et al.* (1995). These networks were: Chesapeake Bay (n = 41, links = 167, Christensen *et al.* 2009), Mid Atlantic Bight (n = 51, links = 515, Okey and Pugliese 2001), Moorea Barrier Reef (n = 39, links = 267, Arias-González *et al.* 1997), mid-1990s Newfoundland Grand Banks (n = 48, links = 525, Heymans and Pitcher 2002) and Tampa Bay (n = 48, links = 340, Walters *et al.* 2005).

Interaction modifications were introduced at densities of 1, 5, 10, 20, 30 and 40 TIMs per species with 100 replicates of each TIM distribution model at each density for each of the trophic networks for a total set of 48 000 communities. The mean strength of the interaction modifications (α) introduced to each trophic network was set at half the mean strength of the positive trophic interactions (range 0.017-0.18) to be comparable with the artificial networks.

Results and Discussion

In the artificial networks, as the density of TIMs included in the model was increased, local stability always decreased while reactivity always increased (Figure 4a, b). Within this overall pattern, a number of TIM distributions led to markedly different responses, discussed below. Although the remainder of the TIM models had impacts on stability that were not meaningfully different to random NTEs, there was a small but discernible split in their reactivity response (Figure S1b). Models that led to NTEs being focussed, clumped or unbalanced (Larger Negative NTEs, Laplace strength distribution, Nearby TIMs, Unbalanced NTEs, Heterogeneous out-degree

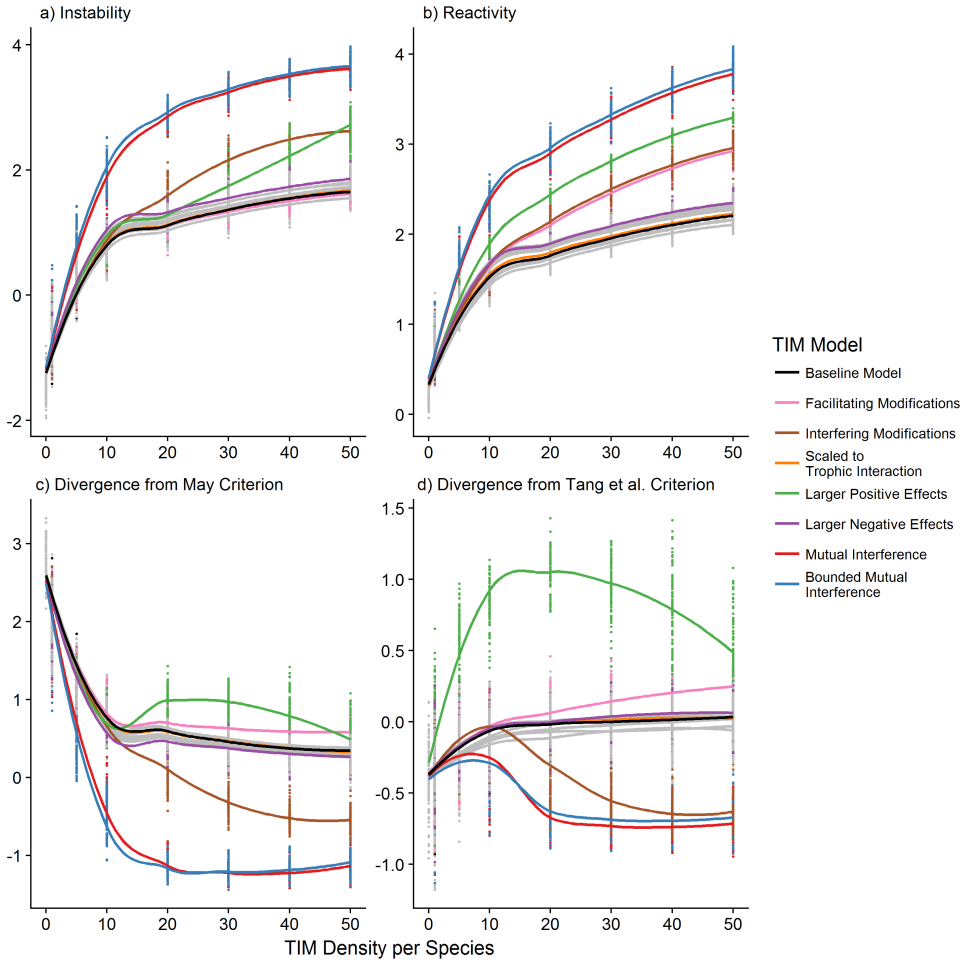


Figure 3.4: Effect of increasing density of TIMs on (a) instability $log\left(\Re\left(\lambda_1^{\mathbf{A}}\right)\right)$, the degree of self-regulation necessary for local asymptotic stability, (b) system reactivity $log(\lambda_1^{\mathbf{H}})$, (c) the log-ratio of the May stability criterion and the observed stability and (d) the log-ratio of the Tang *et al.* stability criterion and the observed stability. TIM distribution models with distinctive responses are highlighted, the remainder are coloured grey and are plotted in Figure S1. Loess fitted lines have been added to highlight differences.

and Reciprocal modifications models) led to a higher reactivity than those that had a more even effect distribution (Baseline, Scaled, Random NTE, Far TIMs, Uniform strength distribution).

The two mutual interference models, representing cases where two resources that share a consumer both negatively affect the consumption of the other (Figure 3.n-o), had the greatest impact on stability and reactivity. At higher levels of TIM density, interfering modifications (which weaken a trophic interaction and are beneficial

for the resource and detrimental for the consumer, at least in the short term, Figure 3.f) caused greater instability and reactivity than other models. Facilitating modifications (Figure 3.e) did not cause a distinct impact on stability, but the impact on reactivity closely matched the interfering modification distribution. The distribution with larger positive NTEs (Figure 3.k) also caused distinct effects, reducing stability at high TIM densities but increasing reactivity faster than baseline models at all TIM densities. Results for further analyses where trophic interactions negatively affected resources more than consumers benefitted followed broadly the same pattern, with the exception that the model with larger positive NTEs had reduced impact as the overall mean interaction strength remained negative (Figure S2 & S3).

Many of the TIM distributions we tested showed a reduced divergence of the true stability from that estimated by the stability criteria of both May and Tang *et al.* (Figure 4c and 4d). This suggests that the TIMs are moving the systems closer to fulfilling the assumptions of random matrix theory under which the criteria are derived, namely that individual interactions are independently and identically distributed (Tao 2012, Allesina and Tang 2015), despite the observable structure being introduced (S.I. Table S2). However, the same TIM models that significantly impacted stability, increase the divergence between the true stability of a system and that estimated by either stability criteria, showing that the TIMs are having consequences which are not captured by the mean, variance and correlation of the matrix elements. All three interference TIM models led to communities that were more stable than expected by the criteria while larger positive NTEs and facilitating TIMs were less stable. Simple, but plausible, distributions of TIMs can therefore be seen to push communities either closer or further (in either direction) from expectations based on the study of random matrices (James *et al.* 2015) than may be expected from analyses of trophic interactions alone.

The structural feature of the resultant matrices that can best explain stability across the set of communities was ρ, the correlation between pairwise elements of the overall interaction matrix $\mathbf{A}$, with an r^2 of 0.884 over all the generated

communities (Figure S4). This can also be observed in the marked superiority of the Tang *et al.* criterion (which includes ρ) over the May criterion (Figure 4c-d), although pairwise correlation was a less good predictor of stability at weak (near zero) levels of correlation (Figure S4a).

Mutual Interference TIMs

The mutual interference model of TIMs is strongly destabilising, despite the lower variance in overall interaction strength (since negative non-trophic interactions overlap with positive trophic interaction terms), which would normally be expected to increase stability (May 1972). This effect is driven largely by emergent pairwise mutualism, long-recognised as destabilising for interaction matrices (May 1973). The NTEs induced by these TIMs are very efficient at breaking down the negative correlation between pairwise elements (Figure S4b), inducing mutualistic effects between resources that share a consumer. However, the maintained divergence from the Tang *et al.* criteria, which includes pairwise correlation, suggests additional higher-level structural contributions.

The mutual interference models result in a high variance in the elements of the NTE matrix $\mathbf{C}$ since they tend to focus negative and positive NTEs on to distinct groups of species (the high-level consumers and low-level resources). However, since in this model resources exert negative NTEs upon their consumers, matrices $\mathbf{B}$ and $\mathbf{C}$ have a low covariance, and the resultant variance of $\mathbf{A}$ is lower than that derived from other NTE distributions. The importance of the sign structure of interference can also be seen in the comparative lack of distinction of the tightly reciprocal interaction modification distribution (Fig 3m) compared to random NTE distributions - it is the specific sign patterning of the links that drives the change to the dynamics, not the topological clustering of the modifications.

Reciprocal negative effects between consumers can be generated by a range of mechanisms, including predator satiation (Jeschke *et al.* 2004), adaptive foraging (Abrams 2010b) and associational defence (Barbosa *et al.* 2009). These effects are widespread (Bruno *et al.* 2003) and are regularly included in general models

of population dynamics (Delmas *et al.* 2017) through multi-species functional responses (Koen-Alonso 2007), yet the resultant dynamic links are rarely considered in network based analyses. The divergence with conclusions drawn from small community modules, where switching is generally considered stabilising (Murdoch and Oaten 1975, May 1977, Valdovinos *et al.* 2010), reinforces the need to consider dynamics across scales and mechanisms.

Sign Effects of TIMs

Interfering TIMs, which are beneficial for resources and detrimental for consumers, have a strongly destabilising effect at high TIM densities. The interfering TIM model differs from the facilitating TIM model only in the sign patterning of the NTEs, yet it has greatly different effects on stability because of the relationship with the underlying trophic interactions. Under these distributions, species at either end of food chains are only susceptible to one sign of NTE, resulting in the banded interaction matrix sign pattern observable in Figure 3e and 3f. Since there are distinct patterns in the underlying trophic interaction distributions (Figure 2) the covariance between matrices $\mathbf{B}$ and $\mathbf{C}$ is higher for facilitating modifications than interfering (Table S2). Hence, a large number of interfering interaction modifications tends to lead to weaker overall pairwise exploitative relationships, despite our model keeping underlying trophic interaction strength fixed. This reduces the variance and pairwise correlation, ρ, of $\mathbf{A}$ faster than randomly signed TIMs (e.g. with a TIM density of 10, ρ = -0.55 compared to -0.61, Table S2). Conversely, facilitating modifications break down the pairwise correlation slightly slower (ρ = -0.62, at TIM density of 10) than random interactions.

Both facilitating and interfering TIM distributions had similar effects on reactivity (Figure 4b). Reactivity (Neubert and Caswell 1997, Tang and Allesina 2014) is dependent on the eigenvalues of $\frac{\mathbf{A}+\mathbf{A}^\intercal}{2}$, effectively a matrix composed of mean pairwise interaction strengths. Both facilitating and interfering TIM distributions result in strong row patterning of this matrix. In biological terms, certain species at either end of food chains accrue consistently stronger interactions,

generating reactivity. While NTEs from TIMs are not directly reciprocal, if either interfering or facilitating modifications are more common, consistent patterns can develop across trophic levels.

In the case where positive NTEs were larger than negative NTEs, changes in stability were driven by the increasingly positive mean interaction strength. This is highlighted by the stability criterion estimate being determined by the expected row sum component, $(S-1)\,\mu$, of the criterion for all but cases with the fewest TIMs. There was no particular impact of the imbalance itself – both the unbalanced NTE model and the model where negative NTEs were consistently larger were not notably different from the random NTE case.

At present, the empirical balance between facilitating and interfering modifications and their distribution throughout ecological communities is effectively unknown, as is the balance between resultant positive and negative consequences for interactors. While the all or nothing cases discussed here represent extreme cases, they show that this data will be essential in determining the impact of non-trophic effects on dynamics.

TIMs and Row Structuring

It has recently been suggested that row-structuring (where the rows of interaction matrices have markedly different means) is a significant contributor to the stability of empirical networks (Jacquet *et al.* 2016), although the effects may be greater on the rate of return to equilibrium than the sign of the eigenvalue (Gibbs *et al.* 2017). Row structuring in trophic networks is a consequence of the consistent dependence of population level interaction strength on interactor density. TIMs may cause row and column structuring by two distinct mechanisms. Firstly, dominant species that take part in strong interactions may be expected to be the receiver of strong NTEs caused by interaction modifications – even a small change in a large interaction could be expected to have a large overall effect on the flow of energy through a community as a whole. Secondly, species that induce a disproportionate number of interaction modifications (ecological engineers (Jones *et al.* 1994, Sanders *et al.*

2014)) have the potential to introduce considerable column-structuring effects. Such ecological engineers causing a large number of interaction modifications may not necessarily be those involved in the strongest trophic interactions. NTEs exerted by such species may serve to break down or replace existing column structure. However, our results suggest that high variation in the number of TIMs each species exerts (out-degree heterogeneity, Figure 3d), representing such a scenario, does not affect stability differently to random NTEs in the artificial trophic networks.

Empirical Trophic Networks

When we repeated our analysis for five empirical marine fishery trophic networks in the set compiled by Jacquet *et al.* (2016) we found distinct results (Figure 5). In contrast to the artificial networks, models where NTEs scaled with the underlying trophic interactions had by far the most significant effects on dynamics of the empirical networks. This occurred despite the mean magnitude of individual NTEs being kept constant between methods of introducing TIMs. In 4 out of 5 cases mutual interference led to more instability, although in the one case (the 'Newfoundland' network) the effect was opposite – the unscaled mutual interference model was stabilising. In another case (the 'Mid Atlantic Bight' network), many of the TIM models led to a small increase in stability, with the largest effect from facilitating modifications.

The empirical networks studied here differ significantly from randomly generated networks (see Jacquet *et al.* (2016) for a full discussion). They include both significant row-structuring and an approximately log-normal interaction trophic strength distribution. A minority of very strong, mostly negative, interactions represent large transfers of biomass between dominant species in the community (SI 5), resulting in a highly leptokurtic distribution of trophic interaction strengths and a very low correlation coefficient (range ρ = -0.014:-0.001). In such a case, unless the TIMs are scaled with the underlying trophic interactions, most interaction modification distributions in our test set effectively only add noise. Consequently, the introduction of TIMs hardly changed the overall pairwise correlation - the

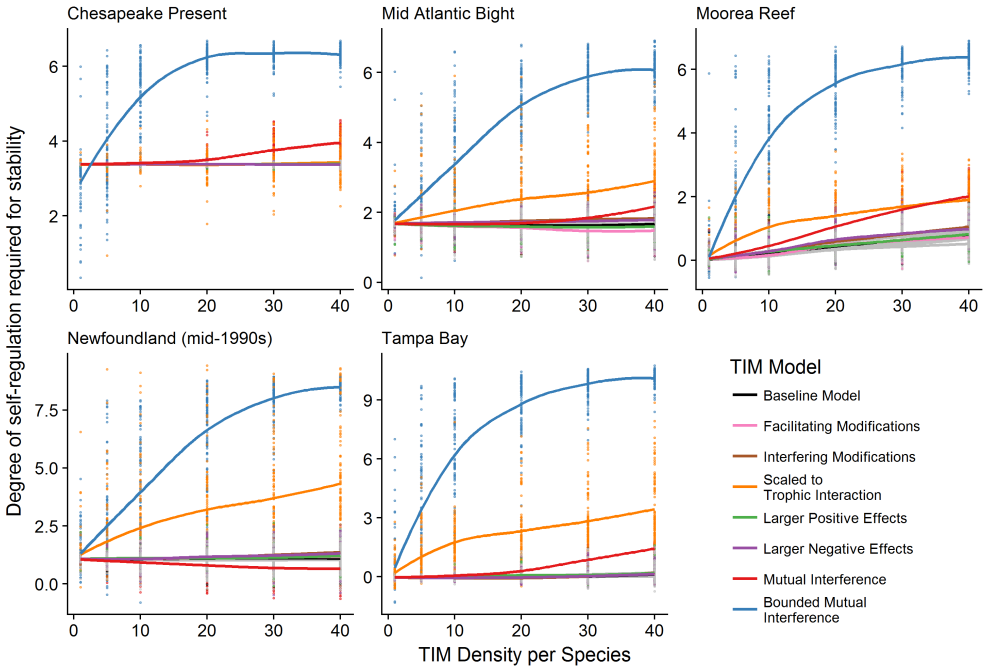


Figure 3.5: Stability responses of five empirically parameterised food webs to increasing density of TIMs. TIM distribution models with distinctive responses are highlighted, the remainder are coloured grey and are plotted in Figure S5. Loess fitted lines have been added.

largest value of ρ across all TIM iterations was just -0.016. The NTEs introduced by the scaled models matched the highly leptokurtic distribution of the trophic interactions leading to an increased variance in NTEs. However, even the increase in variance of the 'scaled' distributions was several orders of magnitude smaller than the variance in the underlying trophic interactions (SI 6). Hence, the stability criteria were almost completely unresponsive to the introduction of TIMs (Figure S6). Nevertheless, a handful of strong NTE links can be observed to cause great destabilisation, while in most cases the comparatively weak links introduced by TIMs from constrained, unscaled, distributions had very little effect on stability.

Conclusion

Our results show that interaction modifications have the potential to cause significant disruptive effects in ecological communities. The inter-relationship between non-trophic and trophic interactions is critical to understanding their consequences,

reiterating the importance of the dpendiencies between superimposed interaction networks (Kéfi *et al.* 2016, Pilosof *et al.* 2017). TIMs can influence the stability of systems through a number of distinct mechanisms beyond introducing additional connectance. They can shift the average interaction sign, change pairwise correlation coefficients, introduce additional row structure and change the interaction strength distribution. Furthermore, given the potential for interaction modifications to short-circuit established trophic interaction motifs such as tri-trophic cascades, the distribution of interaction motifs in ecological communities (Milo 2002, Stouffer *et al.* 2007) may need to be re-examined to incorporate non-trophic effects.

Empirical data on the distribution of interaction modifications in real communities will be essential to discern their true effects. The distribution of non-trophic effects, including those caused by interaction modifications in real communities is at present essentially unknown beyond a limited number of inter-tidal communities (Kéfi *et al.* 2015, Sander *et al.* 2015). The fraction of interspecific interactions driven by interaction modifications is unknown, but likely to be large (Abrams 1983, Werner and Peacor 2003). The set of models used here attempts to map some of the properties real distributions of interaction modifications could have and identify features pertinent to dynamics. Thus, they provide a stepping stone between analytical random matrix approaches (Bairey *et al.* 2016) and empirically parameterised systems.

Ideally, empirical data will need to include information about both the topology and strength of the non-trophic, which is possible, but challenging, to acquire (Mayfield and Stouffer 2017, Terry *et al.* 2017). This could lead to the identification of regular patterns across ecosystems in the features identified here as pertinent to community dynamics. Whilst it is unlikely that there will be strong mechanistic drivers of non-trophic network structure equivalent to the role of body-size within trophic interaction networks (Petchey *et al.* 2008, Brose 2010, Pawar *et al.* 2012), there is nevertheless room for a great improvement in our phenomenological understanding of the distribution of interactions modifications.

Studies focussed exclusively on trophic networks are missing a large portion of the dynamic interactions occurring in ecological communities. Ultimately, the dynamics of ecological communities are dependent on the strength of interactions not whether they are caused by trophic or non-trophic effects. While this study is limited by both its equilibrium setting and by excluding direct non-trophic interactions (such as competition) and the modifications of direct non-trophic interactions (Levine *et al.* 2017, Grilli *et al.* 2017b), it is nonetheless clear that trophic interaction modifications can provide a framework to leverage our understanding of trophic networks to make significant inroads into the study of non-trophic effects. The key questions in ecological dynamics cannot be satisfactorily resolved until non-trophic interactions are fully integrated into community ecology. Until the empirical distribution of non-trophic effects is understood, suggested resolutions of the stability-complexity paradox may be premature.

Data and Code Availability

All generated data and R scripts used in the analysis is available on OSF DOI: 10.17605/OSF.IO/6FNAV

4

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

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Pre-print: https://doi.org/10.1101/377473

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.

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 *et al.* 2017). Trophic interaction modifications (Wootton 1993; Terry, Morris and Bonsall 2017) are class of higher-order process where a consumer-resource interaction is modulated by additional species. Examples include associational defences (Barbosa *et al.* 2009), fear effects (Sih, Englund and Wooster 1998), certain impacts of ecosystem engineers (Sanders *et al.* 2014) and foraging choices (Abrams 2010a). It has been empirically demonstrated that many strong non-trophic effects are caused by such processes (Werner and Peacor 2003; Preisser, Bolnick and Benard 2005; Ohgushi, Schmitz and Holt 2012) with large implications for community structure and dynamics (van Veen, van Holland and Godfray 2005; Barbosa *et al.* 2017; Donohue *et al.* 2017; Matassa, Ewanchuk and Trussell 2018).

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 and Bolker 2007). This allows the direct comparison of non-trophic and trophic interaction strengths (Preisser *et al.* 2005) and network structure (Pilosof *et al.* 2017) but is a representation of a different class of dynamic process (Terry, Morris and Bonsall 2017). While this simplification is fully justified in studies of communities at equilibrium (Grilli *et al.* 2017b), 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 and Hirzel 2005; Goudard and Loreau 2008; Lin and 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 and 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 and Williams 2009; Säterberg, Sellman and Ebenman 2013). However, incorporating the acknowledged flexibility of ecological networks is a perennial challenge for such studies (Montoya, Pimm and Solé 2006).

The impact on the robustness of 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 *et al.* 2010). Approaches have included topological rewiring (Kaiser-Bunbury *et al.* 2010; Staniczenko *et al.* 2010; Thierry *et al.* 2011; Gilljam, Curtsdotter and Ebenman 2015), multi-species functional responses (Uchida and 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 *et al.* 2016), facilitation (Bruno, Stachowicz and Bertness 2003), associational susceptibility (Underwood, Inouye and Hambäck 2014) or mutualistic defence (Holland *et al.* 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; Goudard and Loreau 2008; Garay-Narváez and Ramos-Jiliberto 2009; Lin and Sutherland 2014; Bairey, Kelsic and Kishony 2016), with most theoretical analyses of interaction modifications focussing on small community units (Bolker *et al.* 2003; Abrams 2010b; Holt and Barfield 2013).

