Title: Identifying Important Interaction Modifications in Ecological Systems.

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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.

Key words: interaction modification; food web; non-trophic effect; predictability; trait-mediated indirect effect; trophic interaction; ecological networks;

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 in Supplementary Information.

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. 2006, detailed in SI 1).

The biomass density of each species, $\mathrm{B_i}$, was drawn from a distribution based on the individual body mass as $\mathrm{B_i} = 10^{-2.36+\mathrm{g}+\epsilon}\mathrm{m_i^g}$ 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 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:

$$\frac{dB_i}{dt} = \sum_{i \subset \text{prey of } i}^{i} e_{ii} a_{ii} B_i B_i - \sum_{j \subset \text{predators of } i}^{j} a_{ij} B_i B_j \quad \text{(Eq. 1)}$$

This allows us to specify a community matrix **A**, where each element $\mathbf{A}_{\mathrm{ij}} = \frac{\partial(\mathrm{dB_i/dt})}{\partial \mathrm{B_j}}$, 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 $\mathbf{A}_{\mathrm{ij}} = -\mathrm{a_{ij}B_i}$ while the reverse effect, $\mathbf{A}_{\mathrm{ji}} = \mathrm{e_{ij}a_{ij}B_j}$. Conversion efficiencies, $\mathrm{e_{ij}}$, were drawn from a uniform distribution $\mathcal{U}(0.1,0.2)$. Biomass-density specific attack rates, $\mathrm{a_{ij}}$, 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 $\mathbf{A}_{\mathrm{ii}}$ 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.

TIMs

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

$$a'_{ij} = a_{ij}\left(1 + \sum_{k \in modifiers}^{k} c_{ijk} \log\left(\frac{B_k}{B_k^*}\right)\right) \text{. (Eq. 2)}$$

Species are assumed to not modify their own trophic interactions ($\mathrm{k} \neq \mathrm{i,j}$), 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:

$$\frac{\partial B_i}{\partial B_k} = \ldots - a_{ij} B_i B_j c_{ijk} \frac{1}{B_k^*} \ , \quad \frac{\partial B_j}{\partial B_k} = \ldots + e_{ij} a_{ij} B_i i B_j c_{ijk} \frac{1}{B_k^*} \ . \quad \text{(Eq. 3)}$$

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.

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.

	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

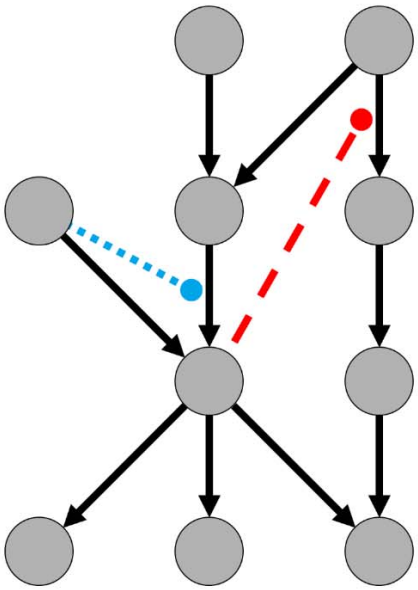

Figure 1. Example values of topological metrics for interaction modifications (dashed lines) within a simple trophic network (solid lines).

Strength of TIMs

Interaction strengths can be simultaneously considered with multiple and 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, and the biomass flux rate, .

Table 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.

