Running Head: Key Interaction Modifications

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 significant challenge, making prioritisation for empirical study essential. We use the trophic interaction modification framework to identify modifications that are most likely to exert significant effects on the dynamics of whole systems, introducing tools to quantify the topological relationship of interaction modifications relative to the underlying network. Using a set of simulated food

webs and randomly distributed interaction modifications we test whether a subset of interaction modifications important for determining the local stability and directional determinability of complex networks can be identified. We show that trophic interaction modifications from rare 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. This work demonstrates that analysis of interaction modifications can be tractable at the network scale and highlights the importance of the inter-relationship between the structure of trophic networks and interaction modifications.

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

Introduction

The study of ecological network dynamics has been dominated by trophic interactions (Dunne and Pascual 2006), but it is increasingly recognised that to improve our understanding of ecosystems non-trophic effects must be considered (Kéfi et al. 2012). Interaction modifications (Wootton 1993), where non-interactor species alter the strengths of links, 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 effects 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 model systems have shown that the effects of TIMs can be considerable, comparable with trophic interactions (Schmitz et al. 2004, Bolnick and Preisser 2005), 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, 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 quantification of the most important processes (Novak et al. 2011) is therefore necessary to improve our understanding of ecological networks.

Here we introduce methods to examine the topological structure of interaction modifications in food webs. 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 predictability and estimation of stability.

Methods

Food web model specification

We used artificial communities at a steady-state equilibrium as a baseline for our analysis. To generate these, initial community trophic network topologies were generated using the niche model algorithm (Williams and Martinez 2000) with species number and trophic connectance fixed at 25 and 0.15. 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). Trophic levels were assigned from the network structure following the pathway method of Levine (1980). The system dynamics were modelled and parameterised following the Allometric Trophic Network (ATN) model approach (Williams and Martinez 2004, Brose et al. 2006b, Delmas et al. 2016), which uses metabolic body-size scaling relationships to parametrise bio-energetic differential equation models (Eq. 1). This model was chosen because of its wide use, limited number of parameters and successful application to experimental data (Boit et al. 2012). The model is of the form:

1) $$\frac{dB_i}{dt} = r_i B_i G_i - x_i B_i + \sum_{j \in prey} x_i y_{ij} F_{ij} B_i - \sum_{j \in predators} x_j \frac{y_{ji}}{e_{ji}} F_{ji} B_j$$

2) $$F_{ij} = \frac{\omega_i B_j^2}{B_0^2 + B_j^2}$$

3) $$G_i = 1 - \frac{B_i}{K}$$

where all parameters and definitions are given in Table 1. Non-trophic dynamic links in the standard ATN model were excluded as they could obscure the TIM effects under study. Hence, the alternative prey interference terms in the functional response (Koen-Alonso 2007) were not incorporated, since prey switching is a cause of TIMs (Abrams 2010). Instead a direct type III functional response was used (Eq. 2). A Type III response was chosen to increase the likelihood of reaching a stable equilibrium rather than a limit cycle or chaotic attractor. Predators with multiple prey had a reduced attack rate on each determined by ω, a predation choice term, which was set at 1/n, where n is the number of prey species the predator consumes. Producer

growth was modelled without interspecific producer competition (Eq. 3), with each producer having a separate, identical, carrying capacity K. Species body-masses M_i were assigned based on trophic level following empirical consumer-resource ratios (Brose et al. 2006a, detailed in SI 1). Model parameters were assigned values following previous studies wherever possible (Table 1).

Community population densities were determined by initiating each species at a biomass of 0.1 and running each system to a steady state before the inclusion of interaction modifications (see SI 1). Of 1000 initial webs, 797 successfully reached a steady-state equilibrium density with a complete network of at least 10 extant species (density greater than 10^{-12}). These were used to form the set of baseline systems. Summary statistics of the structure of the model communities are given in SI 1.