Calls to incorporate the full panoply of non-trophic effects into our understanding of ecological networks have built substantially in recent years (Ings *et al.* 2009; Olff *et al.* 2009; Fontaine *et al.* 2011; Kéfi *et al.* 2012; Ohgushi *et al.* 2012; Levine *et al.* 2017) and the first empirical inventories are being established (Kéfi *et al.* 2015, 2016b). 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:

$$\frac{dB_i}{dt} = B_i \left(r_i - m_i - \frac{B_i}{K_i} - \sum_{j \in \text{ consumers of } i}^{j} \mu_{ij} a_{ij} B_j + \sum_{l \in \text{resources of } i}^{l} \mu_{li} e_{li} a_{li} B_l \right) \tag{4.1}$$

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 and 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 $\geq$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 and Martinez 2000), with 35 species and a connectance of 0.14, removing cannibalistic interactions. Each population density was initially set to 10 and these systems 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 $\mu_{ij} = \prod^k \mu_{ijk}$ (Goudard and Loreau 2008; Golubski and Abrams 2011). 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.

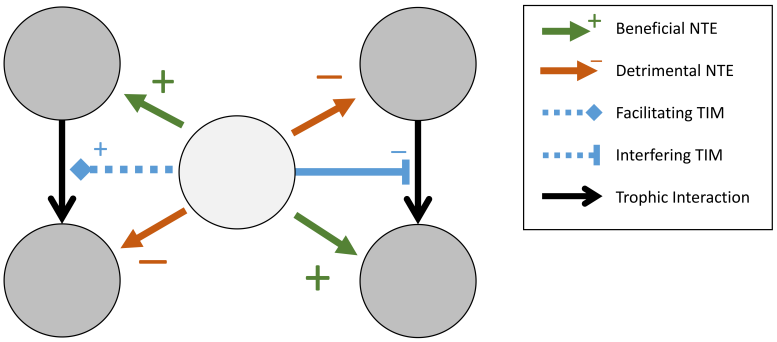


Figure 4.1: Distinctions between terms used to describe interaction modifications and their impacts in terms of the effect of an increase in the density of the modifier species (centre). 'Facilitating' ($\alpha > 0$) and 'interfering' ($\alpha < 0$) trophic interaction modifications (TIMs, dotted arrows) 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:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots \underbrace{-\mu_{ij}a_{ij}B_j}_{\text{Trophic Term with TIM}} \tag{4.2}$$

to:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots \underbrace{-a_{ij}B_j}_{\text{Trophic Term}} \underbrace{+a_{ij}B_j^*\left(1-\mu_{ij}\right)}_{\text{Non-Trophic Term}} \tag{4.3}$$

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

$$\frac{1}{B_j}\frac{dB_j}{dt} = \ldots + \underbrace{e_{ij}a_{ij}B_i}_{\text{Trophic Term}} \underbrace{+e_{ij}a_{ij}B_i^*\left(\mu_{ij}-1\right)}_{\text{Non-Trophic Term}} \tag{4.4}$$

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.

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, $\log_{10}\left(B_k/B_k^*\right)$, 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)[1] 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

[1]This α is a specific case of the c_{ijk} term used in other chapters

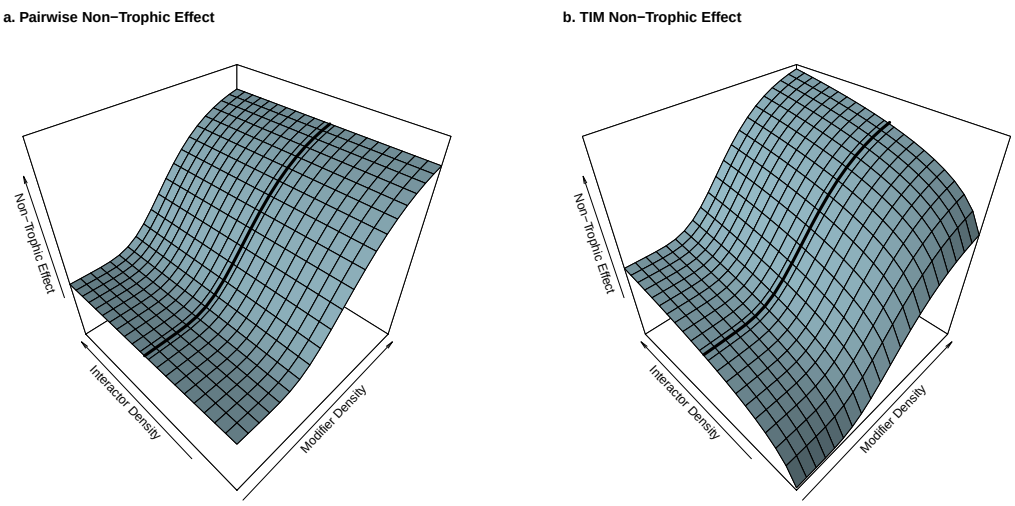


Figure 4.2: Illustrative response surfaces showing the distinction between non-trophic effects caused by pairwise interactions and those from a higher-order interaction modification process involving three species. Per-capita effects are shown in the vertical axis on a logarithmic scale. In both cases, 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.

modifier is at its starting equilibrium point - in effect these strengths are assumed to already incorporate changes to the interaction at the equilibrium.

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

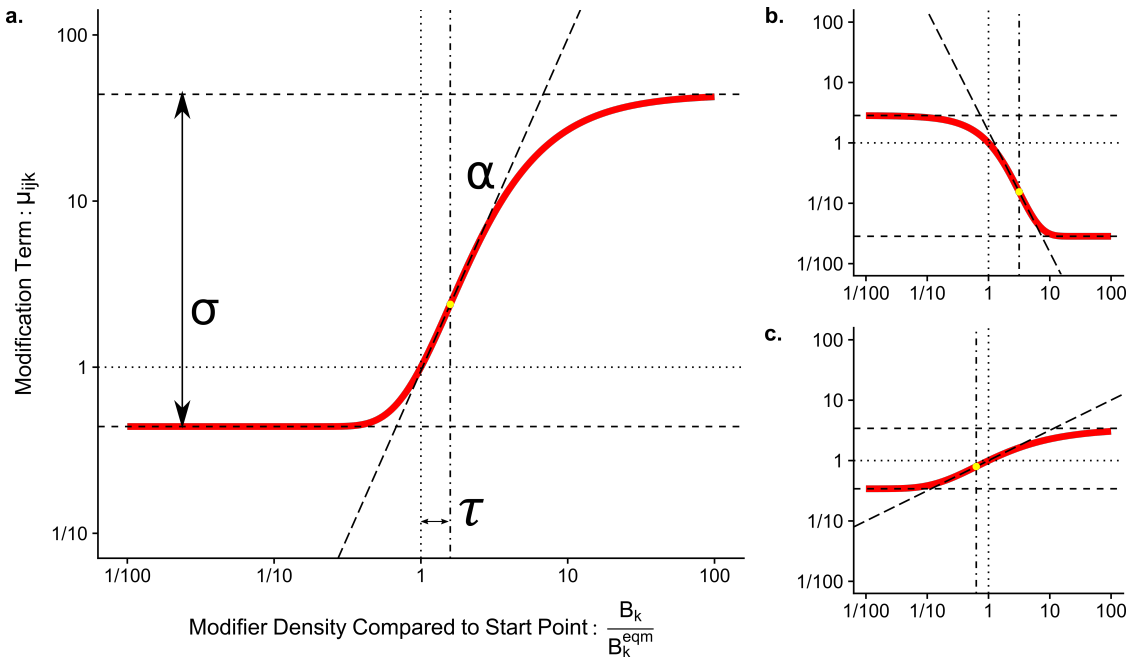


Figure 4.3: Graphical representation of the relationship between the control parameters and the response of the sigmoidal function used to determine the modification term μ_{ijk} from the density of the modifier B_k. Panel a) uses a maximum slope (α) of 2, a distance to threshold (τ) of 0.2 and a range 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.

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 $1/10^{\text{th}}$ 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 and 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 matched 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-NTE: 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.

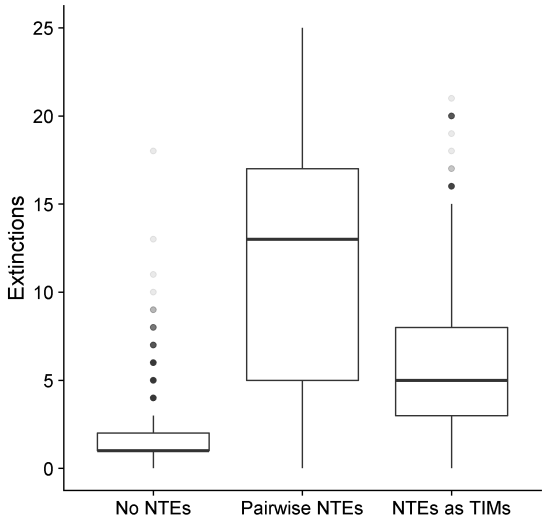


Figure 4.4: Boxplot showing that robustness was significantly lower when TIMs were modelled as pairwise interactions rather than directly as interaction modifications. Both cases produced significantly more extinctions than the no-NTE case.

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).

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

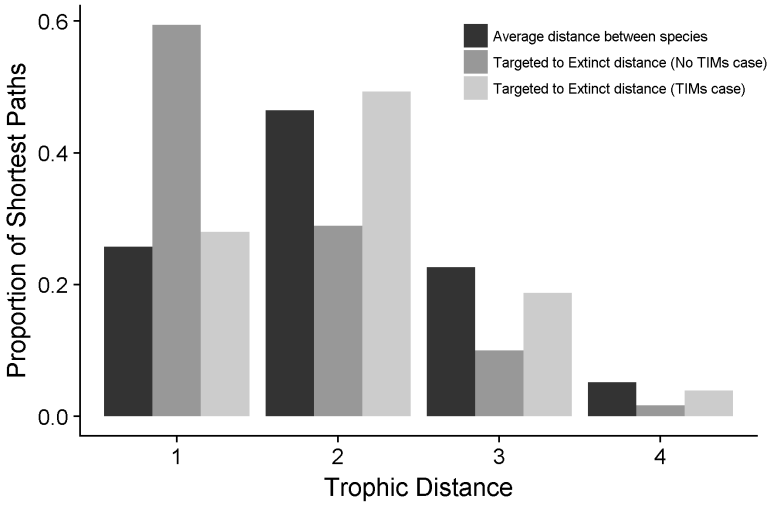


Figure 4.5: Distribution of trophic distances between all species in the communities (black) and between targeted species and secondarily extinct species in communities without TIMs (dark grey) and communities with TIMs (light grey). The distance from the targeted species to the secondarily extinct species in the TIM case was intermediate between the two baseline cases. Trophic distances above 4 were very rare in our model and not shown.

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).

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).

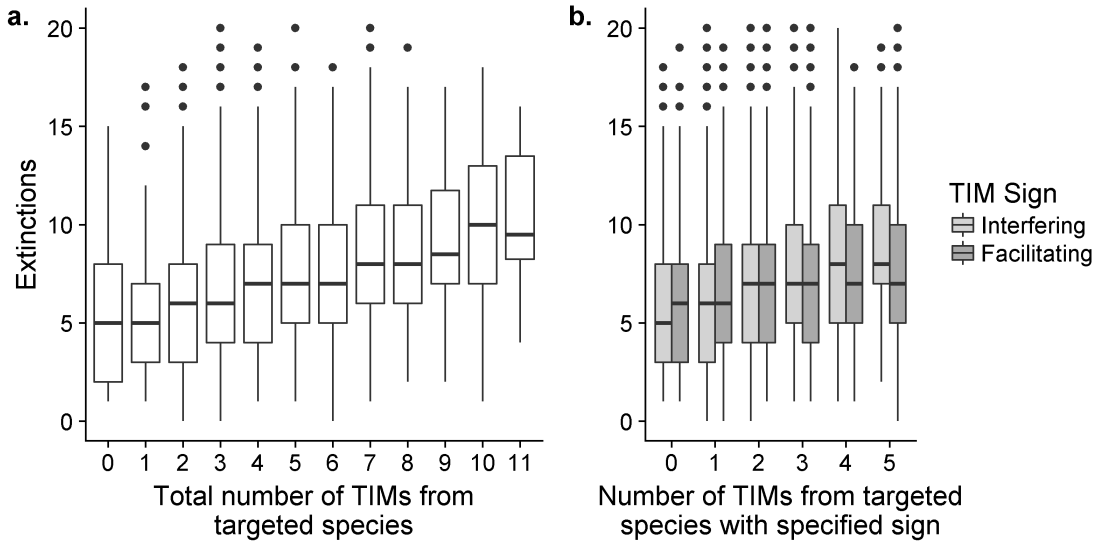


Figure 4.6: Boxplots showing the increase in the resultant number of extinctions as the number of TIMs caused by the targeted species increased. Panel a) shows the response to the total number of TIMs, panel b) shows the distinct responses to the number of each sign of TIM.

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

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

There are two complementary explanations for this impact of detrimental NTEs. Firstly, in a complex model certain species do increase their density, at least for

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

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

Our choice of function to represent interaction modifications, although mathematically complex in form, offers certain advantages compared to previous linear (Arditi *et al.* 2005; Bairey *et al.* 2016), exponential (Goudard and Loreau 2008; Lin and Sutherland 2014) or rational function (Sanders *et al.* 2014) models. In particular, it has ability to directly and independently control salient features

of the function with clear ecological relevance (distance to threshold, maximum rate of change, range 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, 2016b) 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 and Morris 2018)[2] 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 (Thébault and Fontaine 2010; Stouffer and Bascompte 2011; Johnson *et al.* 2014).

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 and 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.

[2]This is a preprint of chapter 3

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 and Barfield 2013; Kéfi, Holmgren and 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 and 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.* 2017b), 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 and Memmott 2013; Säterberg *et al.* 2013; Kaiser-Bunbury *et al.* 2017); as the development and analysis of comprehensive interaction networks expands (Kéfi *et al.* 2016b), interaction modifications must be incorporated appropriately.

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

General Discussion and Outlook

This thesis has sought to advance the study of interaction modifications as distinct processes by demonstrating their tractability at the network scale and establishing their potential impact upon ecological networks. While there remains considerable theoretical and particularly empirical work to be done, I have shown how the unifying framework of the interaction modification approach can bring a greater level of clarity and precision to these highly complex processes. Here, I first review the conclusions of the preceding chapters, then discuss the place of interaction modifications within population ecology, and finally examine different potential avenues to improve the empirical understanding of interaction modifications within entire communities.

Summary of chapters

As part of establishing a grounded framework to develop the study of interaction modifications at the network level I have set out measures of strength (Chapter 1) and topology (Chapter 2) that can be readily applied in theoretical and empirical contexts. As discussed in the introduction, the number of reviews calling for greater attention on non-trophic interactions had reached a saturation point – the first chapter was focussed on moving forward efficiently. At its core is the distinction between interaction modifications and the non-trophic effects that they cause allowing a more dynamically mechanistic approach.

This distinction is not itself new (Abrams 2001), but the difference is linguistically subtle and often lost in the multitude of phrases and acronyms that continue to predominate in this subfield (Chapter 1, Table 1). The diversity of phrases is testament to the pervasiveness of interaction modifications in ecology, but also symptomatic of a focus on categorising processes by natural history rather than

their dynamic consequences. The nature of interaction modifications can lead to them falling through the gaps of variably defined approaches to classifying ecological interactions. For example, interaction modification processes can be classed as either 'direct' or 'indirect' interactions in alternative analyses. Within this context, 'higher-order' is a particularly widespread but problematic phrase (Billick and Case 1994). While its standard meaning is broadly 'not- simple-pairwise', it is invariably assumed to mean something considerably more specific in particular papers. Two recent ecological uses include polynomial pairwise interaction terms (Mayfield and Stouffer 2017) and intransitive competition (Grilli *et al.* 2017b). Furthermore, in wider network theory 'higher-order' can also refer to the path dependency of transfer rates between nodes (Scholtes *et al.* 2016) or simply multi-node network motifs (Benson *et al.* 2016).

Proving that underneath this diversity is a clear process-level division that is more than scholastic semantics has been a key part of the thesis. This in turn allows meaningful comparisons in how the strength of individual trophic interaction modifications can be considered and the distinguishing between direct, secondary and density-mediated interaction modifications. This last point, although at first appearance adding further complication, is crucial in the reconciliation of empirical results with mechanistic models of interaction modifications. Both interaction modification and pairwise non-trophic effect approaches have considerable uses and limitations. Contrasting the two and developing the distinction has been a major part of this thesis as a whole. The large set of strength metrics of interaction modifications in Chapter 1 and their divergence even in simple systems, demonstrates the conceptual depth the interaction modification approach can bring that would overwise be overlooked.

Since Chapter 1 was published as an 'Ideas and Perspectives' article (Terry *et al.* 2017), it has been cited in a variety of studies, including a theoretical analysis of facilitation (Picot *et al.* 2018) and acting as the framing of an experimental demonstration that interaction modifications can alter interaction strengths based on allometric results (Jonsson *et al.* 2018). It has also received a small degree of

pushback in a paper that sought to emphasise the role of energy flux for biodiversity functioning (Barnes *et al.* 2018), although the paper was used as a generic reference for the role of non-trophic effects – the central role of energy flux is also a strong argument for understanding the role of modifications to fluxes.

Building upon this foundation, Chapter 2 focussed on identifying the properties of interacting modifications that exert a particularly strong influence on the community. While necessarily speculative, it demonstrates how interaction modifications can shift expectations of the relative importance of species in a network (a feature also observed in Chapter 4). For instance, rare species that may have relatively little impact as part of a purely trophic network may cause large modifications. It also emphasised the role of interaction strength over topological measures – potentially frustrating shortcuts to identifying key processes based on qualitative food webs. While the exact details of which metric is best able to identify critical subsets of TIMs necessarily depends on the extent of variability of different community properties, the fundamental take-home message is robust. As has been well understood for many decades in food-web research, quantification is critical. An optimistic note was that (for the purposes of linearised dynamics at least), even very straightforward measures of interaction modification strength were as effective as the more complex measures.

Chapters 2 and 3 approach the same question from different angles – how could the distribution of interaction modifications affect the dynamics of a community? In contrast to the more pragmatic approach of Chapter 2, which sought the maximum information from particular interaction modifications, Chapter 3 looks towards more fundamental questions of how the interactions within networks are structured. Chapter 3 shows that under reasonable assumptions of structured distributions of interaction modifications there are considerable impacts on the stability of systems - interaction modifications are therefore likely to be contributing consequential additional structure to the overall interactions in ecological communities.

This work has particular relevance to the ongoing discussion around the use of randomised matrices within ecology (Allesina and Tang 2015, James *et al.* 2015). The majority of analyses seeking to uncover structure in ecological networks

that can resolve the complexity-stability debate has focused almost exclusively on trophic interactions, despite May's (1972) foundational paper including a balance of exploitative, competitive and mutualistic interactions. Those that have investigated non-exploitative interactions, have either added them randomly (Allesina and Tang 2012, Coyte *et al.* 2015) or else focussed exclusively on mutualistic networks (Bastolla *et al.* 2009, James *et al.* 2012, Rohr *et al.* 2014) or competitive networks (Barabás *et al.* 2016, Grilli *et al.* 2017b). Current analytical approaches that include topological structure (Allesina *et al.* 2015) require assumptions that, while appropriate for trophic networks, would break down for interaction modifications. In part, the focus on trophic interaction was justifiable as the empirical base in which to find stabilising patterns is larger (Neutel *et al.* 2002, Tang *et al.* 2014, Johnson *et al.* 2014). The results of Chapter 3 show the importance of the interplay between different classes of interactions and point the way towards what kind of information will need to be generated from future interaction modification networks.

The interaction matrix approach used in this chapter has come under considerable recent criticism as being largely aloof from empirical realities (James *et al.* 2015, Jacquet *et al.* 2016). This chapter makes points on both sides of this debate – current random matrix models are likely to be missing key structural patterns. However, on the plus side, the work shows the power of the approach to inform our understanding of how dynamics of large systems operate (Allesina and Tang 2015) beyond what is currently empirically tangible.

Chapter 4 moved away from a linearised system to investigate the impact of interaction modifications on dynamics away from equilibrium. This generates specific challenges to maintain a genuine and meaningful comparison between pairwise and interaction modification representation of the same processes but is essential to understand fully the role of interaction modifications to address practical questions. By initiating the systems at an equilibrium and centring the interaction modifications around this point, this study was able to overcome the limitations that had severely restricted the conclusions of previous studies (Arditi *et al.* 2005, Goudard and Loreau 2008, Lin and Sutherland 2014). This general

approach of introducing interaction modifications such that, at least initially, they do not shift the underlying interaction strength proved useful in Chapters 2, 3 and 4. In previous studies, interaction modifications were incorporated such that it was not possible to separate the impacts of modifications on interaction strength or additional connectance (Goudard and Loreau 2012).

A considerable focus of the ongoing complexity-stability debate has centred on the definition of stability (Ives 2005). The thesis highlights the challenges on the other side of this relationship, the determination of what exactly complexity is and how to quantify it. There is no single definition of complexity, but it generally considered to be some measure of the number of dynamic links and the number of nodes in a system (MacArthur 1955, May 1973). In Chapter 4 I show the limitations of this approach – the interaction modification model and the pairwise model had the same number of species and the same amount of pairwise connectance yet markedly different stabilities. Further development is needed regarding how this 'higher-order complexity' can be conceptualised and measured, beyond verbal descriptions around the number of moving parts in dynamic systems. Even defining values for 'interaction modification connectance' is not straightforward – the fraction of possible interaction modifications, the total number of interaction modifications, the number of modifications exerted by each species and the number of direct linkages from interaction modifications are all reasonable metrics that measure what are actually distinct values.

In this thesis I have taken two distinct modelling approaches: linearised equilibrial systems (Chapters 2 and 3) and 'full' dynamic systems (Chapter 4). Each approach offers distinct advantages and disadvantages, but taken together are synergistic. While full models, examining the response of populations to large perturbations are attractive as a more 'realistic' analytic framework with less apparently intrusive restrictions, they require their own set of assumptions regarding the setting of the systems and additional parameterisation. Linearised system analysis tools are often criticised for their simplistic assumptions, for example often necessitating an equilibrium state (although see (Klausmeier 2008)). The advantage is the greatly

increased analytical possibilities, drawing upon centuries of mathematical and systems theory work. This debate has being ongoing throughout ecology (Rooney and McCann 2012), since at least the influential work of May (1972). A particular criticism has been the use of local asymptotic stability as a general measure of ecological system stability (Ives 2005). The dominant eigenvalue describes how a system will eventually return to an equilibrium, but neglects the transient dynamics defining how and when the system will reach that point (Hastings 2001). Transient dynamics were indirectly found to play a role in the extinctions observed in Chapter 4. Local stability is also potentially controlled by only a few rare species (Arnoldi *et al.* 2018). Nonetheless, local asymptotic stability is often associated with more meaningful measures of stability (Chen and Cohen 2001) and the extensive literature relating network structure to the dominant eigenvalue made it an important area in which to test the role of interaction modifications. In the absence of comprehensive data about the functional form of interaction modifications, this linearised approach seems a reasonable first approximation.