Metric	Description	General Specification	Calculation
TIM Function Slope	The strength of the relationship between the modifier species density and the interaction rate.	$\frac{\delta}{\delta B_k} a_{ij}$	
Direct Non-Trophic Effect of TIM	The contribution of an individual TIM to the effect from the modifier to an interactor. Also described as	$\left\lvert \mathbf{A}_{ik}^{Full} - \mathbf{A}_{ik}^{c_{ijk}=0} \right\rvert$	$a_{ij} B_i B_j \lvert c_{ijk} \rvert \frac{1}{B_k^*}$

	the trait-mediated indirect effect (Abrams 2008, Okuyama and Bolker 2012).		
Impact on Interaction	The change in the direct interaction strength caused by the TIM. This is a measure of instantaneous effect of a TIM.	$\left\lvert \frac{\delta}{\delta B_k} \mathbf{A}_{ij} \right\rvert$	$a_{ij} B_i \lvert c_{ijk} \rvert \ \frac{1}{B_k^*}$
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.	$\left\lvert \frac{\delta}{\delta B_k^{mod}} [\mathbf{A}^{-1}]_{ij} \right\rvert$	Calculated numerically changing only the density of the modifier term in the TIM function to isolate the TIM effect from those mediated by other interaction chains through the modifier species.

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.

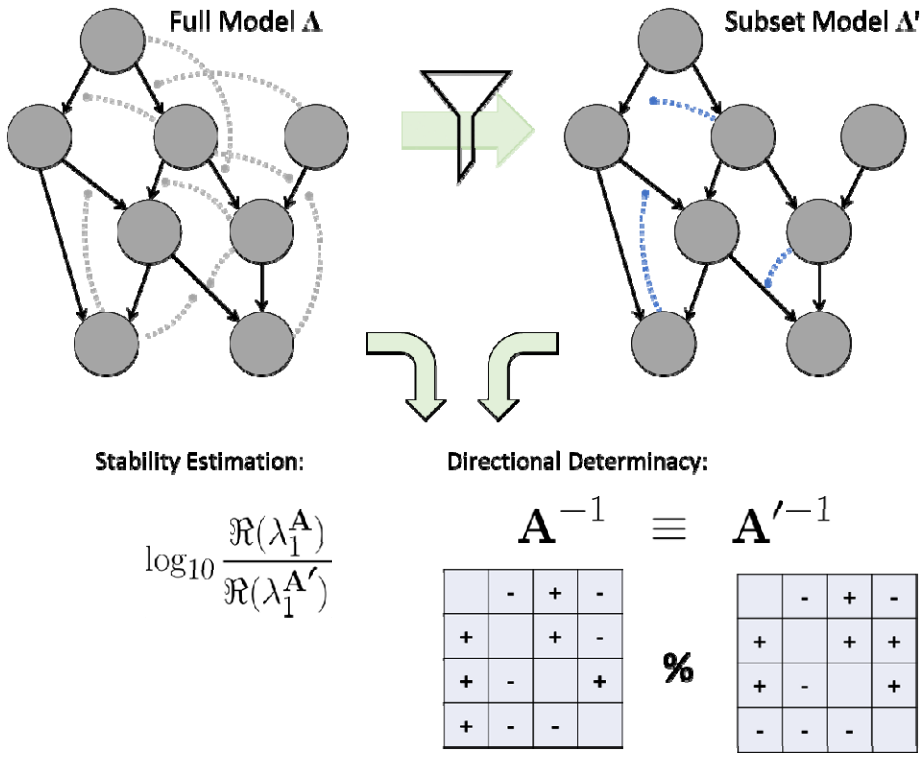

Figure 2. Schematic showing overall approach to test methods for identifying interaction modifications that are influential in the dynamics of model ecological communities. The trophic interaction modifications in the full community model are quantified and 20% retained using a particular metric. The capacity for the subset model to represent the dynamics of the dull model system are then assessed stability estimation and directional determinacy.

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, . 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. 2017), we set each $\mathbf{A}_{ii}$ to 0. In this case, $\Re(\lambda_1^{\mathbf{A}})$ 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 $\log(\Re(\lambda_1^{\mathbf{A}}))$ 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 every 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

212 unfeasible, the *sign* of the net-effects between species, i.e. whether a change in a particular
213 population will lead to an increase or a decrease in another population is a reasonable objective
214 (Yodzis 1988, Novak et al. 2011, Aufderheide et al. 2013).

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

224 Because local asymptotic stability is a prerequisite for calculating directional determinacy,
225 additional communities were generated and unstable communities excluded to create 2000
226 locally stable communities for each of the three values of g and the two approaches to
227 including self-regulation terms. We then followed the same procedure as for local stability to
228 test each metric's ability to identify valuable TIMs. For each web we compared the directional
229 determinacy of a model including the selected subset of interaction modifications to a model
230 including just the trophic interactions.

231 **Results**

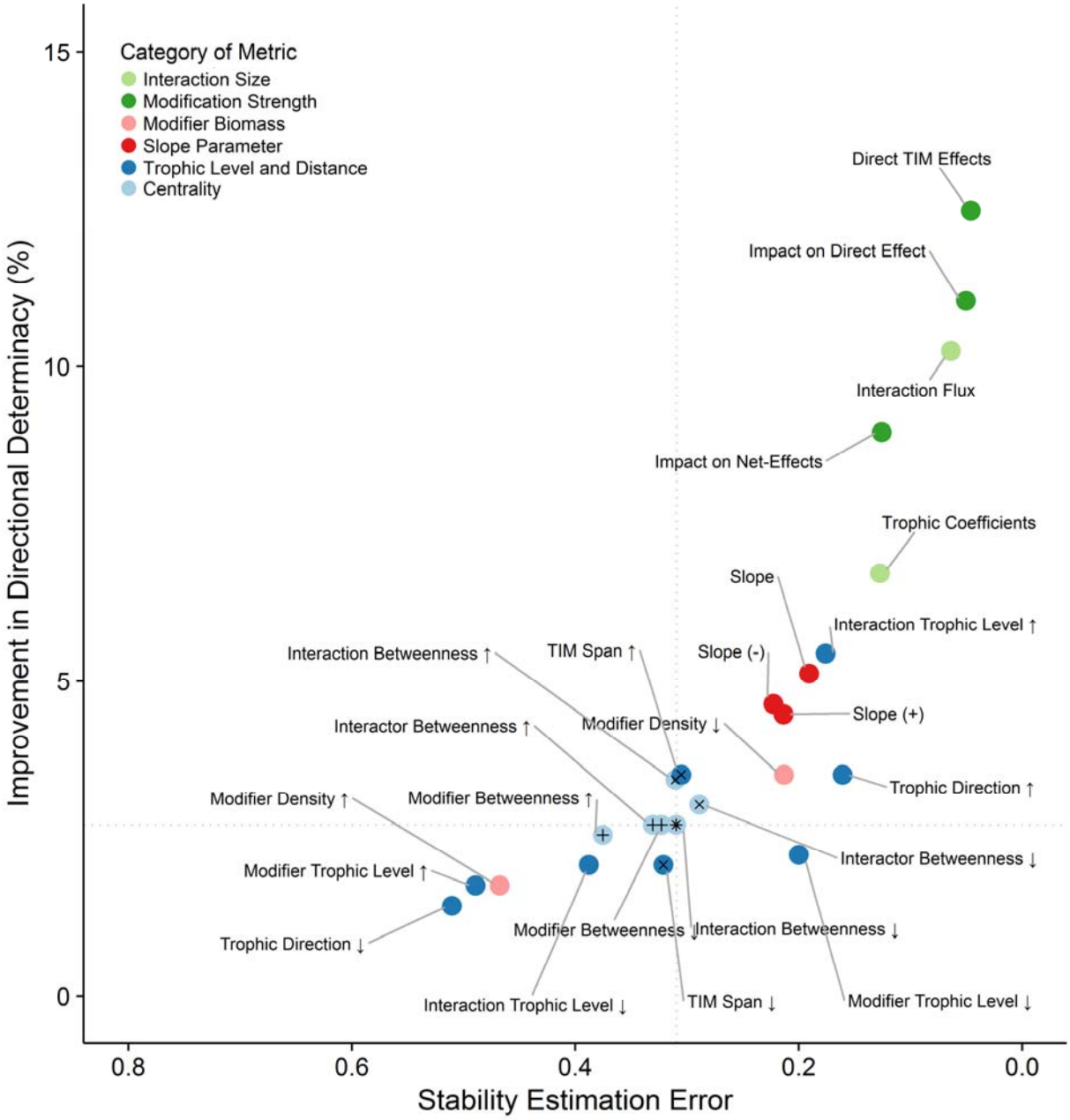

Figure 3. Comparison of the capacity of different metrics to identify TIMs that contribute to the dynamics of whole systems. Arrows indicate whether TIMs were selected for inclusion based on high or low values of the given property. Median error in the estimation of the logarithm of the system stability 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 identify 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, $\alpha = 0.05$), paired by underlying network.