One alternative to local stability that has seen recent emphasis is structural stability, effectively testing the size of the parameter space that is stable for a given model structure (Rohr *et al.* 2014, Saavedra *et al.* 2017). Such changes to model structure could represent perturbations equivalent to the introduction of external mortality as modelled numerically in Chapter 4. With the assumption of linear pairwise interactions, structural stability can be computed directly from an interaction matrix structure (Grilli *et al.* 2017a) and can mitigate some of the disadvantages of a conventional local asymptotic stability analysis. However, as I have shown using simulation methods in Chapter 4, interaction modifications exert dynamics that are fundamentally distinct to that which can be captured within a linearised structure when the systems are heavily perturbed.

In almost every case (the main exception was one of the empirical webs for certain distributions in Chapter 3) the introduction of additional interaction modifications at the network level is profoundly destabilising. This is in contrast with the large number of cases where adaptive foraging interaction modifications have been found

to be stabilising (Kondoh 2003, Valdovinos *et al.* 2010), although there are counter examples (e.g. Gilljam *et al.* 2015). Adaptive foraging, as the name suggests, are specifically structured interaction modifications for the benefit of foragers, but are likely to represent only a minority of overall interaction modifications. Nonetheless, there is reason to expect that real interaction modification distributions are more stable than the random networks used here. The processes present in extant networks are likely to be those that are stable (in the sense of being able to persist long enough to be observed) through a process of non-adaptive selection for systems that are able to persist (Borrelli *et al.* 2015). Until we know those distributions it is too early to say if interaction modifications are such a near-universal destabiliser, but this constraint does not prevent the theoretical exploration of their impacts.

I have based a significant proportion of my analyses on generalised models of population dynamics (Delmas *et al.* 2017) using artificial trophic networks (Williams and Martinez 2000). These have been found to hold up reasonably well in empirical tests (Williams and Martinez 2008, Boit *et al.* 2012), but as importantly they are effectively standard models within ecological modelling, providing a testbed for the role of interaction modifications. Since the only interaction modification networks I could use are necessarily artificial, the increased control and standardisation offered through the use of artificial webs is a significant gain compared to using empirical trophic networks. Theoretical work has the capacity to make assumptions explicit and to some extent controllable. The confrontation of theoretical results with data, such as the fisheries networks in Chapter 3, highlights how the scope of the conclusions drawn from artificial communities will always be constrained by individual peculiarities of real empirical systems. There, the highly leptokurtic interaction strength distribution of the fisheries networks mitigates the impact of interaction modifications unless their strength is scaled to them.

Taken as a whole, this work demonstrates the importance of interaction modifications at a network scale and forms a foundation to be part of the movement towards quantifying interaction modifications in empirical networks. Ultimately, this work is not in itself able to demonstrate their role in ecosystems relative to other

factors - for that a systematic empirical analysis across ecosystems will be necessary, which I discuss below. This work does however play a useful role in cracking open the current vicious circle whereby interaction modifications were generally not empirically studied at the network level due to a lack of evidence of their importance, but the theory is in turn held back by a lack of usable empirical data.

Interaction modifications and other sources of variability

Ecological modelling has two distinct roles: to inform how ecological processes function at an underlying level and to make direct predictions about how systems will develop in the future. It is clear that current models of population dynamics for making predictions are not as reliable as is necessary (Clark *et al.* 2001). Efforts to push back the 'forecast horizon' (Petchey *et al.* 2015) need to carefully consider the most efficient routes to improving estimates.

Comparisons of interaction networks across environmental gradients demonstrate the role of abiotic impacts on interaction strength (Staniczenko *et al.* 2017, Tylianakis and Morris 2017), but single observations struggle to precisely partition the role of biotic and abiotic causes of this variation. The meta-analysis of Chamberlain *et al.* (2014) sought to compare the impact of biotic and abiotic context on different classes (predation, mutualism or competition) of interspecific interactions, including the effect of interaction modifications. They found that abiotic gradients resulted in a larger coefficient of variation of interaction strength than biotic context (0.81 vs 0.52), with no difference between interaction types. However, an opportunistic meta-analysis such as this is heavily susceptible to the selection bias of the original investigators and cannot standardise the magnitude of change in either biotic or abiotic context.

There is a fundamental distinction between changes to per-capita interaction strength that can be attributable to causes that are intrinsic to the system (interaction modifications) and therefore potentially internally foreseeable, and those extrinsic to the system (such as climate). Understanding the balance and interaction

between these types of variation is both challenging and important (Peacor and Cressler 2012). An important future theoretical direction must be to understand how the fact that changes due to interaction modifications are intrinsic (and therefore subject to feedback loops and capable of generating alternative stable states (Kéfi *et al.* 2016a)) rather than extrinsic determine their impact upon real systems.

Interaction modifications could dampen or exacerbate external stochasticity, but to date the only general interaction modification study to incorporate extrinsic noise did not examine this directly (Lin and Sutherland 2014). The overall effect will likely depend on how 'adaptive' interaction modifications are in practice. The large number of interacting timescales necessary in any such analysis are a formidable problem to identifying general conclusions (Hastings 2010). Complicating matters further, interaction modifications and external effects such as climate directly interact to produce a combined effect on interaction strength (Sentis *et al.* 2017). This challenging question has parallels with the questions regarding the role of phenotypic plasticity within evolutionary dynamics (Hendry 2016). Ultimately, satisfactory answers to these questions will require considerably more detailed empirical knowledge of the strength and distribution of interaction modifications than is currently available.

Appropriate levels of abstraction for interaction modifications

The tension between the accuracy promised by an intricate, highly parameterised, 'mechanistic' model and power of judiciously abstracting over non-essential parts to create simple phenomenological representations is critical to successful ecological modelling (Schaffer 1981). Sacrificing specificity for generality can lead to more fundamental insights (Holling 1966) but such results are often destined to remain demonstrations until they can used within more complex and specific models (Evans *et al.* 2013b, Topping *et al.* 2015). Generalised interaction modifications of the type I have used in this thesis lie at an intermediary position, introducing additional dynamic complexity but without directly incorporating physiological

processes. As such they are susceptible to criticisms from both directions in the modelling hierarchy.

It is not necessarily the case that the additional dynamic complexity associated with interaction modifications must be included in all circumstances to understand how a system will respond, even when their impacts are significant. Indeed, the demonstration in Chapter 1's Appendix 5 shows that the stabilising effect attributed to an interaction modification (Křivan and Schmitz 2004, Holt and Barfield 2013) can be very nearly replicated by a simple reduction in interaction strength – the additional feedback loop is not driving the initial stability regime change. Conversely, pushing from the 'increased detail' side, are a very large number of processes affecting foraging that are abstracted into general functional responses, such as stoichiometric constraints (Sperfeld *et al.* 2017) and spatial-temporal variation in resource availability (Senft *et al.* 1987). Interaction modifications ultimately derive from very complex ecology and a simple abstraction will always be found wanting in some aspects. However, particularly at the whole network level, the data is not available to refine models further.

In this thesis I have taken a population-level mass-effect approach, aggregating over individual level variation with mean values (Hastings 2005). Studying the dynamics of population densities intrinsically aggregates over individual level behaviour which can mask important effects (Bolnick *et al.* 2011, Clark *et al.* 2011). Differences between individuals can occur due to the age structure of populations (de Roos and Persson 2006), the distribution of individuals within a heterogeneous habitat (Trussell *et al.* 2006) and individual specialisation (Bolnick *et al.* 2003). Specifically for interaction modifications, individuals with divergent behavioural syndromes can differ in how their interactions are modified (Griffen *et al.* 2012, Toscano and Griffen 2014). Including such factors within a network-scale analysis is very challenging. Individual-based models (DeAngelis and Mooij 2005) that incorporate trait-plasticity can be created (e.g. Peacor *et al.* 2007), but the level of parameterisation and computational intensity required severely restricts the generality of any conclusions. Other approaches that consider within-population

differences, but without individually tracking each organism, such as integral projection models could offer more concise routes to incorporate age structure or trait heterogeneity (Ellner and Rees 2006).

The interaction modification framework is explicitly not grounded in evolutionary or optimisation principles. Where traits can be assumed to be optimised, in some ways analysis is considerably simplified as traits can be assumed to move in an optimal direction (Abrams 1984) but this then requires additional assumptions about the rate of change towards the optimum (Coulson *et al.* 2017). This framework has developed into the field of adaptive dynamics (McGill and Brown 2007), but much research has focused on evolutionary rather than ecological implications. The effect of rapid trait evolution, leading to reciprocal eco-evolutionary feedbacks, has recently been strongly established (Ellner *et al.* 2011, Schoener 2011, Cortez 2011) and demonstrates that natural selection as well as behavioural and phenotypic plasticity can provide sources of interaction modifications on ecological timescales. However, as a generalised approach, the interaction modification framework does not specify the impact on particular physiological traits. Specific trait-based models allow precise trade-offs to be examined, for example a discrete term for time spent foraging would allow direct links to both foraging success and vulnerability (Abrams 2010b). However, whether such an approach is actually superior to the more general approach of modelling separate interaction modifications within complex systems is not clear. While a subset of interaction modifications are caused by adaptive responses this is far from universally the case (Railsback and Harvey 2013). It would be hard for example to find an optimisation-based argument to parameterise the impact of long grass on the ability of a predator to sneak up on its prey (Anderson *et al.* 2010). Optimisation models for foraging have had successes (Stephens and Krebs 1986, Parker and Smith 1990, Abrams 2010b), but these successes are almost always based in relatively restricted settings and require a detailed understanding of the relevant currencies defining the behavioural trade-offs (Davies *et al.* 2012).

The best studied group of interaction modifications, those caused by predators switching between multiple prey options (Abrams 2010a, 2010b, Valdovinos *et al.*

2010), provides a case study for the extent of detail that could be included within a population level approach. Predators are often found to focus their efforts on more common prey, potentially reducing their rate of attack on rarer species (Murdoch and Oaten 1975). The simplest approach to represent this effect would be to take an entirely pairwise approach - it is possible to abstract over the direct influence of other species completely and represent the reduced predation at low densities with a Holling Type-III sigmoidal response (van Baalen *et al.* 2001). At the other end of the spectrum, there are wide range of 'multi-species functional responses' that have been developed to represent such a situation (Gentleman *et al.* 2003, Koen-Alonso 2007). The number of additional features that can be introduced to functional responses is very large, including predator interference (Beddington 1975, Skalski and Gilliam 2001), predator-prey ratios (Abrams and Ginzburg 2000), spatial heterogeneity (Ives 1995) and body-size distributions (Hunsicker *et al.* 2011), amongst others. Models can become highly complex to take into account increasing criteria, for example including 'active-switching' preference terms which in turn can be derived from explicit models of optimisation of energy intake (van Leeuwen *et al.* 2013, Morozov and Petrovskii 2013). Detail in one area can come at the cost of loss of realism in another and complex model forms can be necessary to avoid perverse results such as overall intake declining as the amount of prey available increases (Holt 1983).

Within the interaction modification framework it is possible to use simpler and more consistent models with a direct dynamic link onto the trophic links from the alternative prey. While the precise form of the functional responses is certainly important, for example for the balance between apparent competition and apparent mutualism (Abrams *et al.* 1998), in most cases the shape of the function is unknown. This creates a large role for generalised approaches to dynamics (Gross *et al.* 2009), including the interaction modification framework.

Determination of empirical interaction modification networks

A recurring theme within this thesis is the difficult problem of assessing the role of interaction modifications without an understanding of their distribution within ecological networks. No amount of case studies of small laboratory-based systems (Werner and Peacor 2003) can answer this question as such studies are invariably chosen to confirm existing presuppositions of interaction modifications. How can this gap be closed in the most efficient manner? Experience from previous decades of constructing trophic and mutualistic networks could allow a rapid pace of progress at generating community level inventories of interaction modifications. Although Chapter 2 demonstrates that not all trophic interaction modifications are equal and that it is possible to prioritise, examples of thorough inventories of interaction modifications from across a range of ecosystems will be necessary to understand whether there are consistent patterns in their distribution of the type tested in Chapter 3. Trophic and mutualistic networks show considerable structure (Bascompte 2010) and the single published comprehensive interaction web suggests that this is also true of generic non-trophic interactions (Kéfi *et al.* 2016b). We need to understand if there are consistent patterns in interaction modification distribution, in terms of connectance, direction, strength and motif frequency. For small, simplified systems, understanding the detailed functional form of an interaction modification would be achievable (Chapter 1), although that is probably of a lower initial priority at the community network scale where general values such as the slope, range and threshold (Chapter 4) would be enough. There are broadly four possible approaches to extend the empirical understanding of interaction modifications and other non-trophic processes: inference from spatial variation, inference from temporal variation, amalgamation of specific natural history knowledge and trait-based approaches:

Inference from spatial distribution of populations

The spatial co-occurrence of species offers a tempting avenue to infer inter-specific interactions that has a long and controversial history (Diamond 1973, Weiher and Keddy 1999). Disentangling environmental effects on ecological networks (Tylianakis and Morris 2017, Pellissier *et al.* 2018) from biotic effects, including interaction modifications is fundamentally challenging (Cazelles *et al.* 2016). Recent approaches using Bayesian inference and joint species distribution modelling (Milns *et al.* 2010, Warton *et al.* 2015, Graham and Weinstein 2018) seek to separate the influence of community composition from the impact of environmental variables. In principle, it would be theoretically possible to expand these approaches to include interaction modifications by expanding the underlying model. In practice however, this is likely to be highly unfeasible, especially in the light of recent results highlighting significant shortcomings in the capacity of even the latest techniques in predicting known pairwise interactions from cross-community comparisons (Sander *et al.* 2017, Freilich *et al.* 2018, Barner *et al.* 2018). Separating interaction modifications from indirect interaction chains would be a further, likely insurmountable, challenge. Cross-community comparisons do however certainly have a role in providing indirect supporting evidence for suspected interaction modifications, but this ideally should be backed up by manipulative experiments. Such a study was conducted by van Veen *et al.* (2009) for a aphid-parasitoid interaction modification identified in a laboratory study. They found that the local distribution of an aphid community within a habitat matched their expectation, which they were able to confirm with a manipulative field experiment (van Veen *et al.* 2009).

Direct inference from population dynamics

Fitting models to data of changes in populations through time is an exceptionally powerful approach in defining and testing our understanding of the driving features of dynamic systems (Hilborn and Mangel 1997, Bjørnstad and Grenfell 2001). Serious discrepancies between expectations from pairwise models and experimental observations are a significant piece of evidence for the presence and impact of

interaction modifications (Tack *et al.* 2011, Timóteo *et al.* 2016, Barbosa *et al.* 2017), but they cannot be identified directly by such discordances. Although the data can be challenging to gather (see postscript), where particular interaction modifications are already suspected a model fitting approach is capable of providing considerable insight. For instance van Veen *et al.* (2005) demonstrated that the stability of an aphid-parasitoid system required the inclusion of an interaction modification. More recently, Griffiths *et al.* (2018) using a trait-based model of a protist community showed that including an interaction modification led to a R^2 improvement from 34% to 57% and Donohue *et al.* (2017) showed that interaction modifications were necessary to understand the responses to species removal in a rocky shore community. The prospect of identifying interaction modifications 'cold' purely from time series data is considerably more challenging. In principle, interaction modifications could be identified using statistical 'model-free' approaches (Sugihara *et al.* 2012, Perretti *et al.* 2013, Suzuki *et al.* 2017, Ushio *et al.* 2018). Indeed, in their analysis of a small aquatic system Deyle *et al.* (2016) found that the partial dependency of a predator on its prey is dependent on other species. Since under this approach all interactions are described in terms of their impact of population dynamics, this framework includes 'built-in' testing for their relative importance. However, such methods require either very long (relative to the dynamics of the species involved) or highly replicated time series in order to be accurate. As the size of the system (in terms of the number of state-variables that are tracked) increases, the data requirements grow considerably as there is a greater chance of misleading correlations. Furthermore, without any mechanistic basis, model-free approaches lack both applicability to different regimes and translatability to inform understanding of other similar systems.

Natural history-based approaches

Interaction modifications can rarely be directly observed in the manner of trophic or pollination interactions. The largest-scale attempt to categorise the distribution of non-trophic effects, including those caused by interaction modifications, instead

took the approach of harnessing the extensive knowledge of the species involved in a Chilean rocky shore community that had been developed over many years of separate studies (Kéfi *et al.* 2015). The resultant network includes 104 species, 3296 non-trophic interactions and 1458 trophic interactions. Other examples being developed using this approach include the Tatoosh Island mussel bed system (Sander *et al.* 2015) and a coffee agroecosystem (Perfecto *et al.* 2014, Golubski *et al.* 2016). Currently, given the current state of knowledge, this natural history-focussed approach offers the greatest potential gain for the least investment in resources, at least for directly observable systems. For understanding interaction modifications within microbial systems (Kelsic *et al.* 2015) other approaches would be essential.

This approach makes high demands on expert knowledge of a system, but for many systems this is available, drawing upon decades of experience and previous manipulative experiments. A challenge is the requirement to be able to combine various interaction types into a comparable currency (Vázquez *et al.* 2015). The approach is inherently qualitative, but could be made more quantitative by assigning binned strength estimates, potentially within a Bayesian framework for some analyses to capture uncertainty (Poisot *et al.* 2016). A greater risk is potential biases towards assigning interaction modifications to larger, better studied, species within networks, analogous to issues with 'trophic lumping' in early food webs (Pimm and Kitching 1988). Nonetheless, the general approach has the potential to be more complete than approaches that seek to combine multiple discrete interaction networks found at a single site (Pocock *et al.* 2012).

Trait-based approaches

There has been considerable recent interest in using functional traits as a method to infer interaction network structure (Gravel *et al.* 2013, Morales-Castilla *et al.* 2015, Bartomeus *et al.* 2016). Extending this approach to trophic interaction modifications would have the dual advantage of testing understanding of the fundamental structures of networks and allowing extrapolation to understudied communities (McGill *et al.* 2006). Trait-based approaches would be particularly

valuable for their potential to identify specific cases of interaction modifications between species that do not yet coexist, but may do in the future due to invasion (Pearse and Altermatt 2013).

Trait-based approaches have had some considerable successes in describing trophic networks, which appear to be structured by a relatively low dimensional trait space (Eklöf *et al.* 2013). Traits have also been used effectively for predicting non-trophic interactions for many years, such as Darwin's prediction of an orchid – Hawkmoth interaction (Kritsky 1991). However, the intrinsic diversity of the ecological processes that cause interaction modifications mean that it is unlikely that there are any consistent physiological traits analogous to the role of body size (Emmerson and Raffaelli 2004) across communities. Traits can in some cases be very poor at predicting behavioural responses, for example the lack of fear effects exhibited by many island populations (Sih *et al.* 2010).

A possible more productive route for predicting the presence of interaction modifications in networks would likely to be to expand from directly measurable physiological traits to include positions within a trophic or other interaction network and known interaction modifications. Missed links in networks could then be inferred through matching centrality approaches (Rohr *et al.* 2016). A broader approach would also be necessary, recognising the value of identifying which interactions are not possible (Vizentin-Bugoni *et al.* 2014) and using probabilistic interaction networks to capture the degree of uncertainty about the presence and strength of a link (Poisot *et al.* 2016). However, such approaches can only come after sufficient data gathered through other means has been established to test models upon.

Conclusion

Ecosystems are archetypal complex adaptive systems, composed of many different actors held together with a diversity of processes that together produce considerable emergent properties (Levin 1998). The development of complexity science is in part an admittance that the classic reductionist approach, seeking to determine the smallest fundamental units of mechanism that can scale back up to the whole,

is not appropriate in many situations (Waldrop 1992). Interaction modifications are a key constituent of this complexity – relationships between species cannot be understood without direct reference to other components of the system.

Ecology has benefitted greatly from the developments in systems science (Gardner and Ashby 1970), network theory (Sole and Montoya 2001) and complexity theory (Strogatz 2001) that have led to a beneficial increase in the formality with which ecological problems can be discussed and analysed. The value of this rigour can be seen when certain intuitive assumptions are shown to not be mathematically valid (May 1972) and clarifying what mechanisms are truly fundamental (Chesson 2000). However, ecological systems are inherently more dynamic and heterogeneous than the assumptions of physical science fields from which these methods have been first developed. It should not therefore be surprising that it is necessary to push beyond pairwise methods in ecology. Equivalent extensions are also likely to be relevant within other network-based fields such as neuroscience (Bassett and Sporns 2017), gene regulation (Karlebach and Shamir 2008) and socio-economics (Watts 2004).

This thesis has made progress in scaling up interaction modifications from small modules up to the network scale. The field of non-trophic interactions is rapidly developing - over a quarter of the references used in this thesis have been published since this project started in 2014, including the first empirical network (Kéfi *et al.* 2015). My work shows both the value of this surge of interest and provides useful information about how it can be most profitably harnessed to improve ecological understanding of complex systems.

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Postscript - Experiments

Although the main body of this thesis is predominantly theoretical, the initial intention was for an even balance between theoretical and empirical work. I originally set out to conduct a detailed empirical case study to test the possibility of extracting information about interaction modifications from time series data. Unfortunately, the experiment had to be brought to an early conclusion as the spread of a pathogenic fungi wiped out one of the study species. However, since the design and development of these experiments was a significant fraction of my research time during the doctorate (approximately a year) I briefly summarise them in this postscript.