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). This effect was not noticeable for stability estimation.

The strength properties of TIMs were correlated with each other but topological features considerably less so (Figure 4, SI 6). 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.

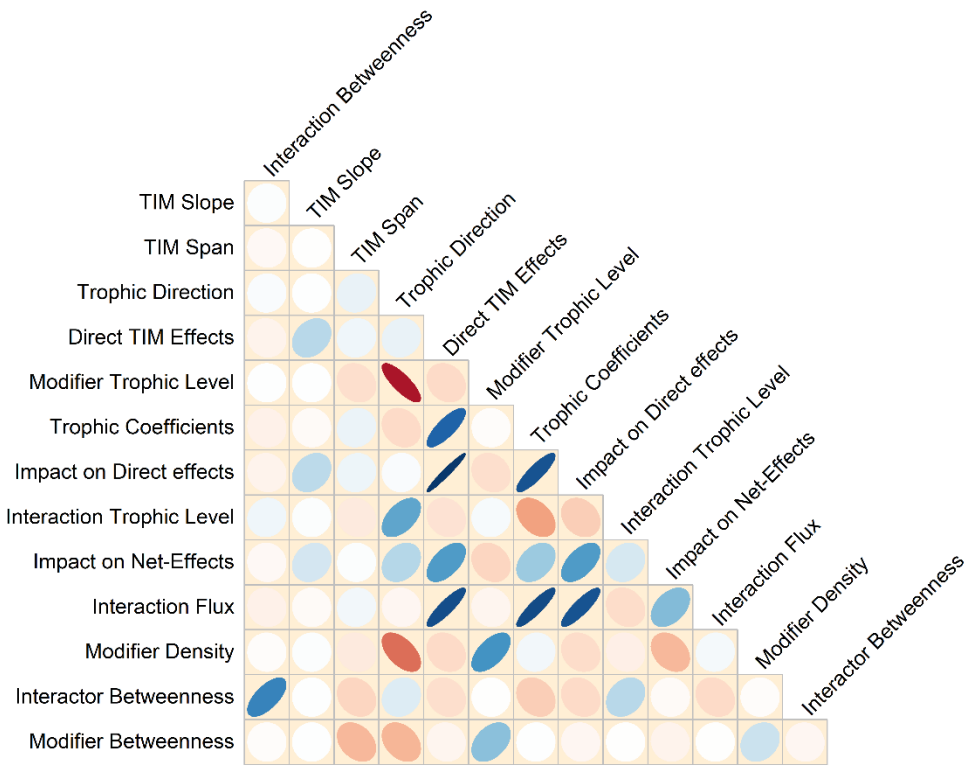

Figure 4. Correlation plot showing relationships between the properties of the TIMs in a model food web community (g = 0.1, producers higher self-regulation than consumers). Ellipses depict Spearman's rank correlations, blue shapes indicating positive correlations and red negative. Corresponding plots for the other model structures are shown in SI 6.

In general, those metrics that addressed aspects of the strength of the interaction modification were the most valuable (shown in green in Fig. 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.

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

269 of the local stability than the strongly negative interaction modifications. This difference was
270 particularly notable for the g=-0.75 case (SI 3). Conversely, selecting interaction modifications
271 for directional determinacy but not for stability.

272 The influence of trophic height depended on the relationship between trophic level and
273 biomass density (controlled by the g parameter) with modifications of high-trophic level
274 interactions becoming comparatively more important when the webs were more top-heavy.
275 The impact of trophic direction was highly dependent on the distribution of self-regulation
276 terms. Where producers are more strongly self-regulated than consumers, 'upwards' TIMs are
277 less influential for directional determinacy.

278 **Discussion**

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

287 TIMs introduce a high level of complexity to ecosystem dynamics. It is therefore reassuring to
288 note that relatively simple and easily observable measures, for example interaction flux, are
289 able to identify the TIMs that drive the system dynamics. Similar sets of TIMs were identified as

290 being important in two distinct types of dynamics – response to press perturbations (directional
291 determinacy) and response to pulse perturbations (local stability). By identifying comparatively
292 high-impact TIMs we can make progress despite the present dearth of empirical distributional
293 data. Below we focus our discussion on specific results and their implications, before looking
294 forward to developing this approach in future work.

295 This study required assumptions regarding the appropriate strength and distribution of TIM
296 values to use. In particular, our results regarding interaction strength are necessarily dependent
297 on the range of the distribution from which the various properties the model are chosen from.
298 If for instance the range of slope parameters was larger compared to the range of biomass
299 densities, the c_{ijk} parameter in our model would have been a more valuable in comparison to
300 the other TIM strength parameters. Empirical distributions of interaction modification strength
301 in a network do not (to our knowledge) yet exist. Meta-analyses of non-trophic effect strength
302 (Bolnick and Preisser 2005, Preisser et al. 2005) suggest an approximate correspondence with
303 trophic interactions. However, the occasional very strong non-trophic effect at the upper tail of
304 the distribution we used (SI 2) is not necessarily unrealistic as the impact of behavioural effects
305 can in certain circumstances be much faster and stronger than consumptive interactions
306 (Abrams 2001). At the other end of the spectrum, it is necessary to set a threshold where a
307 species' influence on an interaction is considered too weak to include. This decision trades-off
308 the mean strength and the overall connectance of the modification distribution. An additional
309 complication is how interaction modifications combine to influence an interaction (Golubski
310 and Abrams 2011). For example, interaction modifications may act antagonistically to each
311 other, with combined modifications exerting less effect than would be expected from the

individual effects. Although strengths 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 modifiers 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 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

356 effect could be driven by at least two mechanisms. Firstly, in our model the assumption of top-
357 down dominated interaction strength imbalance caused by the assimilation term e causes non-
358 trophic effects on prey to be larger than on predators (Eq. 3). This has the result that
359 strengthening TIMs ($+c_{ijk}$) exert larger negative effects (on prey) than positive effects (on
360 predators). Secondly, there will be a topological effect – strengthening TIMs will lead to
361 consistently positive non-trophic effects on high trophic level species and consistently negative
362 impacts on basal species, which will interact with the underlying tropic interaction distribution.

363 **Outlook**

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

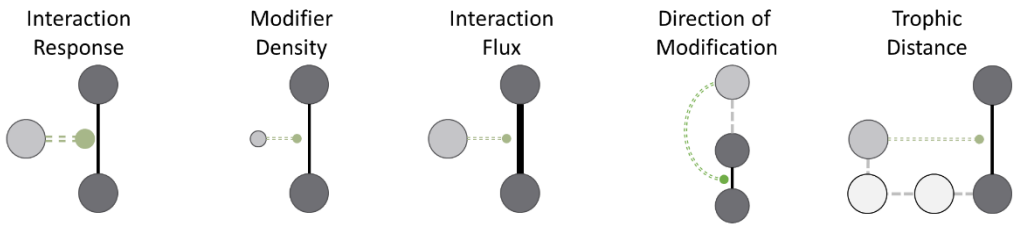

Figure 5. Properties of interaction modifications of relevance to determining their impact.