The objective of this work was to test what information was necessary to sufficiently understand the impact of interaction modifications and to conduct an empirical investigation of how multiple interaction modifications combine. These experiments used caged aphid-parasitoid systems, chosen as these insects have rapid generation times, a simple life history with discrete stages, an extensive literature base (Godfray 1994, Hawkins and Sheehan 1994, Hassell 2000) and offer the ability to directly observe trophic interactions via the mummified aphids. Aphid systems had been used in a number of studies of interaction modification (van Veen *et al* 2005, Frago and Godfray 2014, Kersch-Becker and Thaler 2015, Kehoe *et al* 2016)

I planned to generate a comprehensive dataset encompassing two distinct interaction modifications affecting the attack of pea aphids (*Acyrthosiphon pisum*) by the parasitoid wasp *Aphidius ervi*. The first was interference by a non-host vetch aphid (*Megoura viciae*). This presence of this large, strongly kicking, aphid leads to associational protection for the slightly smaller *A. pisum*. This effect had been demonstrated both in laboratory experiments (van Veen *et al* 2005) and in the field (van Veen *et al* 2009) and so provided a known target. A second interaction modification was hypothesised to be caused by a second parasitoid wasp *Praon*

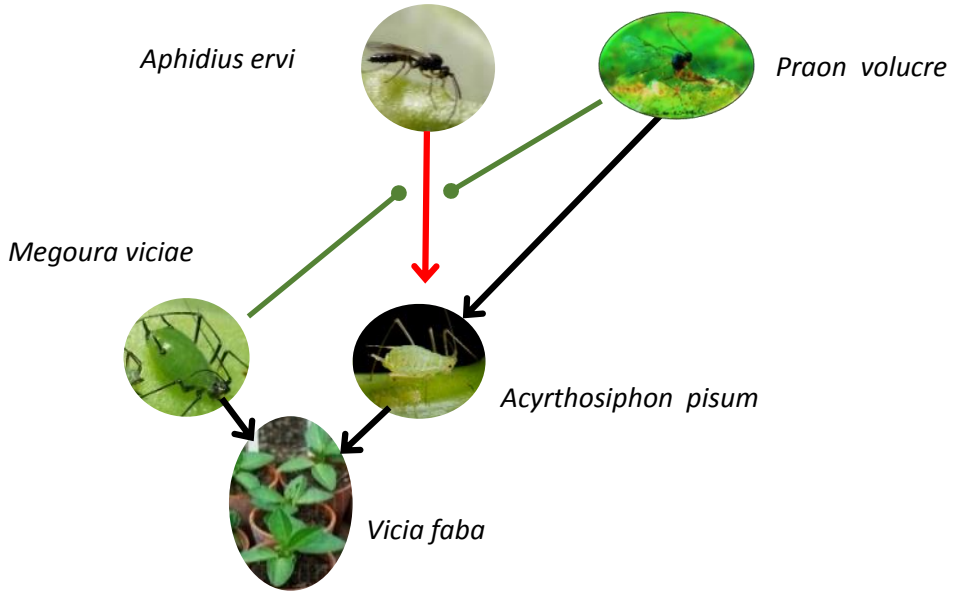


Figure PS.1: Aphid-parasitoid system used in the mesocosm experiments. The trophic interaction that was to be the principle focus of the study is shown with red arrows, other trophic interactions are in black and the interaction modifications with green round-headed arrows.

volucre through interference and multi-parasitism. Previous direct evidence for the result of multi-parasitism by *P. volucre* and *A. ervi* in *A. pisum* did not exist. However, *P. volucre* had been shown to be superior in larval competition with *A. ervi* in *Macrosiphum euphorbiae* aphids (Sidney *et al* 2010) and, a different *Praon* species (*P. pequodorum*) had been shown to be competitively superior in *A. pisum* (Schellhorn *et al* 2002).

There were also likely to be other interaction modifications occurring in the system. Broad bean plants are known to systemically produce volatile chemicals to signal to parasitoids when they are attacked by aphids (Du *et al* 1996, Thompson *et al* 2012, Heil 2014, van Veen 2015). However, given the small size of the cages and the fact that all the plants are attacked this is unlikely to cause notable effects. Other potential modifications such as *M. viciae* reducing the attack rate of *P. volucre* or wasps affecting aphid-aphid competition were also possible and would have been investigated but were not the principle focus.



Figure PS.2: Experimental cages used as mesocosms. Forty 50cm side fine mesh cages were fixed to raised platforms under shade netting, each containing 6 bean plants as a resource. Not seen in shot are smaller cages used to measure key life history parameters of each of the species.

Compared to previous microcosm or mesocosm work (van Veen *et al* 2005, Frago and Godfray 2014, Hammill *et al* 2015, Griffiths *et al* 2018) this study would have had the capacity to understand the relationship between modifications, as well as testing the impact of interaction modifications relative to external variation caused by weather changes during the season. The intention was to initially fit and compare state-space models (Spiegelhalter *et al* 2002, Bolker 2008), including a full suite of environmental data, but then go on to use the dataset to test the capacity of other modelling frameworks to identify the same processes. Key life history values such as aphid reproductive rate, aphid development time and wasp development times were to be based upon strong priors derived from supplementary experiments, allowing the model fitting to focus on the trophic interaction (McCarthy and Masters 2005).

This was to be followed by a highly replicated fully-factorial set of short term functional response experiments carried out in a controlled temperature room in order to parameterise a 4-dimensional response surface of the *A. ervi*-*A. pisum* interaction with the inclusion of the two other species. These experiments would provide a baseline to directly compare the data from the time series.



Figure PS.3: Effects of the pathogenic fungi on *A. pisum*. Also observable (left of centre) is an *A. ervi* mummification cocoon with its characteristic golden spherical shape and several first-instar *A. pisum* nymphs

Ten replicates of four species combinations (*A. ervi*-*A. pisum* only, + *P. volucre*, + *M. viciae*, + both *P. volucre* and *M. viciae*) were censused as frequently as possible, which in practice was approximately every ten days. The two aphids were easily distinguishable by colour and shape, while the two wasps could be distinguished by the shape of the cocoon they made with the parasitised aphid. *A. ervi* pupates within the body of the aphid and forms a round golden cocoon. *P. volucre* pupates underneath the body of the mummy in a silken tent. Aphids were supplied with 6 pots of bean plants, half of which were replaced as part of each census.

When designing the experiment the greatest identified threat was the potential for overheating in the full sun. This was mitigated by erecting a large shade canopy (Figure 2). However, in the event June 2016 (the month following the introduction of the wasps to the mesocosms) was the least sunny June ever recorded in the 135 year history of the Radcliffe Weather Observatory, with only 104.4 hours of clear sun for the whole month and nearly double the average number of rain days (Munday and Creese 2016). The ultra-fine mesh of the cages, necessary to exclude external parasitoids and hyperparasitoids, inevitably impeded airflow leading to very damp conditions inside the cages.

This contributed to an outbreak of an entomopathogenic fungal infection (likely *Pandora neoaphidis*) affecting *A. pisum* (Figure 3). If the outbreak had been contained then its effect could likely have been accounted for in the modelling relatively

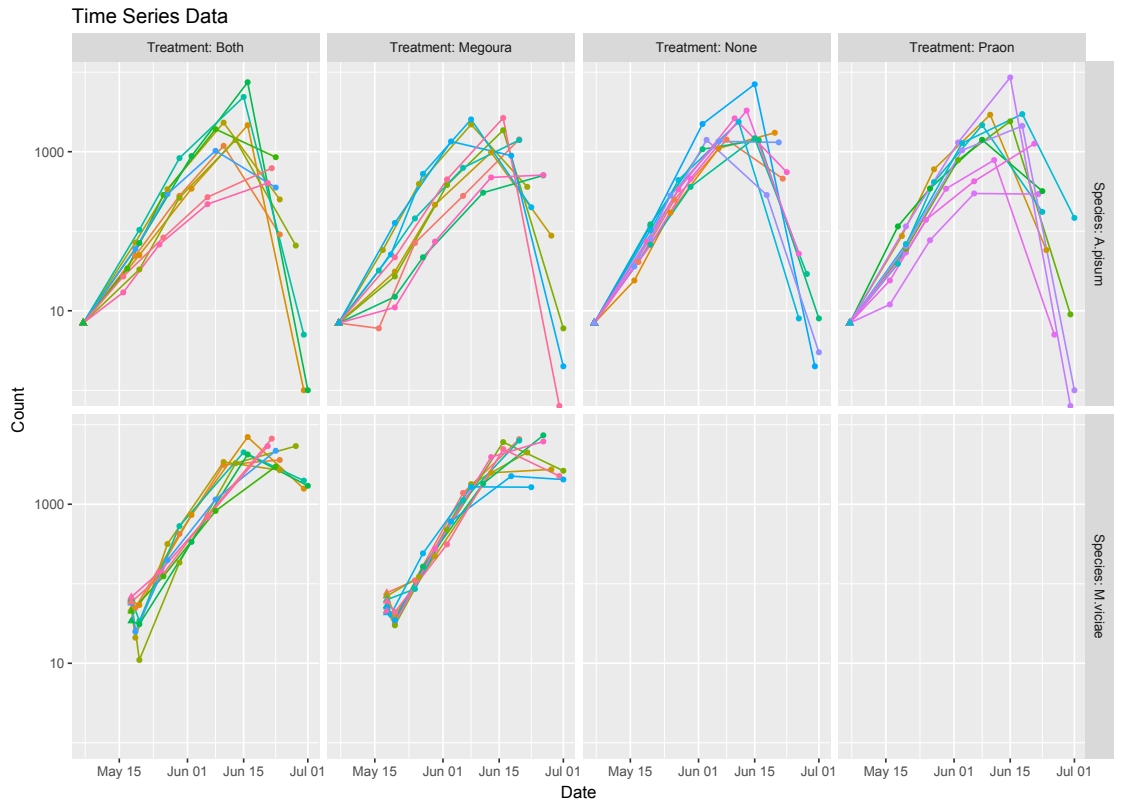


Figure PS.4: Time series of total numbers of aphids, summing over original separate counts of adults and numphs of each aphid species. Each line shows a separate cage. Treatments are defined in terms of additional species to the core *A. pisum* - *A. ervi* interaction. After intial exponential growth of both populations, *M. viciae* appeared to have reached a carrying capacity by mid-June. However, *A. pisum* rapidly declined in all treatments as the infection spread.

simply - prior work shows that *A. ervi* are unable to detect entomopathogenic fungi when ovipositing *A. ervi* (Baverstock *et al* 2005). However, the plague rapidly led to the complete extirpation of all *A. pisum* (Figure 4).

Once the infection took hold, there was little to stop the airborne spread. In order to simplify the population dynamic modelling, the *A. pisum* were derived from a single clone so there was no genetic variability in susceptibility. Furthermore, this clone had been cured of its symbionts using antibiotics to ensure a high attack success rate of the parasitoids, but this had the additional effect of also leaving it highly susceptible to pathogenic attack (Lukasik *et al* 2013).

Attempts were made to restart the populations, but difficulties getting sufficient parasitoid wasp stocks from the suppliers and the rapidly declining seasonal window in which to gather sufficient data forced the experiments to be discontinued. Simple

ANOVA analysis of the rate of parasitism in the *A. ervi* single generation that was able to hatch, showed no apparent difference between the treatments, but the aphid densities were at that point still relatively low.

Although the experiments were ultimately not successful in gathering the required data, they demonstrate that replicated time series experiments are within reach. There remains a need for experiments that push beyond short-term, highly controlled laboratory demonstrations of interaction modifications and mesocosm approaches such as that which I attempted provide a valuable route.

Appendices

A

Supplementary Material for Chapter 1

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5: Comparison of TIMs with Direct Parameter Changes . . 171

1: Interaction Modification Functions

Table A.1: Expressions that have been suggested or used for the modification of functional response parameters. c_{ijk} = modification parameter (k's effect on the consumption of i by j), x_k = modifier density, T_0 = half-saturation density of modification, a = plays role in determining steepness of threshold, direction of effect and intercept, d= point of inflection, also affects intercept. M_{nti}= value when x_k tends to infinity, M_0 = baseline value, v = curve abruptness, u = modifier density when μ (modification effect) = 0.5. Some models have been adapted from the original source for consistency in the table.

Name	Examples of Use	Function	Lower Bounded above 0?	Upper Bounded?	Contains threshold?	Number of free parameters
Linear	Arditi *et al.* (2005)	$\max\{0, 1 + x_k c_{ijk}\}$	N	N	N	1
Exponential	Křivan & Schmitz (2004), Okuyama & Bolker (2012)	$exp(c_{ijk}, x_k)$	N	N	N	1
Power Law	Goudard & Loreau (2008), Lin & Sutherland (2014)	$(1 + x_k)^{c_{ijk}}$	N	Y	N	1
Interference	Paixão *et al.* (2014)	$\frac{1}{1 - c_{ijk} x_k}$	N	N	N	1
Saturating	Kéfi *et al.* (2012) Sanders *et al.* (2014)	$\frac{\exp c_{ijk} \times x_k + T_0}{x_k + T_0}$	Y	Y	N	2
Logistic	Kéfi *et al.* (2012)	$\frac{M_{nti} - M_0}{1 + e^{a(x_k - d)}} + M_0$	Y	Y	Y	3
Dose Response	Ramos-Jiliberto *et al.* (2008)	$1 + \frac{c_{ijk}(x_k)^v}{(x_k)^v + u^v}$	Y (if $c_{ijk} < -1$)	Y	Y	3

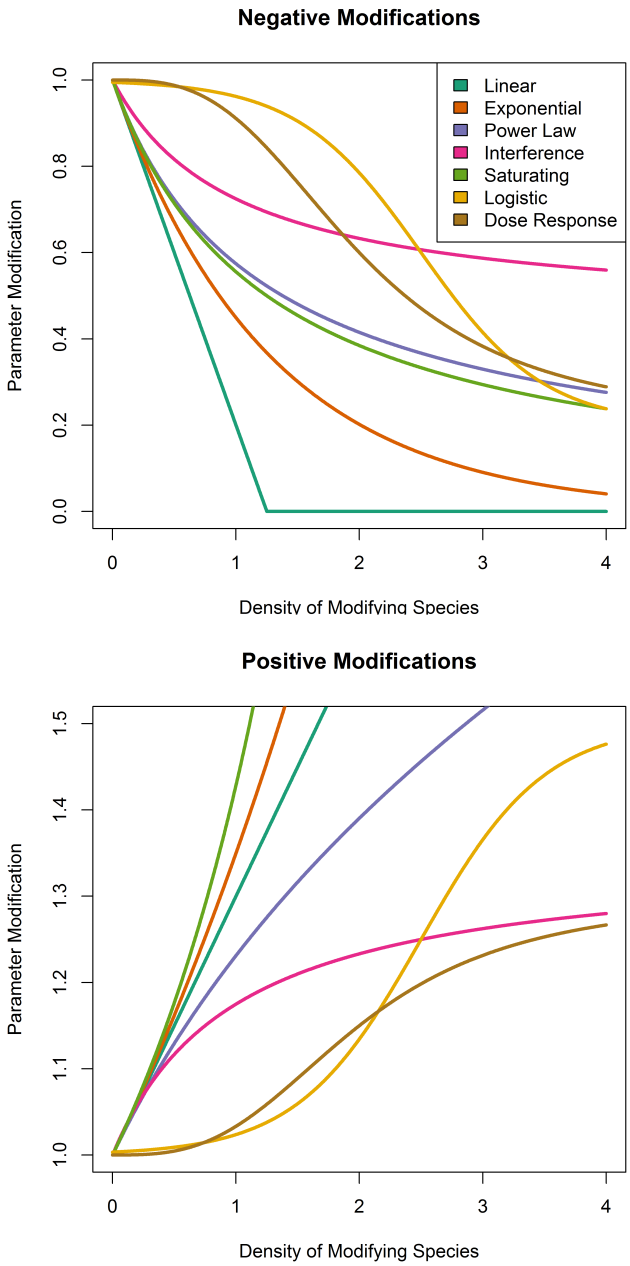


Figure A.1: Graphical depictions of example modification functions in Table 1. For the negative modifications $T_0 = 1$, $M_{nti} = 0.2$, $M_0 = 1$, d = 2.5, u=2, v=3, c_{ijk} = -0.8, a= -2. For positive modifications values are the same except: $c_{ijk} = 0.3$, $M_{nti} = 1.5$.

2: Derivation of Relative Change in B_{CR} TIM Metric

B_{CR} is an interaction strength metric that represents the biomass potential of the resource that is captured by the consumer. It was originally put forward by Gilbert *et al.* (2014) in their study of the effect of temperature on interaction strength given temperature affects multiple parameters simultaneously. It has been used by Nilsson & McCann (2016) to show that this metric (which they term 'New IS') relates in a straightforward and meaningful way to stability. It uses biomass accumulation of the resource and consumer relative growth to define B_{CR} in terms of biomass flow through the consumer- resource system. This flow is related to static measures of the resource biomass (K/R^*) and has the advantage of being interpretable both experimentally and theoretically. K in this context is seen as an aggregate of supply rate and resource loss rate and R is the denisty of the resource.

B_{CR} is defined (Gilbert *et al.* 2014, Eq 3.) where both resource and consumer are able to coexist as:

$$B_{CR} \propto \frac{\text{[Consumption Efficency][Resource Biomass Accumulation]}}{\text{[Consumer Loss]}} =$$

$$\frac{[ef(R)][K]}{[m(C)]} = \frac{K}{R^*} = \frac{R \text{ without consumer}}{R \text{ with consumer}}$$

B_{CR} measures can be represented by aggregates of parameters. Both papers present how these values can be derived from parameter sets for different models with different functional responses. It can be used for higher trophic levels using appropriate measures of equilibrium biomasses of prey in place of K. Eg: Type I functional response (Gilbert et al 2014, Eq 5.):

$$B_{CR} \propto \frac{R^* \text{ without consumer}}{R^* \text{ with consumer}} = \frac{K}{m/ea} = \frac{eaK}{m}$$

We suggest a metric of the strength of a TIM could be the ratio of this new metric with and without the TIM:

$$\Delta B_{CR} = \frac{B_{CR} + TIM}{B_{CR}\ 0\ TIM} = \frac{\frac{R \text{ without consumer+TIM}}{R \text{ with consumer+TIM}}}{\frac{R \text{ without consumer 0 TIM}}{R \text{ with consumer 0 TIM}}}$$

Since the TIM would not be having an effect when there is no consumer this can be simplified twice:

$$TIM = \frac{\frac{R \text{ without consumer}}{R \text{ with consumer+TIM}}}{\frac{R \text{ without consumer}}{R \text{ with consumer 0 TIM}}} = \frac{R \text{ with consumer+TIM}}{R \text{ with consumer 0 TIM}}$$

This gives some stronger justification for using this otherwise quite simple metric of TIMs, the change in equilibrium density of the resource caused when the TIM is present. It has the advantage of being composed of calculable parameters.

As an example, here we calculate the change in B_{CR} in a minimal three species Lotka-Volterra with logistic growth and a TIM from a modifier species denoted by $f(M)$, where M and C are the densities of the modifier and the resource respectively:

$$\frac{dM}{dt} = eaMC - nM$$

$$\frac{dC}{dt} = ef(M)aCR - aMC - mC$$

$$\frac{dR}{dt} = r(1 - R/K)R - f(M)aCR$$

The effect of the TIM could be defined from the non-zero equilibria, showing that in this case the strength of the TIM depends on a particular subset of parameters and the magnitude of ΔB_{CR} is not directly related to $f(M)$ due to the 1- term.

$$C^* = n/ea$$

$$R^* = K(1 - \frac{af(M)C^*}{r}) = K(1 - \frac{f(M)n}{er})$$

$$M^* = ef(m)R^* - m/a) = ef(m)K(1 - \frac{f(m)n}{er}) - m/a)$$

$$\Delta B_{CR} = \frac{R\text{with consumer+TIM}}{R\text{with consumer 0 TIM}} = \frac{K(1 - \frac{f(M)n}{er})}{K(1 - \frac{n}{er})} = \frac{1 - \frac{f(M)n}{er}}{1 - \frac{n}{er}}$$

3: Measuring TIMs in Cycling Systems

One approach to quantify the impact of a TIM on the dynamics of a particular system would be to measure the coefficient of variation (CV) of key values such as μ or biomass flux. This approach is not always straightforward as fluctuations in biomass flux that would be present in the system without the TIM would need to be taken into account.

As an example system, the non-linear tri-trophic system detailed below can be parameterised to give stable cycles, as indicated by the positive CV of predator density in Fig S3a when c = 0.

$$\frac{dP}{dt} = \frac{\mu e_p a_p HP}{1 + \mu h_p a_p H} - m_p P$$

$$\frac{dH}{dt} = \frac{e_h a_h RH}{1 + h_h a_h R} - \frac{\mu a_p HP}{1 + \mu h_p a_p H} - m_h H$$

$$\frac{dR}{dt} = GR\left(1 - \frac{R}{k}\right) - \frac{a_h RH}{1 + h_h a_h R}$$

$$\mu = \exp\left(c_{ijk} R\right)$$

$a_h = 5, h_h = 1.24, m_h = 0.4, e_h = 1, a_p = 0.8, h_p = 2.5, m_p = 0.08, e_p = 1, c_{ijk} = 0, G = 1, K = 0.58$

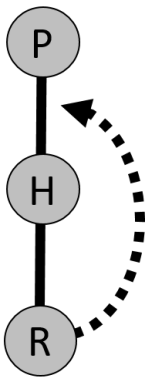


Figure A.2: Diagram of modelled community

When an exponential TIM from the resource onto the predator-herbivore interaction is included, it can be seen that initially moving c_{ijk} above or below 0 leads to an increase in the CV of the parameter modification (μ) (Fig S3b). With larger positive values of c_{ijk}, the values for CV of μ continue to rise. However, in this model a negative TIM is stabilising (Fig S3a) and past a point (marked '*') the CV of μ starts to decline to 0 as the system is forced towards an equilibrium (Fig S2b). A strongly negative TIM has in this case had a strong effect on the macro-dynamics of the system, but in doing so has masked its own dynamic effect.

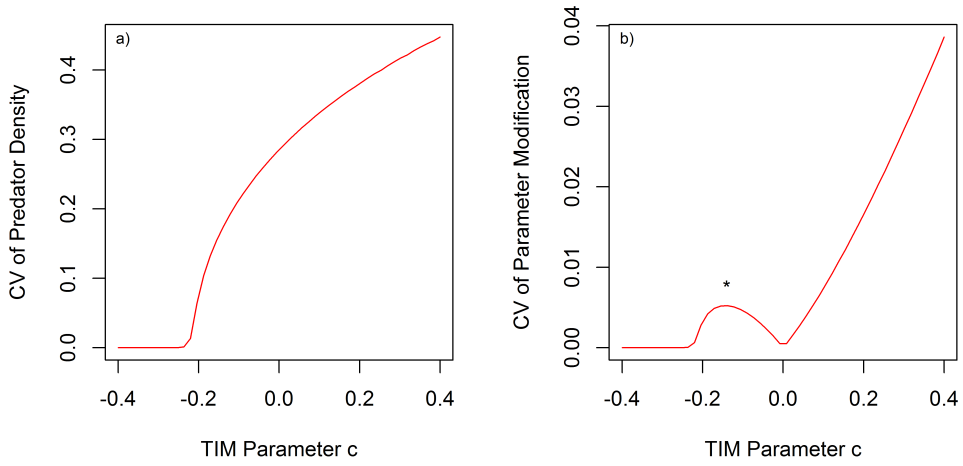


Figure A.3: Plots of metrics for TIMs in a cycling system. a) coefficient of variation (CV) of the predator population density, b) CV of the parameter modification term (μ)

4: Model Details for Metric Comparisons

Model structures and parameters used in the Figure 3 of the main text.