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 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 fixed value for the slope can give improvements of mean directional determinacy of 10.5% 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).

393 Equilibrium studies such as ours allow a precise analysis of particular processes in isolation from
394 other sources of variation. However, this approach does not incorporate the full spectrum of
395 impacts TIMs can have in dynamic systems and future work should seek to address this gap.
396 Furthermore, trophic interaction strengths are not purely determined by biotic factors – there
397 is also extensive dependence on the abiotic environment (Wootton and Emmerson 2005, Poisot
398 et al. 2015). The balance of the impact of exogenous and endogenous sources of interaction
399 strength variation is unknown. The two processes can interact, with TIMs varying depending on
400 abiotic conditions (Sentis et al. 2017) and interaction modifications allowing species to resist
401 abiotic variability (Bruno et al. 2003). The extent to which interaction strength variation will
402 frustrate ecological prediction is unclear. However, at least some of this variation can be
403 accounted for by dependence on other species in the community which, in principle, is
404 quantifiable (Terry et al. 2017).

405 **Conclusion**

406 To improve our understanding of ecosystems it will be necessary to incorporate important
407 dynamic processes whether they are consumer-resource links, direct non-trophic effects or
408 interaction modifications (Fontaine et al. 2011). This potential complexity poses a daunting
409 challenge but not all interaction modifications are equal. We have shown that considering
410 interaction modifications as distinct entities opens up a range of analyses and that although the
411 underlying mechanisms may be complex, relatively simple heuristics may be useful in
412 identifying significant processes in food webs. Where interaction modifications are suspected,
413 but unquantified, our work provides guidance to determine where further research could bring
414 the greatest improvement in understanding. Fully incorporating interaction modifications into

415 the fold of ecosystem ecology will be a long, but rewarding, endeavour. We hope that our work
416 will encourage further studies, both experimental and theoretical, to understand these critical
417 components of ecosystem dynamics.

418 **Data Statement**

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

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425 **References**

426 Abrams, P. A. 2001. Describing and Quantifying Interspecific Interactions: A Commentary on
427 Recent Approaches. - Oikos 94: 209–218.

428 Abrams, P. A. 2008. Measuring the impact of dynamic antipredator traits on predator-prey-
429 resource interactions. - Ecology 89: 1640–1649.

430 Arditi, R. et al. 2005. Rheagogies: Modelling non-trophic effects in food webs. - Ecol. Complex.
431 2: 249–258.

432 Aufderheide, H. et al. 2013. How to predict community responses to perturbations in the face
433 of imperfect knowledge and network complexity. - Proc. R. Soc. London B Biol. Sci. 280:
434 20132355.

435 Barabás, G. and Allesina, S. 2015. Predicting global community properties from uncertain
436 estimates of interaction strengths. - J. R. Soc. Interface 12: 20150218.

437 Barabás, G. et al. 2017. Self-regulation and the stability of large ecological networks. - Nat. Ecol.
438 Evol. 1: 1870–1875.

439 Bender, E. A. et al. 1984. Perturbation Experiments in Community Ecology: Theory and Practice.
440 - Ecology 65: 1–13.

441 Berlow, E. L. et al. 2004. Interaction Strengths in Food Webs: Issues and Opportunities. - J.
442 Anim. Ecol. 73: 585–598.

443 Bolnick, D. I. and Preisser, E. L. 2005. Resource competition modifies the strength of trait
444 mediated predator–prey interactions: a meta-analysis. - Ecology 86: 2771–2779.

445 Brose, U. et al. 2006. Consumer-resource body-size relationships in natural food webs. - Ecology
446 87: 2411–2417.

447 Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. - Trends Ecol. Evol. 18:
448 119–125.

449 Coyte, K. Z. et al. 2015. The ecology of the microbiome: Networks, competition, and stability. -
450 Science 350: 663–666.

451 Dambacher, J. M. and Ramos-Jiliberto, R. 2007. Understanding and Predicting Effects of
452 Modified Interactions Through a Qualitative Analysis of Community Structure. - Q. Rev.
453 Biol. 82: 227–250.

454 Dambacher, J. M. et al. 2003. Qualitative predictions in model ecosystems. - Ecol. Modell. 161:

455 79–93.

456 Doak, D. F. et al. 2008. Understanding and predicting ecological dynamics: are major surprise
457 inevitable? - Ecology 89: 952–961.

458 Dunne, J. A. and Pascual, M. 2006. Ecological Networks: Linking Structure to Dynamics in Food
459 Webs. - Oxford University Press.

460 Fontaine, C. et al. 2011. The ecological and evolutionary implications of merging different types
461 of networks. - Ecol. Lett. 14: 1170–1181.

462 Golubski, A. J. and Abrams, P. A. 2011. Modifying modifiers: what happens when interspecific
463 interactions interact? - J. Anim. Ecol. 80: 1097–1108.

464 Golubski, A. J. et al. 2016. Ecological Networks over the Edge: Hypergraph Trait-Mediated
465 Indirect Interaction (TMII) Structure. - Trends Ecol. Evol. 31: 344–354.

466 Goudard, A. and Loreau, M. 2008. Nontrophic Interactions, Biodiversity, and Ecosystem
467 Functioning: An Interaction Web Model. - Am. Nat. 171: 91–106.

468 Iles, A. C. and Novak, M. 2016. Complexity Increases Predictability in Allometrically Constrained
469 Food Webs. - Am. Nat. 188: 87–98.

470 Kéfi, S. et al. 2012. More than a meal… integrating non-feeding interactions into food webs. -
471 Ecol. Lett. 15: 291–300.

472 Kéfi, S. et al. 2015. Network structure beyond food webs: mapping non-trophic and trophic
473 interactions on Chilean rocky shores. - Ecology 96: 291–303.

Kéfi, S. et al. 2016. How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience. - PLOS Biol. 14: e1002527.

Koslicki, D. and Novak, M. 2018. Exact probabilities for the indeterminacy of complex networks as perceived through press perturbations. - J. Math. Biol. 76: 877–909.

Laska, M. S. and Wootton, J. T. 1998. Theoretical Concepts and Empirical Approaches to Measuring Interaction Strength. - Ecology 79: 461–476.

Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. - J. Theor. Biol. 83: 195–207.

Levine, J. M. et al. 2017. Beyond pairwise mechanisms of species coexistence in complex communities. - Nature 546: 56–64.

Lin, Y. and Sutherland, W. J. 2013. Color and degree of interspecific synchrony of environmental noise affect the variability of complex ecological networks. - Ecol. Modell. 263: 162–173.

May, R. M. 1973. Stability and Complexity in Model Ecosystems. - Princeton University Press.

Mougi, A. and Kondoh, M. 2012. Diversity of Interaction Types and Ecological Community Stability. - Science 337: 349–351.

Neutel, A.-M. et al. 2002. Stability in Real Food Webs: Weak Links in Long Loops. - Science 296: 1120–1123.

Newman, M. 2010. Networks: An Introduction. - Oxford University Press.

Novak, M. et al. 2011. Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. - Ecology 92: 836–846.

Novak, M. et al. 2016. Characterizing Species Interactions to Understand Press Perturbations: What Is the Community Matrix? - Annu. Rev. Ecol. Evol. Syst. 47: 409–432.

Ohgushi, T. et al. 2012. Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives. - Cambridge University Press.

Okuyama, T. and Bolker, B. M. 2012. Model-based, response-surface approaches to quantifying indirect interactions. - In: Ohgushi, T. et al. (eds), Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives. Cambridge University Press, pp. 186–204.