'Linear' model:

$$\frac{dA}{dt} = a'AB - mA$$

$$\frac{dB}{dt} = bBC - a'AB - nB$$

$$\frac{dC}{dt} = rC\left(1 - \left(\frac{C}{K}\right)\right) - bBC$$

$$a' = a + cC$$

a = 5, b = 3, r = 4, c = 0, m = 1, n = 1, K = 1

'Non-linear' model:

$$\frac{dA}{dt} = \frac{a'AB}{1 + a'hB} - mA$$

$$\frac{dB}{dt} = \frac{bBC}{1 + bhC} - \frac{a'AB}{1 + a'hB}\breve{}nB$$

$$\frac{dC}{dt} = rC\left(1 - \frac{C}{K}\right) - \frac{bBC}{1 + bhC}$$

$$a' = ae^{cR}$$

a = 6, b = 5, r = 2, c = 0, m = 1, n = 1, h= 0.4, K = 1

'Aphid-Parasitoid' model of van Veen *et al.* (2005):

$$\frac{dA}{dt} = \frac{saAB}{1 + bB + cC + dA} - mA$$

$$\frac{dB}{dt} = r_B B\left(1 - \alpha_{BB}B - \alpha_{BC}C\right) - \frac{aAB}{1 + bB + cC + dA}$$

$$\frac{dC}{dt} = r_C C\left(1 - \alpha_{CC}C - \alpha_{CB}C\right)$$

Parameters have been renamed for consistency with the other models. In order to fit the populations on the same scale, the population densities of the aphids and parasitoids are displayed on a log-scale.

A = Parasitoid wasp (*A. ervi*), B = Host aphid (*A. pisum*), C= Competitor aphid (*M. viciae*). a =0.000382, a_{BC}=0.00037, a_{CB}=0.000397, r_B =3.22, r_C =2.82, a_A =0.281, s =0.5, d =1.26, b =0.0233, m =0.634. Fitted value of c=0.043

5: Comparison of TIMs with Direct Parameter Changes

In stable systems, the introduction of a TIM can have equivalent effects to directly changing TIM parameters. As a demonstration, we examine the tri-trophic system detailed in Appendix 3 above, with a TIM introduced using an exponential link function and a standard set of parameters where the producer modifies the top predator-consumer interaction.

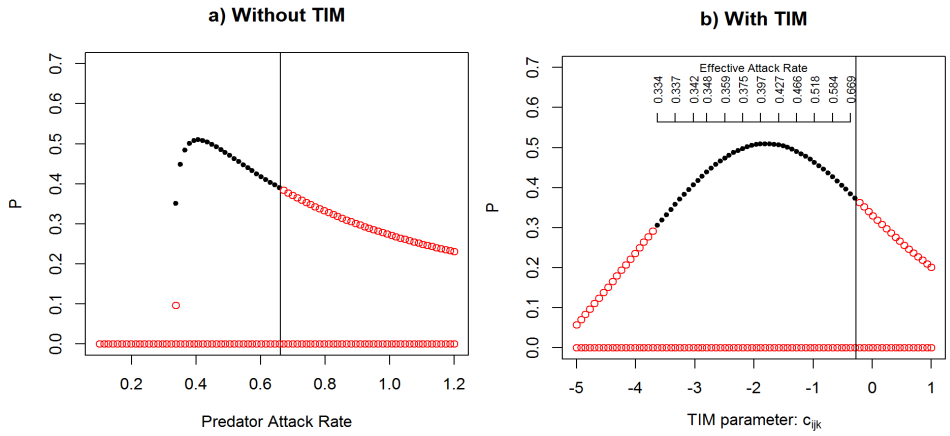


Figure A.4: Stability diagrams comparing direct modification of attack rates (a) to the introduction of a TIM (b). Stable roots are shown as black dots, unstable with red circles.

Stability is calculated from eigenvalues of the Jacobian at the system roots. A system with parameters that would lead to a cycling system can be stabilised either by reducing the attack rate of the predator directly (Fig S4a), or by increasing the negative effect of the TIM (Fig S4b). The stabilising effect of the TIM cannot therefore be directly attributed to the extra dynamic components of the TIM. For this an additional step is necessary, for example a close examination of the point at which the stability is attained. It is possible to infer the resultant post-modification attack rate and compare to direct modification diagram. Here the system with direct change becomes unstable at an attack rate of approximately 0.66. With the TIM the equivalent boundary between stability and instability occurs at c_{ijk} = -0.267, which is equivalent in this model to a μ of 0.876 and hence a predator attack rate of 0.7.

This means that this system with a resultant attack rate of 0.68 would be stable when produced by this TIM, but unstable in a system with fixed parameter values, demonstrating an additional role for the dynamic processes. Note that towards the left of the diagrams in this system there is a very strong divergence between the impact of lower fixed attack rates (which do not permit even unstable systems to exist) and large negative effects of the modification, which can lead to persistent (albeit very large) cycles.

B

Supplementary Material for Chapter 2

Contents

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1: Further Details of the Specification of Artificial Communities

Defining body masses

Body masses are assigned in a similar manner to Iles and Novak (2016). 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 body masses were specified on a logarithmic scale (base 10):

i Producers were assigned a body mass of 0.

ii Primary consumer (Trophic level 2)) body-masses were drawn from a normal distribution: $\mathcal{N}(0.65, \sigma = 1.52)$, 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:

$$0.65 + \sum_{1,\ldots,h} \mathcal{N}\left(2.73, \sigma = \frac{1.6}{\sqrt{h}}\right)$$

This results in body-masses distributed in a relatively hierarchical manner with trophic level

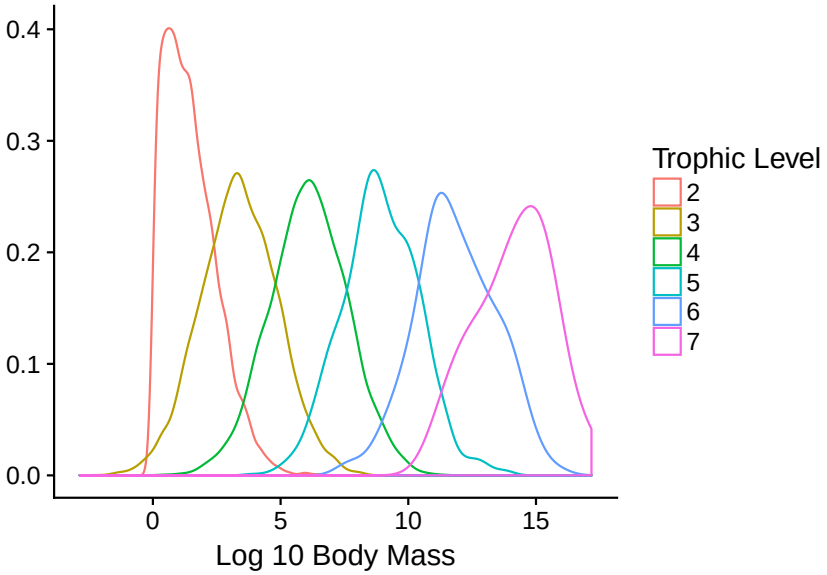


Figure B.1: Histogram of body mass distribution with trophic level. Note all Producers have a body mass of 1 (i.e. 0 on the logarithmic scale)

Defining attack rates

Biomass density specific attack rates a_{ij} were set based on documented relationships (Pawar *et al.* 2012) between consumer-resource size ratios and attack rates. We used a scaling exponent (β) of 0.95, intermediate between empirical values for 2D and 3D foraging behaviour. We also introduce a generality penalty term term ω_j, which is a simple prey preference term equal to 1/n, the number of prey species of predator j. We don't include a unit correction term described in the original paper since this would be a constant term in our interaction matrices.

$$a_{ij} = m_j^{\beta-1}\omega_j \frac{(m_i/m_j)^{0.46}}{1+(m_i/m_j)^2}$$

2: Distribution of Trophic and Non-Trophic Effect Strengths

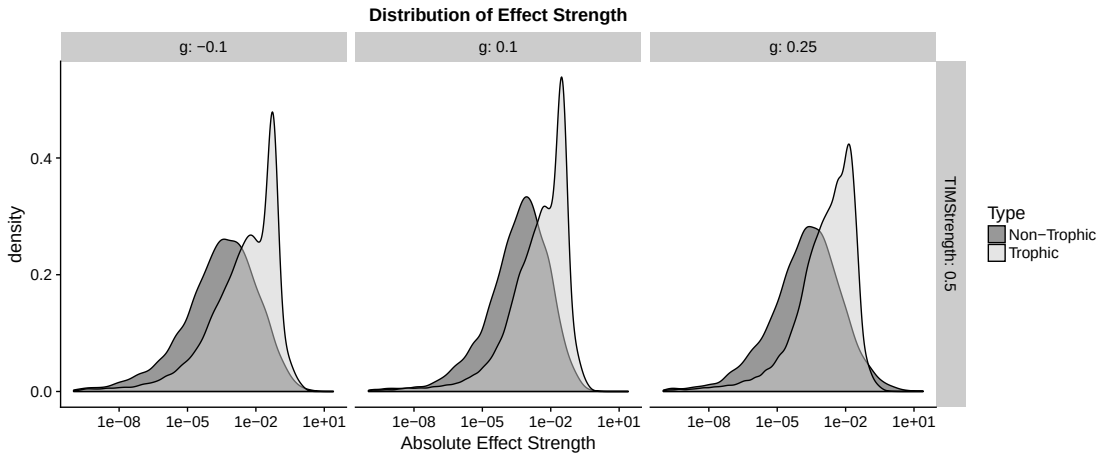
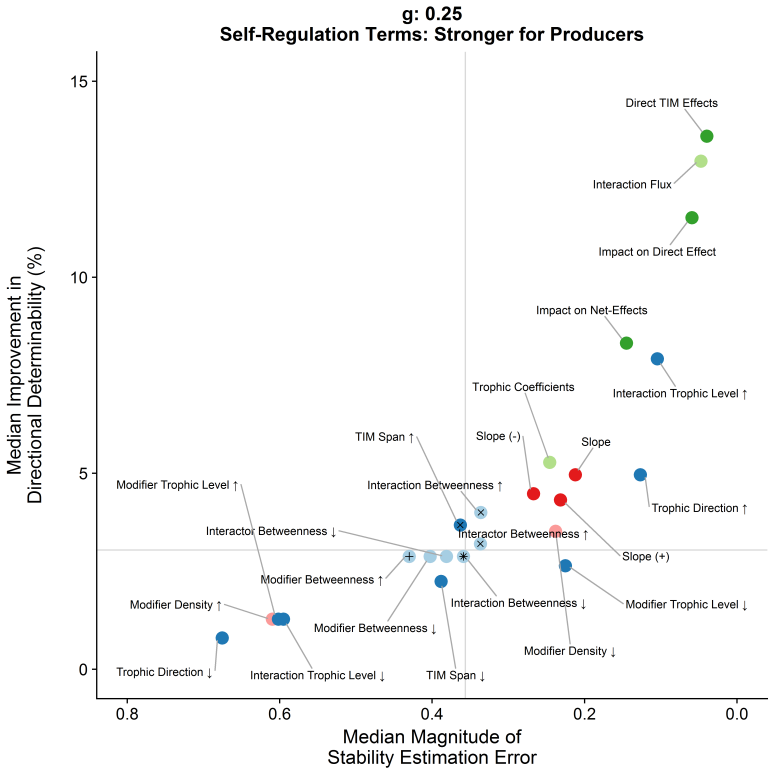


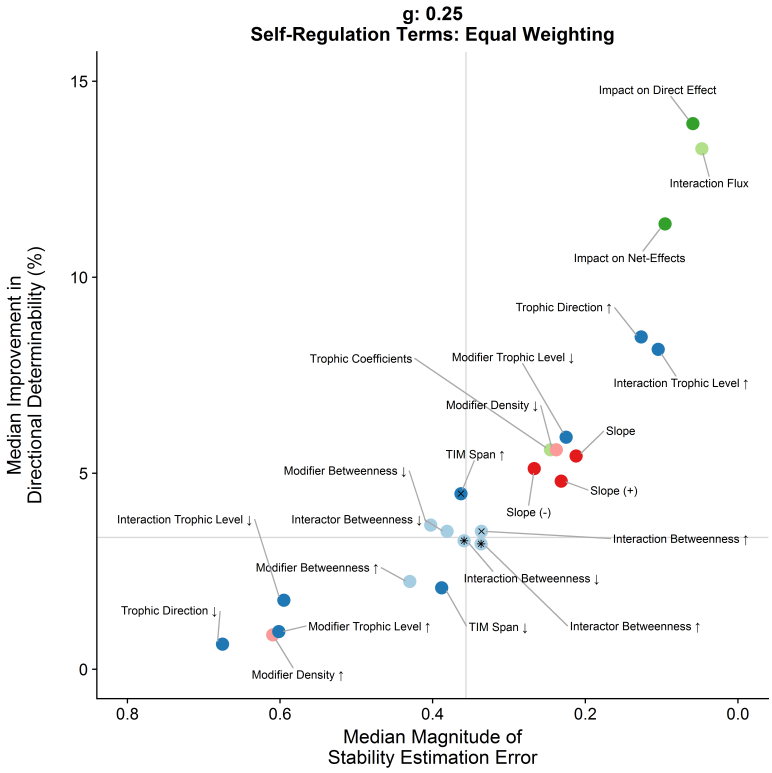
Figure B.2: Comparison of the magnitude of the strength of trophic and non-trophic pairwise interaction elements under three different parameterisation of the trophic network.

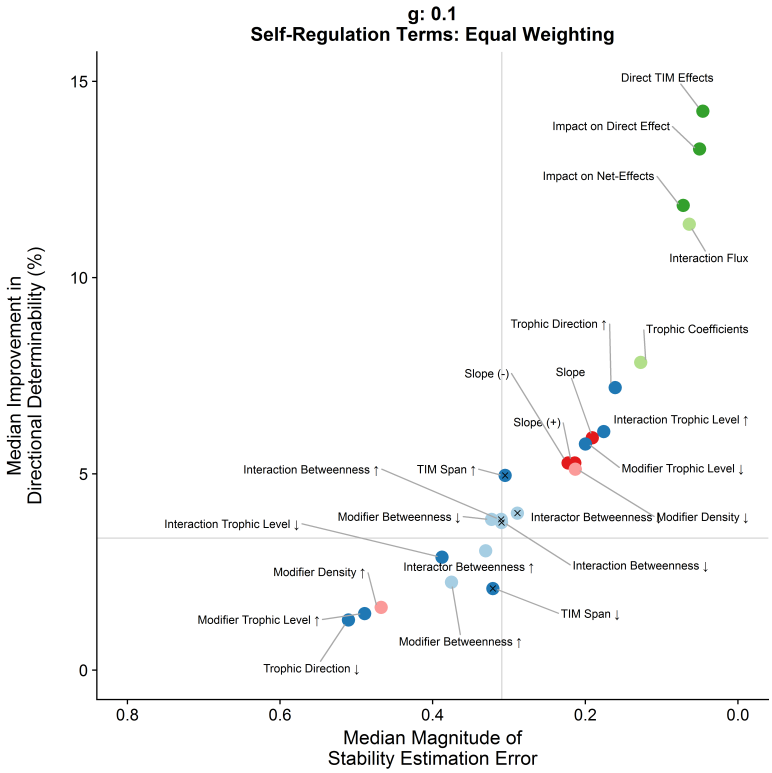
3: Supplementary Results

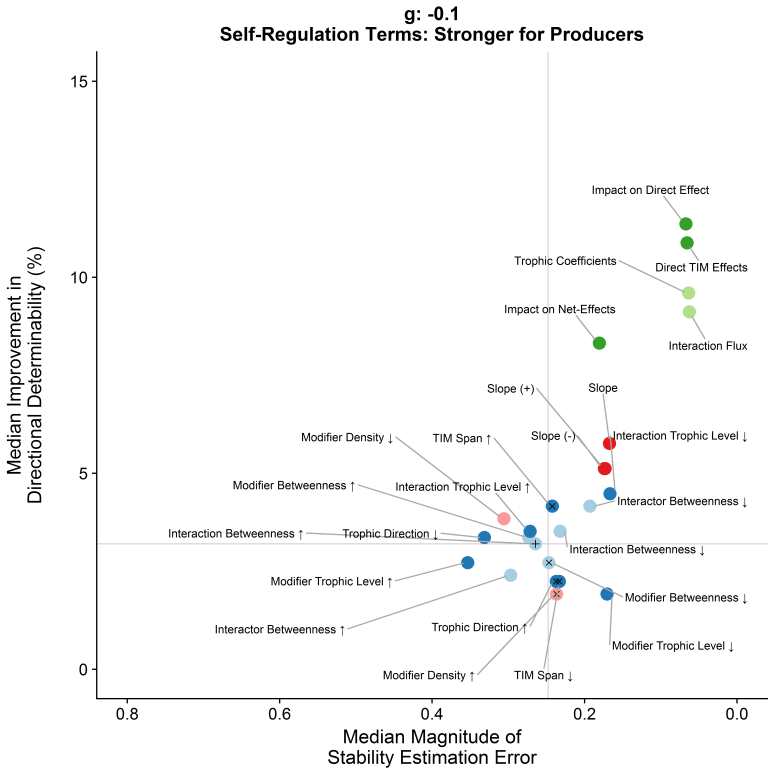
Alternative trophic parameterisations

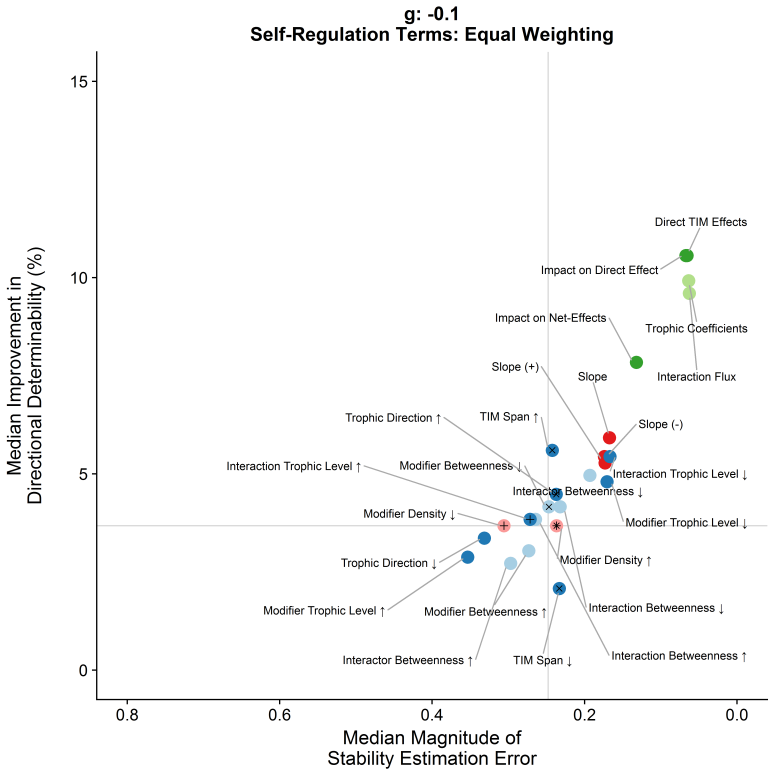
Figures equivalent to Figure 3 of the main text showing broadly similar results when two properties of the trophic parameterisation are changed - the body-mass:abundance scaling factor, g, and the distribution of self-regulation terms, as discussed in the main text.




g: 0.25
Self-Regulation Terms: Equal Weighting
Median Improvement in Directional Determinability (%)
Median Magnitude of Stability Estimation Error
Impact on Direct Effect
Interaction Flux
Impact on Net-Effects
Trophic Direction ↑
Interaction Trophic Level ↑
Trophic Coefficients
Modifier Trophic Level ↓
Modifier Density ↓
Slope
TIM Span ↑
Modifier Betweenness ↓
Slope (+)
Slope (-)
Interaction Trophic Level ↓
Interactor Betweenness ↓
Interaction Betweenness ↑
Modifier Betweenness ↑
Interaction Betweenness ↓
Trophic Direction ↓
Modifier Trophic Level ↑
TIM Span ↓
Interactor Betweenness ↑
Modifier Density ↑


g: 0.1
Self-Regulation Terms: Equal Weighting
Median Improvement in Directional Determinability (%)
Median Magnitude of Stability Estimation Error
Direct TIM Effects
Impact on Direct Effect
Impact on Net-Effects
Interaction Flux
Trophic Direction ↑
Trophic Coefficients
Slope (-)
Slope
Slope (+)
Interaction Trophic Level ↑
Interaction Betweenness ↑
TIM Span ↑
Modifier Trophic Level ↓
Modifier Betweenness ↓
Interactor Betweenness ↓
Modifier Density ↓
Interaction Trophic Level ↓
Interactor Betweenness ↑
Interaction Betweenness ↓
Modifier Density ↑
TIM Span ↓
Modifier Trophic Level ↑
Modifier Betweenness ↑
Trophic Direction ↓


g: -0.1
Self-Regulation Terms: Stronger for Producers
Median Improvement in Directional Determinability (%)
Median Magnitude of Stability Estimation Error
15
10
5
0
0.8
0.6
0.4
0.2
0.0
Impact on Direct Effect
Trophic Coefficients
Direct TIM Effects
Impact on Net-Effects
Interaction Flux
Slope (+)
Slope
Modifier Density ↓
TIM Span ↑
Slope (-)
Interaction Trophic Level ↓
Modifier Betweenness ↑
Interaction Trophic Level ↑
Interactor Betweenness ↓
Interaction Betweenness ↑
Trophic Direction ↓
Interaction Betweenness ↓
Modifier Trophic Level ↑
Modifier Betweenness ↓
Interactor Betweenness ↑
Trophic Direction ↑
Modifier Trophic Level ↓
Modifier Density ↑
TIM Span ↓


g: -0.1
Self-Regulation Terms: Equal Weighting
Median Improvement in Directional Determinability (%)
Median Magnitude of Stability Estimation Error
15
10
5
0
0.8
0.6
0.4
0.2
0.0
Direct TIM Effects
Impact on Direct Effect
Impact on Net-Effects
Trophic Coefficients
Slope (+)
Slope
Interaction Flux
Trophic Direction ↑
TIM Span ↑
Slope (-)
Interaction Trophic Level ↑
Modifier Betweenness ↓
Interaction Trophic Level ↓
Interaction Betweenness ↓
Modifier Density ↓
Modifier Trophic Level ↓
Trophic Direction ↓
Modifier Density ↑
Modifier Trophic Level ↑
Modifier Betweenness ↑
Interaction Betweenness ↓
Interactor Betweenness ↑
TIM Span ↓
Interaction Betweenness ↑