Pawar, S. et al. 2012. Dimensionality of consumer search space drives trophic interaction strengths. - Nature 486: 485–489.

Peckarsky, B. L. et al. 2008. Revisiting the Classics: Considering Nonconsumptive Effects in Textbook Examples of Predator – Prey Interactions. - Ecology 89: 2416–2425.

Petchey, O. L. et al. 2015. The ecological forecast horizon, and examples of its uses and determinants (D Vasseur, Ed.). - Ecol. Lett. 18: 597–611.

Pilosof, S. et al. 2017. The multilayer nature of ecological networks. - Nat. Ecol. Evol. 1: 101.

Pocock, M. J. O. et al. 2012. The robustness and restoration of a network of ecological networks. - Science 335: 973–7.

Poisot, T. et al. 2015. Beyond species: why ecological interaction networks vary through space and time. - Oikos 124: 243–251.

513 Preisser, E. L. et al. 2005. Scared to death? The effects of intimidation and consumption in
514 predator-prey interactions. - Ecology 86: 501–509.

515 R Core Team 2017. R: A Language and Environment for Statistical Computing. in press.

516 Reuman, D. C. et al. 2009. Allometry of Body Size and Abundance in 166 Food Webs. - Adv. Ecol.
517 Res. 41: 1–44.

518 Schmitz, O. J. et al. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. -
519 Ecol. Lett. 7: 153–163.

520 Sentis, A. et al. 2017. Predator diversity and environmental change modify the strengths of
521 trophic and nontrophic interactions. - Glob. Chang. Biol. 23: 2629–2640.

522 Tack, A. J. M. et al. 2011. Can we predict indirect interactions from quantitative food webs? - an
523 experimental approach. - J. Anim. Ecol. 80: 108–118.

524 Tang, S. et al. 2014. Correlations between interation strengths drives stability in large ecological
525 networks - Supp Info. - Ecol. Lett. 17: 1094–1100.

526 Terry, J. C. D. et al. 2017. Trophic interaction modifications: an empirical and theoretical
527 framework. - Ecol. Lett. 20: 1219–1230.

528 van Altena, C. et al. 2016. Patterns in intraspecific interaction strengths and the stability of food
529 webs. - Theor. Ecol. 9: 95–106.

530 van Veen, F. J. F. et al. 2005. Stable Coexistence in Insect Communities Due to Density- and
531 Trait-Mediated Indirect Effects. - Ecology 86: 3182–3189.

532 Werner, E. E. and Peacor, S. D. 2003. A Review of Trait-Mediated Indirect Interactions in
533 Ecological Communities. - Ecology 84: 1083–1100.

534 Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. - Nature 404:
535 180–183.

536 Williams, R. J. and Martinez, N. D. 2008. Success and its limits among structural models of
537 complex food webs. - J. Anim. Ecol. 77: 512–519.

538 Williams, R. J. et al. 2002. Two degrees of separation in complex food webs. - Proc. Natl. Acad.
539 Sci. 99: 12913–12916.

540 Woodward, G. et al. 2005. Body size in ecological networks. - Trends Ecol. Evol. 20: 402–409.

541 Wootton, J. T. 1993. Indirect Effects and Habitat Use in an Intertidal Community: Interaction
542 Chains and Interaction Modifications. - Am. Nat. 141: 71–89.

543 Wootton, J. T. and Emmerson, M. 2005. Measurement of Interaction Strength in Nature. -
544 Annu. Rev. Ecol. Evol. Syst. 36: 419–444.

545 Yodzis, P. 1988. The Indeterminacy of Ecological Interactions as Perceived Through Perturbation
546 Experiments. - Ecology 69: 508–515.

547 Yodzis, P. and Innes, S. 1992. Body Size and Consumer-Resource Dynamics. - Am. Nat. 139:
548 1151–1175.

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