Directional determinacy



Figure B.3: Boxplot showing extent of variance around the median values plotted in the main text figure for each of the metrics in the shift in directional determinacy on inclusion of TIMs as selected by a particular metric

Stability estimation

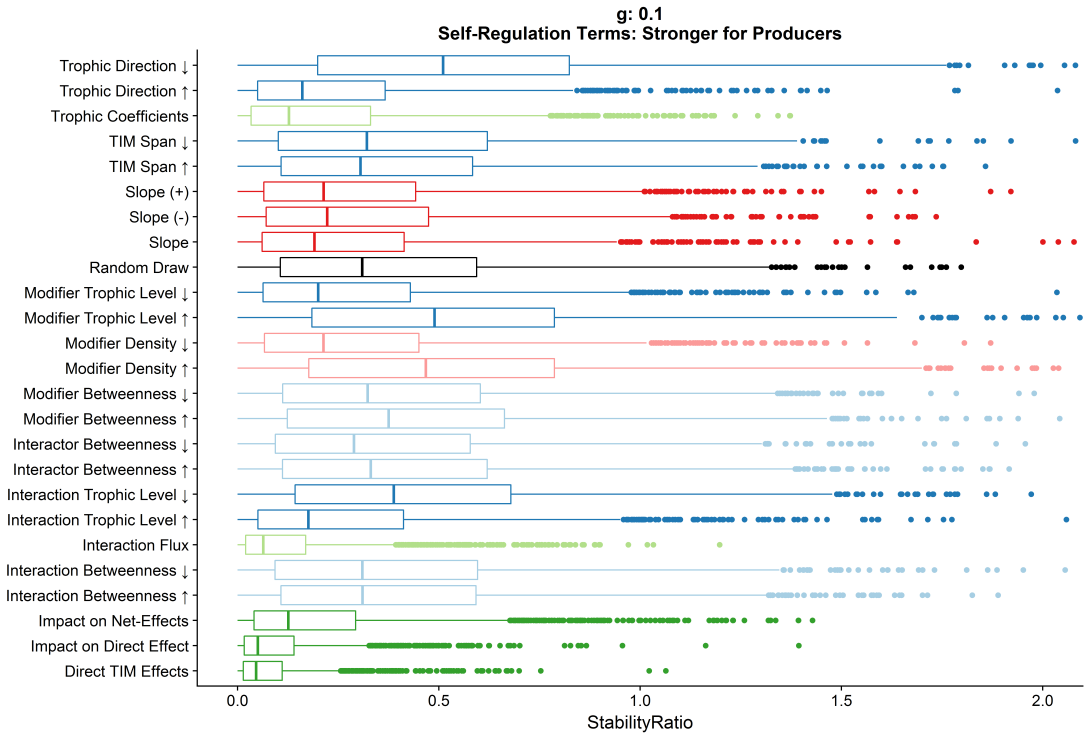


Figure B.4: Boxplot showing extent of variance around the median values plotted in the main text figure for each of the metrics in the stability estimation error on inclusion of TIMs as selected by a particular metric

4: Condition Numbers of Matrices

The accuracy of numerical inversion of matrices can be sensitive to machine tolerances. The amount of errors that introduced by a matric manipulation can be descibed by a *condition number*, often κ. A rule of thumb that is often suggested is: If the entries in $\mathbf{A}$ and $\mathbf{B}$ are accurate to r significant digits, and if the condition number of $\mathbf{A}$ is approximately κ , then the computed solution of $\mathbf{A}x = \mathbf{B}$ should usually be accurate to at least $r - \log_{10}(\kappa)$ significant digits.For 'normal' matrices, the condition number for inverting can be directly calculated as the ratio of the largest and smallest eigenvalues $\mid \frac{\lambda_{max}}{\lambda_{min}} \mid$. However this does not hold for non-normal matrices, such as our communities, so we calculate κ directly using `base::rcond()`.

The figure below shows that although our $\mathbf{A}$ matrices were relatively ill-conditioned, the numerical accuracy of the inversion was still than the vast majority of (98.4%) of net-effect elements, in most cases by many orders of magnitude higher. We can therefore be confident of the numerical stability of our results.

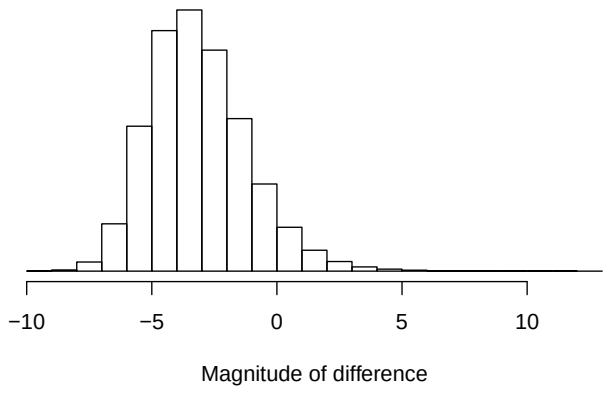


Figure B.5: Histogram of differences between reciprocal condition number of interaction matrices and magnitude of net-effect elements

5: Statistical Results

Table B.1: Results tables containing the results of statistical significance tests for other parameterisations are provided as .csv files in the online supplementary material named after the model parameters used to generate them. D.D.= 'Directional Determinacy'

Metric	Metric Category	Mean D.D.	Median D.D. Change	D.D. p-value	Count D.D.>10% Worse	Median Stability Error	Stability p-value
Interaction Flux	Interaction Size	0.787	0.102	0.000	31	0.064	0.000
Trophic Coefficients	Interaction Size	0.753	0.067	0.000	22	0.127	0.000
Direct TIM Effects	Modification Strength	0.805	0.125	0.000	15	0.046	0.000
Impact on Direct Effect	Modification Strength	0.793	0.110	0.000	20	0.050	0.000
Impact on Net-Effects	Modification Strength	0.771	0.090	0.000	7	0.126	0.000
Slope	Slope Parameter	0.738	0.051	0.000	14	0.191	0.000
Slope (+)	Slope Parameter	0.730	0.045	0.000	14	0.214	0.000
Slope (-)	Slope Parameter	0.734	0.046	0.000	41	0.223	0.000
Modifier Density (Higher)	Modifier Biomass	0.703	0.018	0.000	61	0.468	0.000
Modifier Density (Lower)	Modifier Biomass	0.721	0.035	0.000	39	0.213	0.000
Modifier Betweenness (Higher)	Centrality	0.715	0.026	0.993	9	0.375	0.000
Modifier Betweenness (Lower)	Centrality	0.713	0.027	0.462	21	0.323	0.043
Interactor Betweenness (Higher)	Centrality	0.716	0.027	0.758	17	0.331	0.007
Interactor Betweenness (Lower)	Centrality	0.719	0.030	0.000	38	0.289	0.107
Interaction Betweenness (Higher)	Centrality	0.723	0.034	0.000	10	0.310	0.841
Interaction Betweenness (Lower)	Centrality	0.717	0.027	0.151	27	0.310	0.611
Modifier Trophic Level (Higher)	Trophic Level	0.704	0.018	0.000	11	0.489	0.000
Modifier Trophic Level (Lower)	Trophic Level	0.707	0.022	0.000	7	0.200	0.000
Interaction Trophic Level (Higher)	Trophic Level	0.741	0.054	0.000	30	0.176	0.000
Interaction Trophic Level (Lower)	Trophic Level	0.708	0.021	0.000	33	0.388	0.000
Trophic Direction (Higher)	Trophic Level	0.721	0.035	0.000	19	0.161	0.000
Trophic Direction (Lower)	Trophic Level	0.702	0.014	0.000	49	0.510	0.000
TIM Span (Higher)	Trophic Distance	0.723	0.035	0.000	19	0.305	0.962
TIM Span (Lower)	Trophic Distance	0.709	0.021	0.000	6	0.321	0.172
Random Draw	Random Draw	0.714	0.027	NA	29	0.309	NA

6: Correlation Between TIM Properties for Alternative Trophic Parameterisations

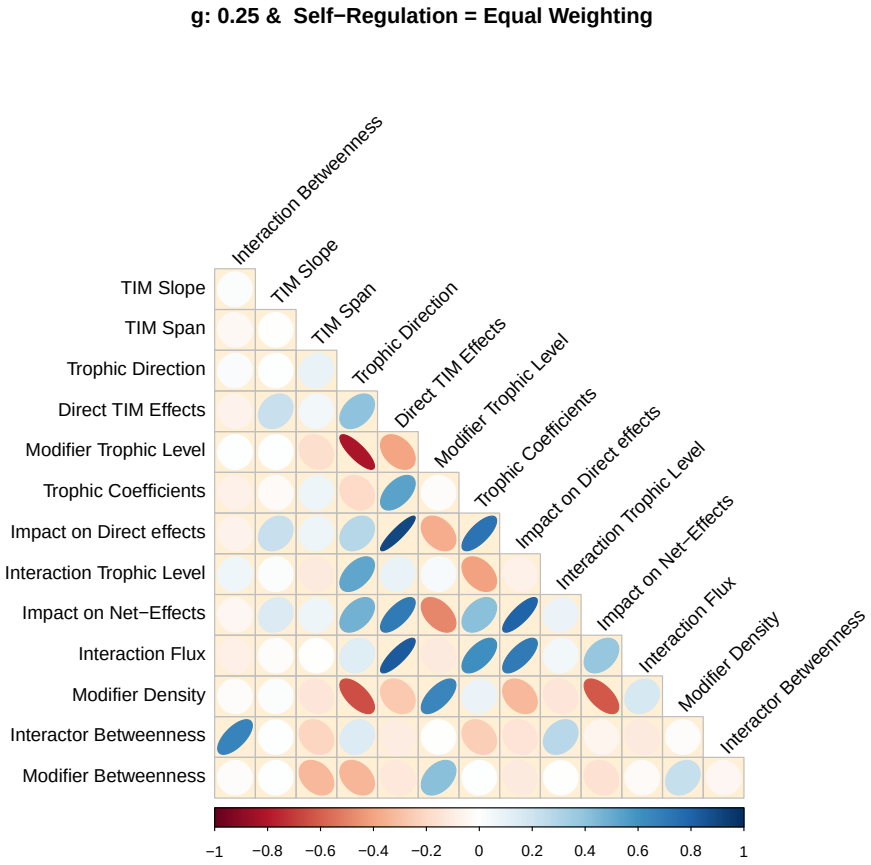


Figure B.6: Correlation between TIM properties when the biomass - abundance scaling, g, = 0.25 and self-regulation terms weighted equally for all species

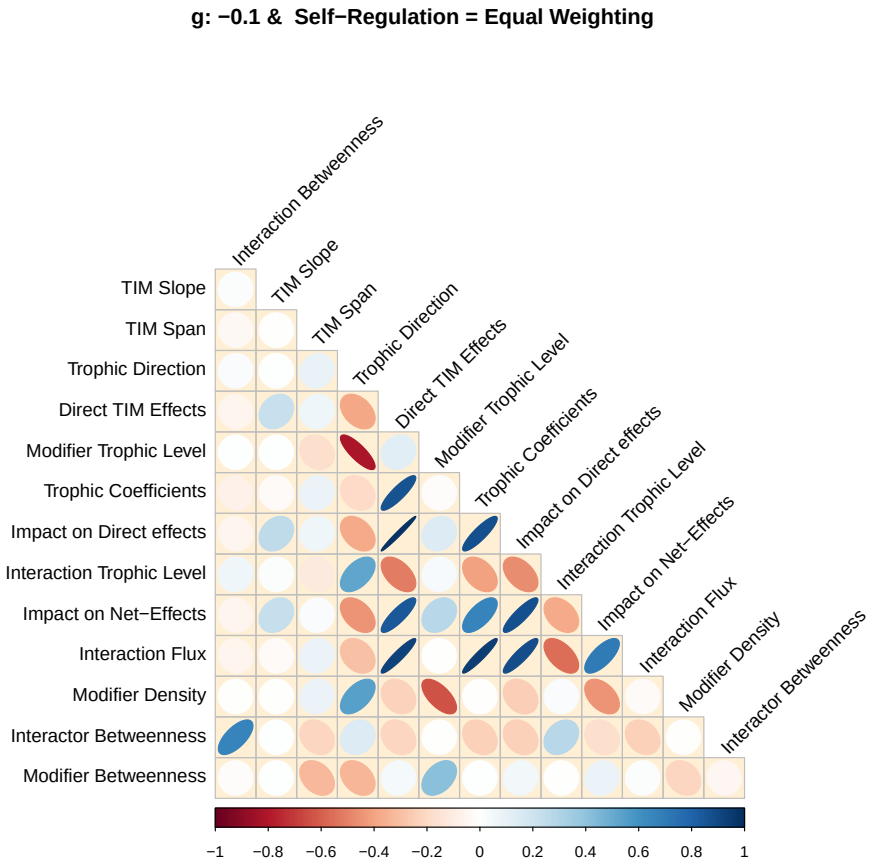


Figure B.7: Correlation between TIM properties when the biomass - abundance scaling, g, = -0.1 and self-regulation terms weighted equally for all species

7: Exploratory Strength Randomisation Study

To look at the importance of accurately understanding the TIM slope parameters we conducted a simple randomisation study. Using a set of 500 stable communities generated as described in the main text, using $g = 0.1$ and the parameterisation with stronger producer competition.

For each community we conducted two randomisation experiments using the custom function `Randomise_Cijk_Values()`:

1. Re-drawing the c_{ijk} slope parameters from a uniform distributuon, retaining the correct sign

2. Assigning every c_{ijk} parameter a value of 0.25, retaining the correct sign

In each case the full model and the randomisation model were compared for stability estimation and directional deterimacy as in the main text.

Parameter Values	Directional Determinacy	Stability Estimation
Random	0.0978	0.1504
Fixed	0.1553	0.1265

C

Supplementary Material for Chapter 3

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1: Model Specifications

Table C.1: Description of models used to distribute interaction modifications and determine non-trophic effects. Letters match the diagrams in the main text. α is the mean magnitude of interaction modification strength, b_{ij} denotes trophic interaction coefficients, i denotes the resource, j the consumer and k the modifier species of a given interaction modification. Parameter ϕ is a standardisation terms used in the Normal distribution to maintain $\mathbb{E}(|c_{ijk}|) = \alpha : \phi = (\alpha\sqrt{\pi})/\sqrt{2}$. γ fulfills the same role in the scaled model: $\gamma = \frac{2\alpha(|a_{ij}|+|a_{ji}|)}{2\mathbb{E}(a_{ij} \in Predation)})$

	Model	Topological Distribution	Interaction modification parameter (c_{ijk}) distribution	Translation from c_{ijk} to NTEs ($\mathbf{C}_{ik}$ and $\mathbf{C}_{jk}$)
Baselines				
	Random NTEs	Each non-diagonal element of C equally likely to be non-zero	NA	Elements of $\mathbf{C}$ drawn directly from $\mathcal{N}(0, \phi)$
a)	Random TIMs with normally distributed strengths and equal NTEs	Each potential TIM equally likely to be present.	$\mathcal{N}(0, \phi)$	$\mathbf{C}_{ik} = -c_{ijk}$ $\mathbf{C}_{jk} = c_{ijk}$
Topological Distribution				
b)	Nearby TIMs Only	Only TIMs where the modifier is trophically linked to at least one of the interactors	"	"
c)	Far TIMs Only	Only TIMs where the modifier is not trophically linked to either of the interactors	"	"
d)	Heterogeneous TIM out-degree ('Ecological Engineers')	Each species is assigned a distinct probability of being a modifier from a beta distribution.	"	"
Distribution of TIM effects				
e)	Facilitating TIMs only	Each potential TIM equally likely to be present.	$\mid \mathcal{N}(0, \phi) \mid$	"
f)	Interfering TIMs only	"	$- \mid \mathcal{N}(0, \phi) \mid$	
g)	Fat-tailed strength distribution.	"	$Laplace(\mu : 0, b : \alpha)$	

h)	Uniformly distributed strength	"	$\mathcal{U}\left(-2\alpha,\ 2\alpha\right)$	
i)	Strength Scaled to Trophic Interaction	"	$\mathcal{U}\left(-\gamma, \gamma\right)$	"
Non-trophic effect balance				
j)	The positive and negative NTEs are uneven for each TIM	"	$\mathcal{N}(0, \phi)$	$\begin{cases} \mathbf{C}_{ik} = -0.5c_{ijk}, \\ \mathbf{C}_{jk} = 1.5c_{ijk} \\ \\ \mathbf{C}_{ik} = -1.5c_{ijk}, \\ \mathbf{C}_{jk} = 0.5c_{ijk} \end{cases}$
k)	Positive NTEs greater than negative	"	$\mid \mathcal{N}(0, \phi) \mid$	$\begin{cases} \mathbf{C}_{ik} = -0.5c_{ijk}, \\ \mathbf{C}_{jk} = 1.5c_{ijk} \\ \\ \mathbf{C}_{ik} = 1.5\ c_{ijk}, \\ \mathbf{C}_{jk} = -0.5c_{ijk} \end{cases}$
l)	Negative NTEs greater than positive	"	"	$\begin{cases} \mathbf{C}_{ik} = 0.5c_{ijk}, \\ \mathbf{C}_{jk} = -1.5c_{ijk} \\ \\ \mathbf{C}_{ik} = -1.5c_{ijk}, \\ \mathbf{C}_{jk} = 0.5c_{ijk} \end{cases}$
Paired TIMs				
m)	Tight Reciprocal.	TIMs distributed in reciprocal pairs. The set of three species i,j, and k are involved in two TIMs.	$\mathcal{N}(0, \phi)$	$\mathbf{C}_{ik} = -c_{ijk}$, $\mathbf{C}_{jk} = \ c_{ijk}$
n)	Reciprocal interference.	TIMs are paired around a consumer and two resources. Each resource reduces the consumption of the other by the shared consumer.	$-\mid \mathcal{N}(\mu = 0, \phi) \mid$	"
o)	Bounded reciprocal interference.	"	$-\mathcal{U}\left(0,\ a_{jk}\right)$	"

2: Structural Properties of Artificial Networks

Table C.2: Mean value of structural properties of the communities with TIMs introduced under different models at a TIM density of 10 per species. To aid interpretation those models that differed significantly (linear model, p<0.05, n=100 per model) from the baseline of equally distributed TIMs with a Normal strength distribution (first row) for a particular structural feature are shown in bold with a (+) or (-) indicating the direction of difference. Exact values of estimated differences, t-values, and p-values are listed in 'Full Statistical Results.csv', available at https://osf.io/8zrsm/

		Connectance		Variance					Structuring		Total Degree Heterogeneity	
TIM Model	Total	Non-Trophic	Total	Non-Trophic	Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Row Structure	Column Structure	In-degree	Out-degree
Baseline Model	0.416	0.281	0.386	0.133	0	0.000282	-0.63	0.024	0.011	0.0283	0.0089
Random NTEs	**0.437** (+)	**0.297** (+)	0.39	**0.138** (+)	0	-0.000159	-0.62	**0.011** (-)	0.011	**0.0082** (-)	**0.0082** (-)
Nearby TIMs	**0.322** (-)	**0.241** (-)	0.385	0.133	0	-0.000419	-0.626	**0.021** (-)	**0.019** (+)	**0.0188** (-)	**0.0186** (+)
Far TIMs	**0.467** (+)	**0.266** (-)	0.387	0.134	0	0	-0.628	0.025	**0.0081** (-)	**0.0323** (+)	**0.0063** (-)
Heterogenous TIM Out-degree	**0.391** (-)	**0.248** (-)	0.383	0.132	0	-0.000466	-0.632	**0.022** (-)	**0.021** (+)	**0.0235** (-)	**0.0297** (+)
Facilitating Modifications	0.416	0.28	**0.429** (+)	**0.145** (+)	0	**0.0157** (+)	-0.637	**0.032** (+)	**0.013** (+)	0.0283	0.0091
Interfering Modifications	0.416	0.281	**0.365** (-)	**0.145** (+)	0	**-0.0161** (-)	**-0.577** (+)	**0.021** (-)	0.011	0.0283	0.0091
Uniformally Distributed Strengths	0.416	0.281	**0.365** (-)	**0.114** (-)	0	-0.000302	**-0.663** (-)	0.022	0.011	0.028	0.0088
Laplace Distributed Strengths	0.415	0.28	**0.419** (+)	**0.167** (+)	0	-7.81e-5	**-0.58** (+)	0.025	**0.013** (+)	0.028	0.0091
Scaled Strengths	0.416	0.281	0.389	**0.137** (+)	0	4.69e-5	-0.623	0.024	0.012	0.0281	0.009
Reciprocal Modifications	**0.295** (-)	**0.221** (-)	0.387	0.133	0	9e-4	-0.629	**0.019** (-)	**0.018** (+)	**0.016** (-)	**0.016** (+)
Reciprocal	**0.293** (-)	**0.191** (-)	**0.304** (-)	**0.227** (+)	0	**-0.0881** (-)	**-2.28e-5** (+)	**0.012** (-)	**0.013** (+)	**0.0142** (-)	**0.0142** (+)
Interference											
Bounded Reciprocal Interference	**0.294** (-)	**0.191** (-)	**0.299** (-)	**0.265** (+)	0	**-0.109** (-)	**0.137** (+)	**0.012** (-)	**0.013** (+)	**0.0141** (-)	**0.0141** (+)
Unbalanced NTEs	0.414	0.279	**0.416** (+)	**0.165** (+)	0	-7e-4	**-0.58** (+)	0.025	0.012	0.0288	0.0089
Larger Positive NTEs	0.415	0.281	**0.43** (+)	**0.17** (+)	**0.09** (+)	**0.00387** (+)	**-0.583** (+)	**0.029** (+)	0.011	0.0282	0.0089
Larger Negative NTEs	0.417	0.282	**0.413** (+)	**0.169** (+)	**-0.09** (-)	**-0.00413** (-)	**-0.568** (+)	0.024	**0.012** (+)	0.0285	0.0088

3: Additional Stability and Reactivity Results

Non-highlighted TIM models

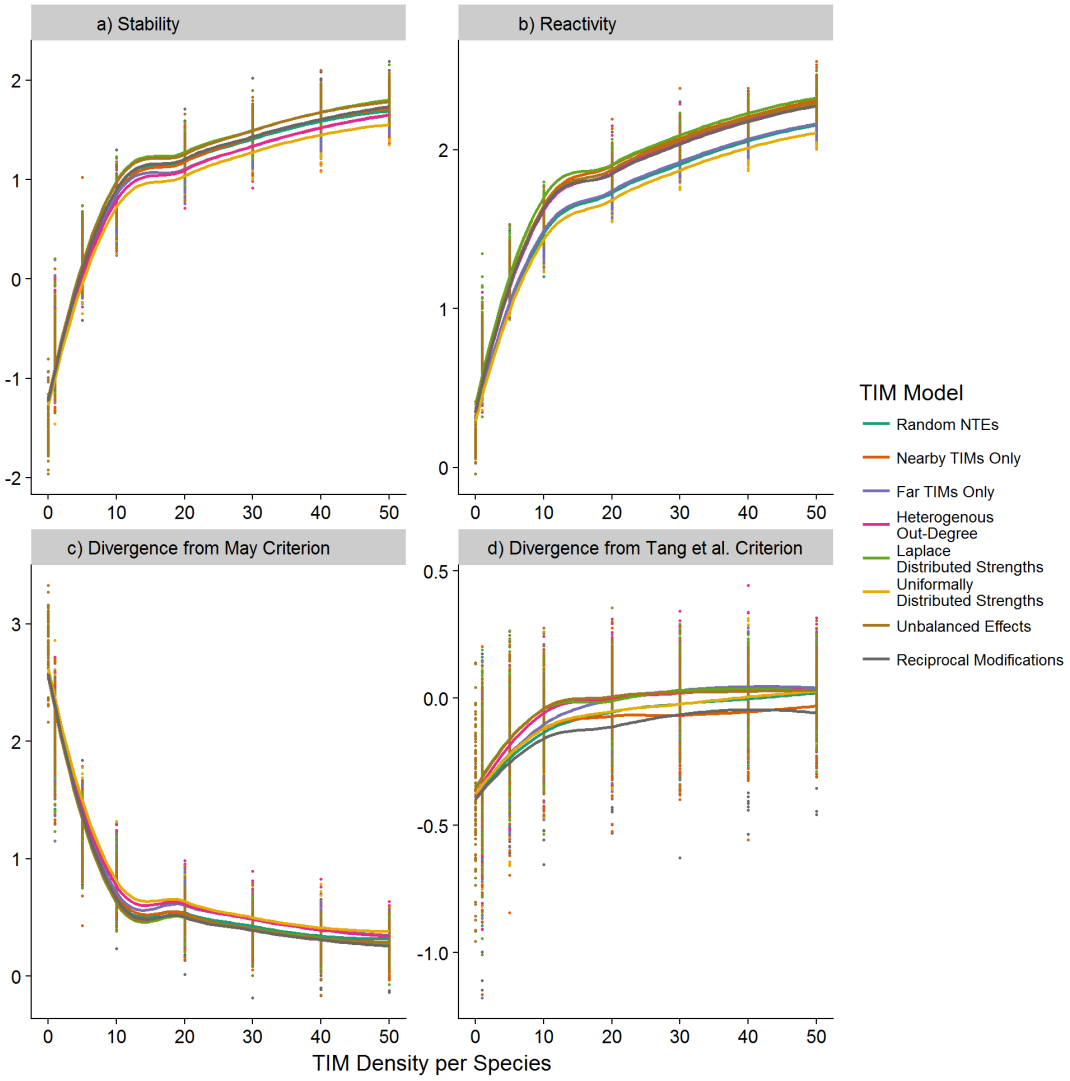


Figure C.1: Responses of models that were coloured grey in the main text Figure 4. Effect of increasing density of TIMs on (a) stability $log(R(\lambda_1^{\mathbf{A}}))$, the degree of self-regulation necessary for local asymptotic stability, (b) system reactivity $log(\lambda_1^{\mathbf{H}})$, (c) the log-ratio of the May stability criterion and the observed stability and (d) the log-ratio of the Tang *et al.* stability criterion and the observed stability.

Repeats with stronger top-down effects

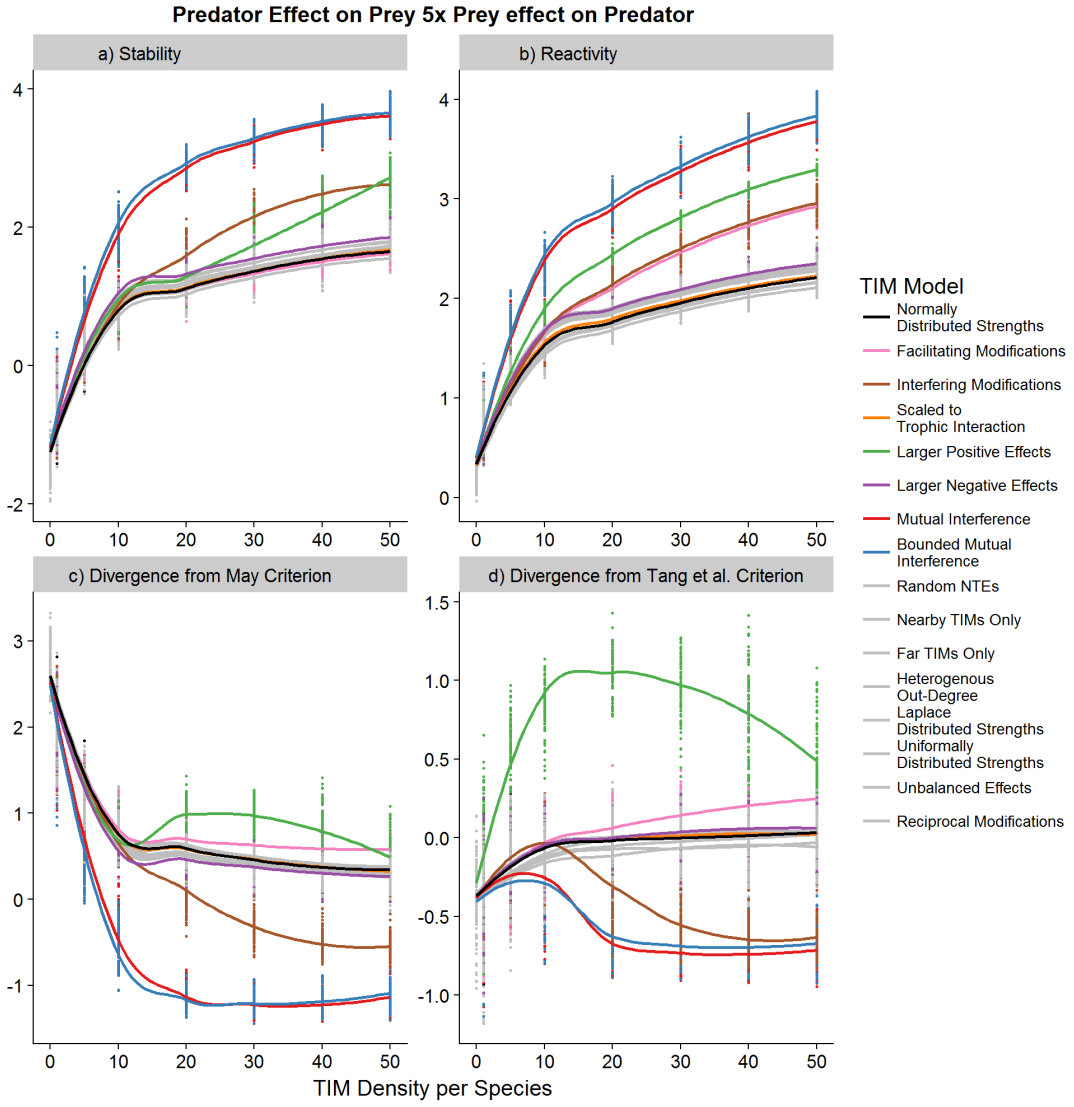


Figure C.2: Repeat of results shown in main text Figure 4 with an underlying trophic interaction distribution where resources were negatively affected by consumers on average 5x as much as consumers were affected by resources. Panels show effect of increasing density of TIMs on (a) stability $log(R(\lambda_1^{\mathbf{A}}))$, the degree of self-regulation necessary for local asymptotic stability, (b) system reactivity $log(\lambda_1^{\mathbf{H}})$, (c) the log-ratio of the May stability criterion and the observed stability and (d) the log-ratio of the Tang *et al.* stability criterion and the observed stability. The impact of TIMs are comparable with the main text results, with the exception that larger positive NTEs (green line) do not lead to destabilisation and facilitation TIMs (pink line) no longer have a distinctive effect.

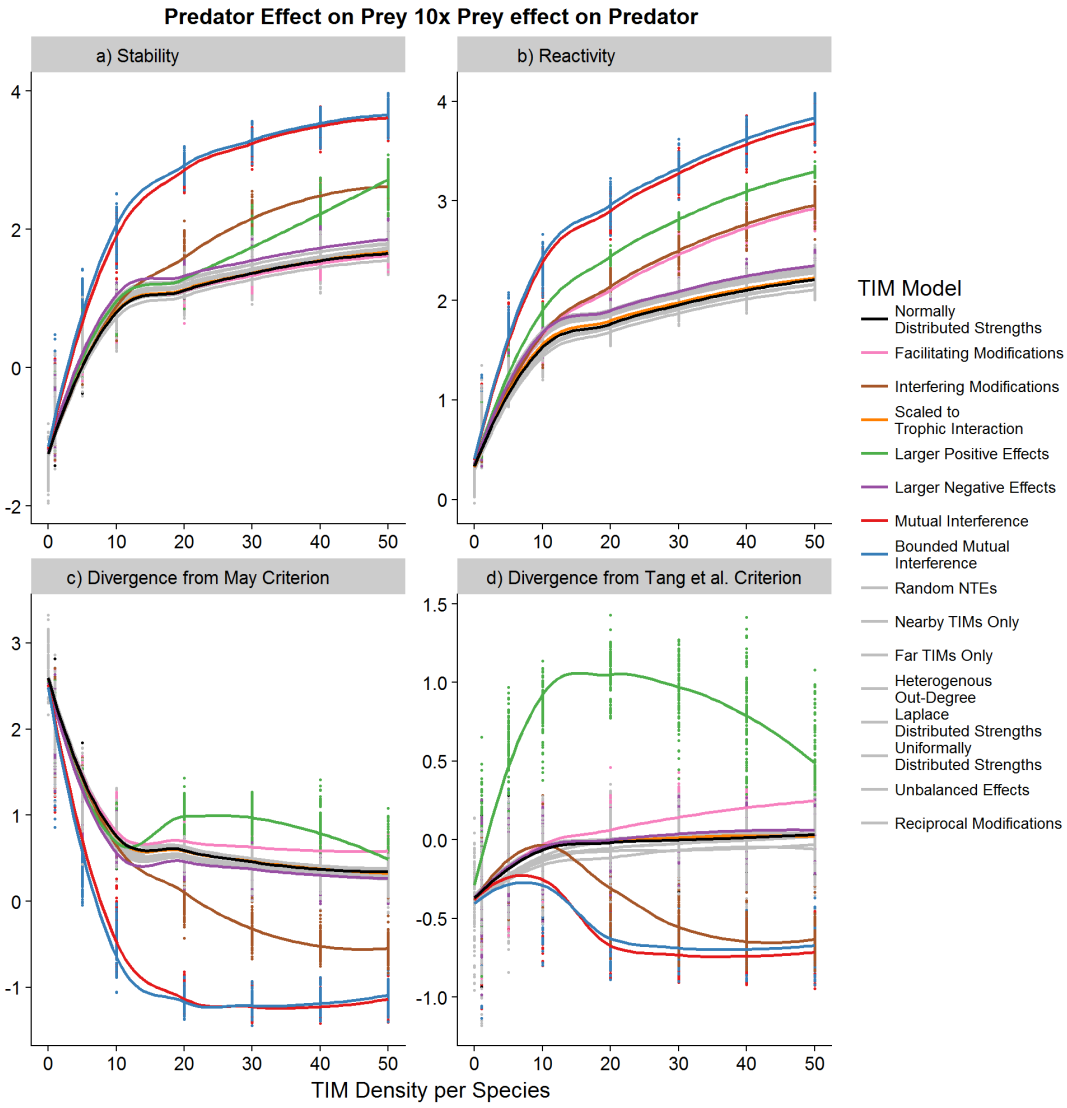


Figure C.3: Repeat of results shown in main text Figure 4 with an underlying trophic interaction distribution where resources were negatively affected by consumers on average 10x as much as consumers were affected by resources. Panels show effect of increasing density of TIMs on (a) stability $log(R(\lambda_1^{\mathbf{A}}))$, the degree of self-regulation necessary for local asymptotic stability, (b) system reactivity $log(\lambda_1^{\mathbf{H}})$, (c) the log-ratio of the May stability criterion and the observed stability and (d) the log-ratio of the Tang *et al.* stability criterion and the observed stability. As with the results shown in Figure S2, the impact of TIMs are comparable with the main text results, with the exception that larger positive NTEs (green line) do not lead to destabilisation and facilitation TIMs (pink line) no longer have a distinctive effect. The grey line that has a less destabilising effect and which maintains the greatest deviation from the Tang et al. Criterion is the Reciprical Modifications model.

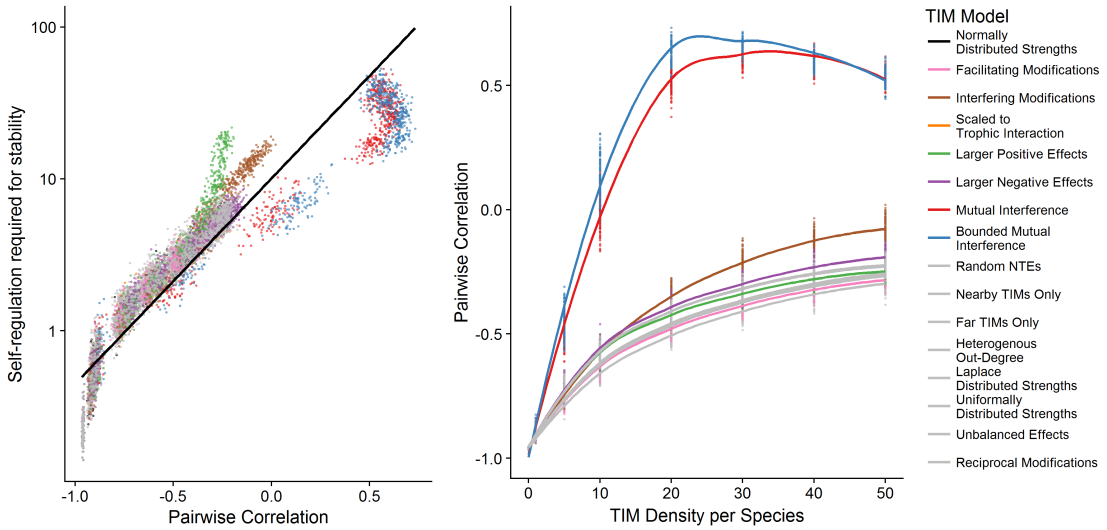
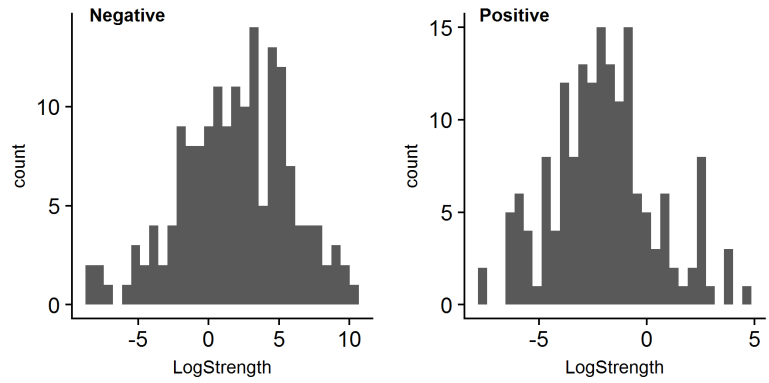


Figure C.4: a) Scatter plot across all replicates and models of the relationship between the pairwise correlation between overall interactions and the stability of the system ($log(R(\lambda_1^A))$) with the artificial trophic networks. The line shows a linear model. It can be seen that the pairwise correlaiton is a very strong predictor of stability. b) shows the impact of TIM density on the pairwise correlation across the different models, with the most diveregence models highlighted. The two mutual interference models most rapidly break down the original negative correlation caused by the specification of the trophic interactions

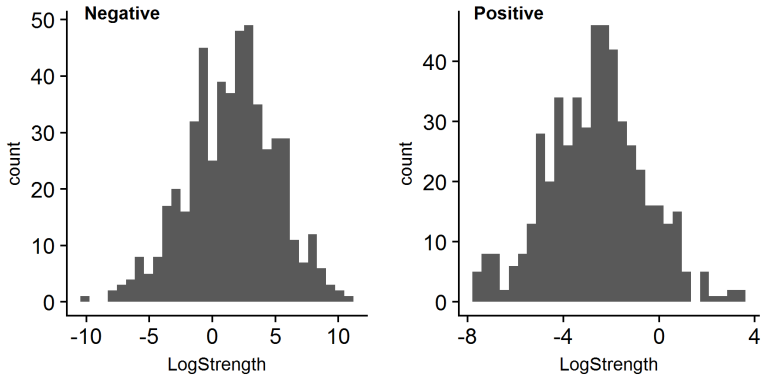
4: Empirical Network Interaction Strength Distribution

Plots of the approximately log-normal distribution of trophic interaction strengths in the five empirical webs, split by whether the interactions were positive or negative.

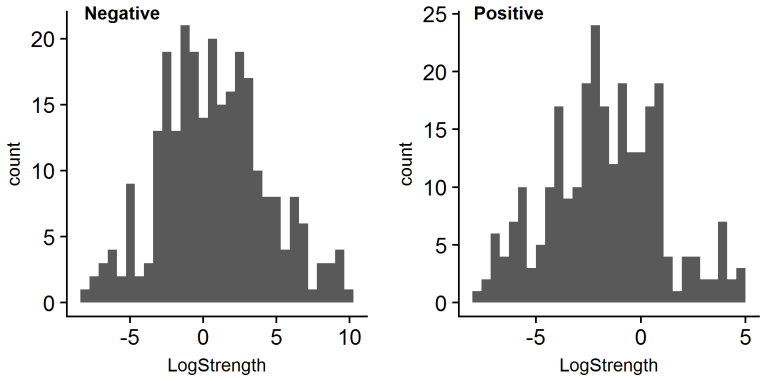
Chesapeake Present



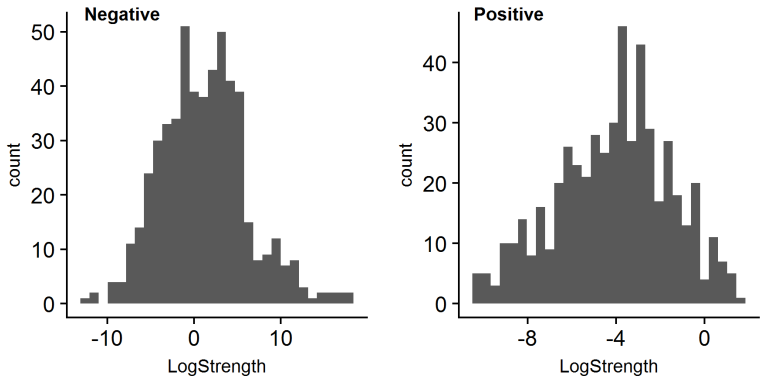
Mid Atlantic Bight



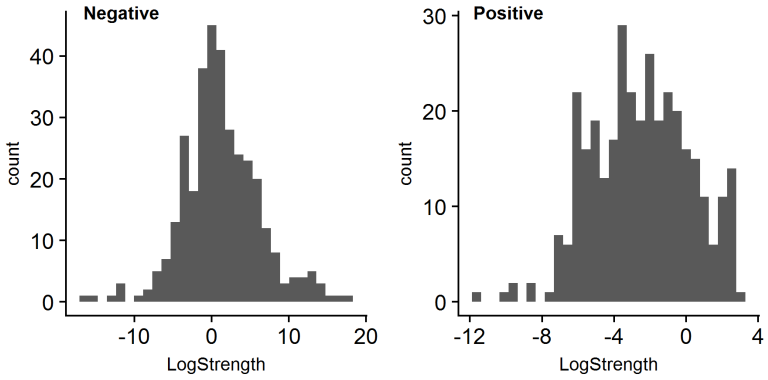
Moorea Reef



Newfoundland (mid-1990s)



Tampa Bay



5: Structural Properties of Empirical Networks with TIMs

Chesapeake Present

Table C.3: Table showing structural properties of Chesapeake Present network with added TIMs.

	Connectance		Variance					Structuring		Total Degree Heterogeneity	
TIM Model	Total	Non-Trophic	Total	Non-Trophic	Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Row Structure	Column Structure	In-degree	Out-degree
Baseline Model	0.492	0.377	869000	0.00337	-70.030	-0.0941	-0.00650	48100	41810	0.0362	0.0111
Random NTEs	0.532	0.412	869000	0.00364	-70.031	0.0073	-0.00650	48100	41810	0.0099	0.0099
Nearby TIMs	0.378	0.320	869000	0.00344	-70.030	0.3670	-0.00650	48100	41810	0.0259	0.0255
Far TIMs	0.558	0.355	869000	0.00349	-70.030	0.0000	-0.00650	48100	41810	0.0401	0.0082
Heterogenous TIM Out-degree	0.455	0.327	869000	0.00344	-70.030	-0.0823	-0.00650	48100	41810	0.0288	0.0409
Facilitating Modifications	0.495	0.381	869000	0.00429	-70.030	4.4100	-0.00650	48110	41810	0.0363	0.0107
Interfering Modifications	0.494	0.379	869000	0.00421	-70.030	-4.4000	-0.00650	48100	41810	0.0365	0.0109
Uniformally Distributed Strengths	0.494	0.380	869000	0.00296	-70.030	-0.1420	-0.00650	48100	41810	0.0368	0.0109
Laplace Distributed Strengths	0.494	0.380	869000	0.00444	-70.030	0.0288	-0.00650	48100	41810	0.0371	0.0105
Scaled Strengths	0.493	0.379	869000	0.05420	-70.030	0.9050	-0.00650	48110	41810	0.0366	0.0105
Reciprocal Modifications	0.346	0.286	869000	0.00349	-70.030	-0.6240	-0.00650	48100	41810	0.0221	0.0221
Reciprocal Interference	0.296	0.210	869000	0.00744	-70.030	-1.2700	-0.00648	48100	41810	0.0287	0.0287
Bounded Reciprocal Interference	0.297	0.211	869000	16.60000	-70.030	-0.3050	-0.00562	48240	41810	0.0288	0.0288
Unbalanced NTEs	0.493	0.379	869000	0.00431	-70.030	-0.1620	-0.00650	48100	41810	0.0369	0.0111
Larger Positive NTEs	0.495	0.381	869000	0.00441	-70.014	-1.2100	-0.00650	48100	41810	0.0367	0.0109
Larger Negative NTEs	0.494	0.380	869000	0.00439	-70.047	1.3000	-0.00650	48100	41810	0.0363	0.0112

Mid Atlantic Bight

Table C.4: Table showing structural properties of Mid Atlantic Bight network with added TIMs.

	Connectance		Variance					Structuring		Total Degree Heterogeneity	
TIM Model	Total	Non-Trophic	Total	Non-Trophic	Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Row Structure	Column Structure	In-degree	Out-degree
Baseline Model	0.578	0.321	2230000	0.000797	-102.46	-0.07710	-0.00517	102400	92660	0.0345	0.0170
Random NTEs	0.607	0.341	2230000	0.000831	-102.46	0.06320	-0.00517	102400	92660	0.0159	0.0162
Nearby TIMs	0.518	0.306	2230000	0.000801	-102.46	-0.05530	-0.00517	102400	92660	0.0306	0.0307
Far TIMs	0.677	0.273	2230000	0.000806	-102.46	0.00000	-0.00517	102400	92660	0.0379	0.0065
Heterogenous TIM Out-degree	0.558	0.280	2230000	0.000801	-102.46	0.01140	-0.00517	102400	92660	0.0325	0.0324
Facilitating Modifications	0.579	0.322	2230000	0.000903	-102.46	2.04000	-0.00517	102400	92660	0.0347	0.0166
Interfering Modifications	0.580	0.323	2230000	0.000893	-102.46	-2.01000	-0.00517	102400	92660	0.0349	0.0166
Uniformally Distributed Strengths	0.580	0.323	2230000	0.000682	-102.46	0.22400	-0.00517	102400	92660	0.0346	0.0167
Laplace Distributed Strengths	0.579	0.321	2230000	0.001010	-102.46	0.29900	-0.00517	102400	92660	0.0350	0.0170
Scaled Strengths	0.581	0.324	2230000	0.027900	-102.46	-0.37600	-0.00517	102400	92660	0.0354	0.0167
Reciprocal Modifications	0.496	0.294	2230000	0.000818	-102.46	0.00738	-0.00517	102400	92660	0.0292	0.0292
Reciprocal Interference	0.461	0.243	2230000	0.001150	-102.46	-0.57300	-0.00517	102400	92660	0.0380	0.0380
Bounded Reciprocal Interference	0.461	0.242	2230000	0.955000	-102.46	-8.53000	-0.00497	102400	92660	0.0379	0.0379
Unbalanced NTEs	0.579	0.322	2230000	0.001000	-102.46	-0.06970	-0.00517	102400	92660	0.0347	0.0166
Larger Positive NTEs	0.580	0.324	2230000	0.000996	-102.46	-0.21300	-0.00517	102400	92660	0.0347	0.0164
Larger Negative NTEs	0.580	0.324	2230000	0.001020	-102.47	0.36600	-0.00517	102400	92660	0.0347	0.0168

Moorea Reef

Table C.5: Table showing structural properties of Moorea Reef network with added TIMs.

TIM Model	Connectance		Variance		Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Structuring		Total Degree Heterogeneity	
	Total	Non-Trophic	Total	Non-Trophic				Row Structure	Column Structure	In-degree	Out-degree
Baseline Model	0.601	0.402	734000	0.00678	-69.757	-0.09790	-0.0137	61640	17500	0.0348	0.0134
Random NTEs	0.635	0.428	734000	0.00697	-69.757	-0.36400	-0.0137	61640	17500	0.0125	0.0124
Nearby TIMs	0.519	0.370	734000	0.00663	-69.757	-0.00765	-0.0137	61640	17500	0.0299	0.0299
Far TIMs	0.692	0.332	734000	0.00672	-69.757	0.00000	-0.0137	61640	17500	0.0350	0.0071
Heterogenous TIM Out-degree	0.564	0.338	734000	0.00670	-69.757	-0.08510	-0.0137	61640	17500	0.0307	0.0357
Facilitating Modifications	0.600	0.400	734000	0.00760	-69.757	2.88000	-0.0137	61640	17500	0.0347	0.0136
Interfering Modifications	0.601	0.400	734000	0.00772	-69.757	-2.62000	-0.0137	61640	17500	0.0350	0.0133
Uniformally Distributed Strengths	0.601	0.400	734000	0.00572	-69.757	-0.15400	-0.0137	61640	17500	0.0346	0.0130
Laplace Distributed Strengths	0.601	0.402	734000	0.00875	-69.757	0.43200	-0.0137	61640	17500	0.0345	0.0130
Scaled Strengths	0.599	0.399	734000	0.13900	-69.757	0.74500	-0.0137	61660	17500	0.0347	0.0134
Reciprocal Modifications	0.482	0.340	734000	0.00668	-69.757	-0.19000	-0.0137	61640	17500	0.0284	0.0284
Reciprocal Interference	0.489	0.311	734000	0.01010	-69.757	-2.09000	-0.0137	61640	17500	0.0254	0.0254
Bounded Reciprocal Interference	0.489	0.312	734000	24.90000	-69.757	-21.00000	-0.0133	61720	17490	0.0256	0.0256
Unbalanced NTEs	0.600	0.400	734000	0.00841	-69.757	0.34700	-0.0137	61640	17500	0.0348	0.0132
Larger Positive NTEs	0.602	0.402	734000	0.00833	-69.733	0.56000	-0.0137	61640	17500	0.0348	0.0130
Larger Negative NTEs	0.600	0.399	734000	0.00835	-69.780	-0.32000	-0.0137	61640	17500	0.0347	0.0134

Newfoundland (mid-1990s)

Table C.6: Table showing structural properties of Newfoundland (mid-1990s) network with added TIMs.

		Connectance		Variance					Structuring		Total Degree Heterogeneity	
TIM Model		Total	Non-Trophic	Total	Non-Trophic	Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Row Structure	Column Structure	In-degree	Out-degree
Baseline Model		0.633	0.340	3.92e+12	4.52e-05	-81415	4.0800	-0.00169	8.037e+10	2.827e+11	0.0346	0.0139
Random NTEs		0.658	0.360	3.92e+12	4.81e-05	-81415	-0.1150	-0.00169	8.037e+10	2.827e+11	0.0141	0.0140
Nearby TIMs		0.576	0.327	3.92e+12	4.58e-05	-81415	2.5100	-0.00169	8.037e+10	2.827e+11	0.0305	0.0304
Far TIMs		0.735	0.269	3.92e+12	4.67e-05	-81415	0.0000	-0.00169	8.037e+10	2.827e+11	0.0382	0.0044
Heterogenous Out-degree	TIM	0.611	0.293	3.92e+12	4.56e-05	-81415	54.1000	-0.00169	8.037e+10	2.827e+11	0.0323	0.0275
Facilitating Modifications		0.633	0.341	3.92e+12	5.22e-05	-81415	293.0000	-0.00169	8.037e+10	2.827e+11	0.0345	0.0138
Interfering Modifications		0.636	0.343	3.92e+12	5.30e-05	-81415	-261.0000	-0.00169	8.037e+10	2.827e+11	0.0348	0.0136
Uniformally Distributed Strengths		0.634	0.341	3.92e+12	3.91e-05	-81415	-2.8600	-0.00169	8.037e+10	2.827e+11	0.0348	0.0137
Laplace Distributed Strengths		0.635	0.342	3.92e+12	5.88e-05	-81415	29.0000	-0.00169	8.037e+10	2.827e+11	0.0341	0.0136
Scaled Strengths		0.634	0.342	3.92e+12	5.20e-03	-81415	-3.5700	-0.00169	8.037e+10	2.827e+11	0.0346	0.0140
Reciprocal Modifications		0.557	0.317	3.92e+12	4.70e-05	-81415	9.6400	-0.00169	8.037e+10	2.827e+11	0.0286	0.0286
Reciprocal Interference		0.536	0.270	3.92e+12	6.51e-05	-81415	-0.3020	-0.00169	8.037e+10	2.827e+11	0.0355	0.0355
Bounded Reciprocal Interference		0.535	0.269	3.92e+12	7.42e-02	-81415	-0.0971	-0.00169	8.037e+10	2.827e+11	0.0354	0.0354
Unbalanced NTEs		0.633	0.342	3.92e+12	5.79e-05	-81415	7.1500	-0.00169	8.037e+10	2.827e+11	0.0345	0.0142
Larger Positive NTEs		0.633	0.343	3.92e+12	5.86e-05	-81415	-62.2000	-0.00169	8.037e+10	2.827e+11	0.0347	0.0137
Larger Negative NTEs		0.633	0.341	3.92e+12	5.79e-05	-81415	33.8000	-0.00169	8.037e+10	2.827e+11	0.0345	0.0139

Tampa Bay

Table C.7: Table showing structural properties of Tampa Bay network with added TIMs.

TIM Model		Connectance		Variance		Mean Interaction Strength	Trophic:Non-Trophic Covariance	Pairwise Correlation	Structuring		Total Degree Heterogeneity	
		Total	Non-Trophic	Total	Non-Trophic				Row Structure	Column Structure	In-degree	Out-degree
Baseline Model		0.517	0.335	6.05e+11	0.001120	-26885	-179.00	-0.0012	1.478e+10	2.808e+10	0.0459	0.0147
Random NTEs		0.553	0.361	6.05e+11	0.001180	-26885	-73.80	-0.0012	1.478e+10	2.808e+10	0.0140	0.0138
Nearby TIMs		0.442	0.307	6.05e+11	0.001130	-26885	-237.00	-0.0012	1.478e+10	2.808e+10	0.0352	0.0358
Far TIMs		0.588	0.287	6.05e+11	0.001130	-26885	0.00	-0.0012	1.478e+10	2.808e+10	0.0513	0.0076
Heterogenous Out-degree	TIM	0.486	0.288	6.05e+11	0.001120	-26885	-16.80	-0.0012	1.478e+10	2.808e+10	0.0393	0.0347
Facilitating Modifications		0.514	0.332	6.05e+11	0.001340	-26885	845.00	-0.0012	1.478e+10	2.808e+10	0.0455	0.0144
Interfering Modifications		0.515	0.333	6.05e+11	0.001340	-26885	-969.00	-0.0012	1.478e+10	2.808e+10	0.0456	0.0145
Uniformally Distributed Strengths		0.516	0.336	6.05e+11	0.000957	-26885	148.00	-0.0012	1.478e+10	2.808e+10	0.0456	0.0146
Laplace Distributed Strengths		0.515	0.333	6.05e+11	0.001420	-26885	248.00	-0.0012	1.478e+10	2.808e+10	0.0452	0.0146
Scaled Strengths		0.514	0.333	6.05e+11	0.139000	-26885	-538.00	-0.0012	1.478e+10	2.808e+10	0.0457	0.0146
Reciprocal Modifications		0.428	0.295	6.05e+11	0.001130	-26885	-71.00	-0.0012	1.478e+10	2.808e+10	0.0317	0.0317
Reciprocal Interference		0.386	0.229	6.05e+11	0.002250	-26885	-48.20	-0.0012	1.478e+10	2.808e+10	0.0372	0.0372
Bounded Reciprocal Interference		0.387	0.230	6.05e+11	4.000000	-26885	-1.39	-0.0012	1.478e+10	2.808e+10	0.0374	0.0374
Unbalanced NTEs		0.516	0.334	6.05e+11	0.001410	-26885	-19.30	-0.0012	1.478e+10	2.808e+10	0.0457	0.0145
Larger Positive NTEs		0.516	0.335	6.05e+11	0.001430	-26885	-185.00	-0.0012	1.478e+10	2.808e+10	0.0452	0.0147
Larger Negative NTEs		0.515	0.333	6.05e+11	0.001430	-26885	260.00	-0.0012	1.478e+10	2.808e+10	0.0453	0.0146

6: Non-highlighted TIM Models

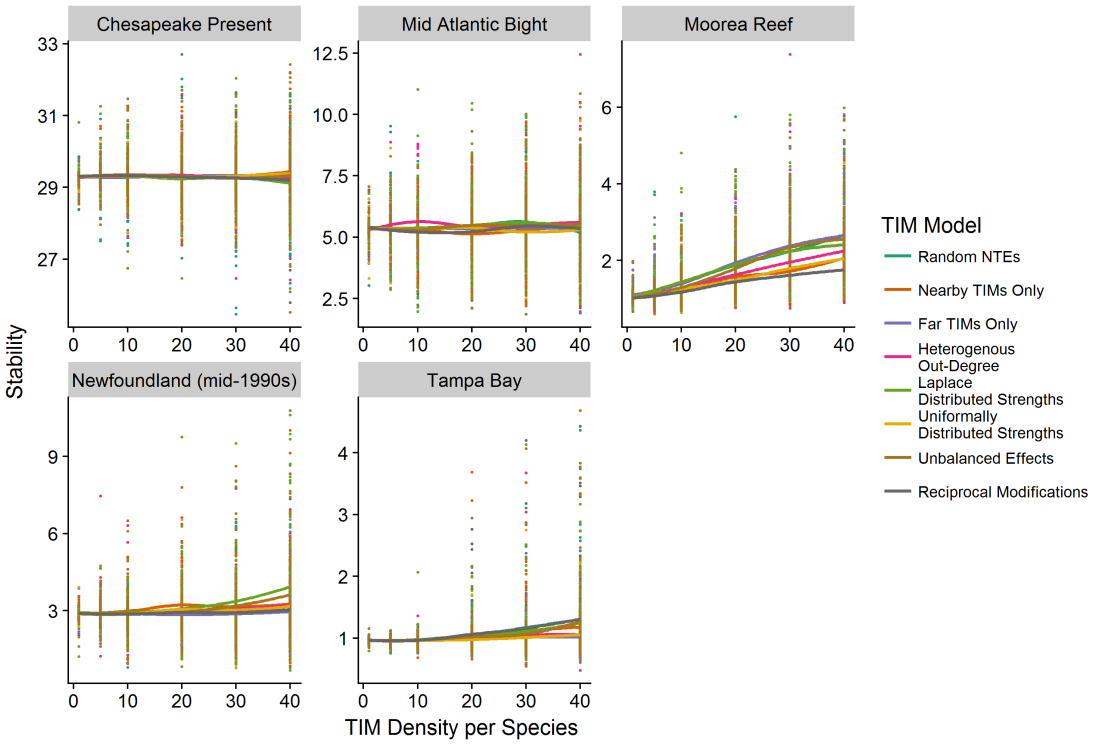


Figure C.5: Stability response of the introduction of TIMs in the empricial webs under the models not highlighted in main text Figure 5.

7: Stability Criteria in the Empirical Networks

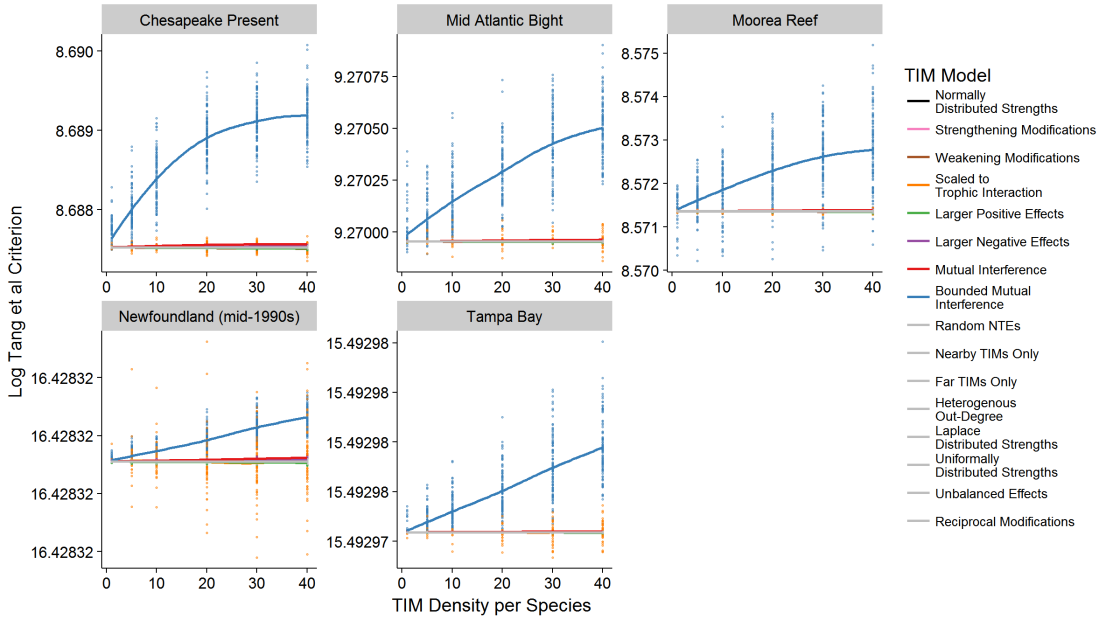


Figure C.6: The minimal response of the Tang *et al.* stability criterion to the introduction of TIMs. Note the very restricted y-axis of each facet.

D

Supplementary Material for Chapter 4

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1: Method for Determining Body Masses

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:

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

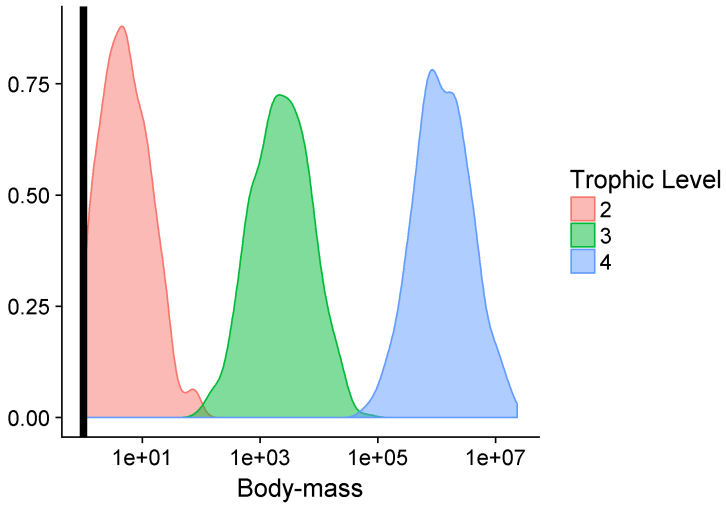


Figure D.1: Density plot showing distribution of body masses across integer trophic levels. Black line shows producer body mass. Note the relatively small overlap in body masses and logarithmic scale.

2: Starting Communities

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

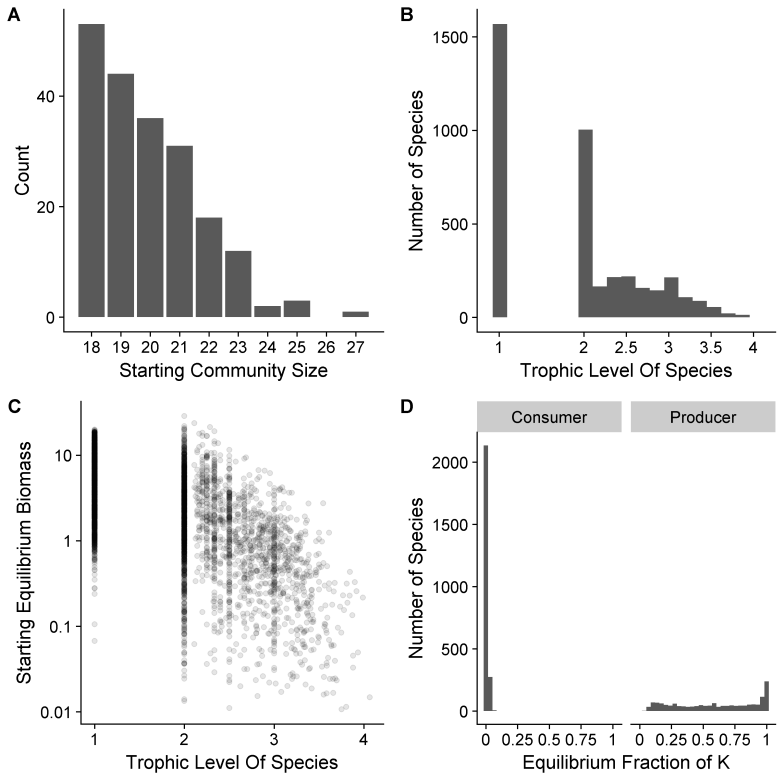


Figure D.2: Further details about the properties of the 200 equilibrium communities used in robustness analysis. A: Histogram showing distribution of number of species in each community. Eighteen species was chosen as a lower cut off-point. B: Distribution of 3983 species across trophic levels, as calculated 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 generalised form of the Gompertz equation is:

$$f(\theta_{ijk}, x) \ = g\left(a\ e^{-be^{-cx}} - d\right) \tag{D.1}$$

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

$$\log_{10}\left(\mu_{ijk}\right) = f\left(\theta_{ijk},\ x\right) \tag{D.2}$$

The core results that we wish to achieve are:

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

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

iii $f''\left(\theta_{ijk}, \tau\right) = 0$, the point of inflection occurs at $x - \tau$

iv $\left|f\left(\theta_{ijk}, \infty\right) - f\left(\theta_{ijk}, -\infty\right)\right| = \sigma$, 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 $a = \sigma$. Criterion ii) can be simply met as $\max\left(\frac{df}{dx}\right) = \frac{gac}{e}$, 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 $d = ae^{-b}$, 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 Equilibria

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 material. 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: Direction of Initial Population Response

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% were negative and 19.5% were positive.

6: Partition of Interaction into Trophic and Non-Trophic Components

For case where species 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:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots \underbrace{-\mu_{ij}a_{ij}B_j}_{\text{Trophic Term with TIM}} \tag{D.3}$$

First expand μ_{ij} as:

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots - \ (1 \ + (\mu_{ij} - 1))a_{ij}B_j \tag{D.4}$$

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

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots \underbrace{-a_{ij}B_j}_{\text{Trophic Term}} \ + \underbrace{a_{ij}B_j(1-\mu_{ij})}_{\text{Non-Trophic Term}} \tag{D.5}$$

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

$$\frac{1}{B_i}\frac{dB_i}{dt} = \ldots \underbrace{-a_{ij}B_j}_{\text{Trophic Term}} \ + \underbrace{a_{ij}B_j^*(1-\mu_{ij})}_{\text{Non-Trophic Term}} \tag{D.6}$$

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 instead can be followed to find the impact on the other species.