Adding TIMs

TIMs were represented with a function that links the density of the modifier species with the functional response (Eq. 4). Here we used an extension of the sigmoidal function suggested by Kéfi et al. (2012), parameterised such that at the equilibrium density of the modifier the resultant modification term is 1 (i.e. there is no change to the interaction strength at the equilibrium point) and the point of inflexion of the function is at the equilibrium point:

4) $$F'_{ij} = F_{ij} \prod_{k \in modifiers}^{k} \left(M_0 + \frac{M_{max} - M_0}{(1 + e^{-c_{ijk}(log_{10}(B_k) - log_{10}(B_k^*))})^{1/\nu_k}} \right) \quad , \quad \nu_k = \frac{log(2)}{log(\frac{M_{max}}{1-M_0})} .$$

Through the use of this parameterisation and by conducting analyses at a fixed set of species densities, the distribution of trophic interaction strengths is maintained. 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). Since the Jacobian-based analyses we conduct are linearisations, an equivalent linear TIM function would have the same result, however this sigmoidal function allows consistency with additional analyses using extended dynamics. The TIM slope parameter (c_{ijk}) controls the direction and magnitude of the modification. A positive c_{ijk} causes an increased level of the modifier to increase the underlying trophic interaction while a negative value results in a reduction in the interaction as the modifier density increases. The sign of the realized functional response rate is always unaffected and so energy flow between species is never reversed. Although reversals are possible (Barkai and McQuaid 1988), they are unlikely to be widespread. The dependence on the logarithm of the modifier biomass ensures that modifications are scaled to the relative change in density of the modifier.

When multiple TIMs affect a single interaction, they are combined multiplicatively. The most prevalent combination of interaction modifications in nature is unknown, although there have been suggestions that interaction modifications are likely to act antagonistically to each other (Golubski and Abrams 2011), meaning that combined modifications have less effect than would be expected from the individual effects. For this analysis, since the starting condition is assumed to be the post-modification interaction strengths, the complications such considerations might introduce is reduced.

TIMs were added so that each potential TIM (combination of an existing trophic interaction and a third-party species) was present with probability of 0.1 (non-trophic connectance *sensu*

122 Goudard and Loreau (2008)). This choice of TIM connectance was arbitrary and would not
123 affect the results since the aim of the study is to determine relative importance of TIMs. TIMs
124 were assigned a slope parameter (c_{ijk}) drawn from a uniform distribution -0.3:0.3. This
125 distribution of slope parameters resulted in a distribution of Jacobian elements components
126 due to TIMs in approximately the range of trophic interactions (SI 2).

127 Empirical distributions of interaction modification strength in a network do not (to our
128 knowledge) yet exist although an approximate correspondence with trophic interaction
129 strengths is a reasonable estimate from meta-analyses (Preisser et al. 2005). In our simulations,
130 average direct pairwise TIM effects were smaller than trophic effects, but there was a notable
131 upper tail of interactions (SI 2). 3.17% of non-zero TIM-attributable Jacobian element
132 components had a magnitude larger than 1, the upper bound of trophic effects. This occasional
133 very strong direct effect caused by an interaction modification is not necessarily unrealistic as
134 the impact of behavioural effects can in certain circumstances be much faster and stronger
135 than consumptive interactions (Abrams 2001). Nonetheless, we repeated the analysis capping
136 such outlier interactions in line with the maximum trophic interaction element and found
137 similar results (SI 2).

138 **Ranking by TIM metrics and Generation of Reduced Models**

139 The TIM metrics listed in Table 2 and discussed below were calculated for each TIM.
140 Correlations between the TIM metrics across all the webs were assessed with Spearman's rank
141 correlation tests. For each web the TIMs were ranked according to each metric, using the
142 ranking methods detailed in Table 2. For each web, for each metric, the 'top' 30% of TIMs were

identified and a 'Reduced' system was generated including just those TIMs. A 'random' draw of 30% of TIMs was also generated for each web to establish a baseline. 30% was chosen as giving a good spread between the metrics – a subset with too few TIMs for inclusion led to very little change in predictability, while if too many were included the difference between the metrics was less clear (SI 3). The Jacobian matrices (**J**) for each of the 'Full', 'Reduced' and 'No TIM' models were calculated numerically at the equilibrium density with the *numDeriv* R package.

Strength of TIMs

It is well established that no single aspect of interaction strength is sufficient to categorise trophic interactions completely (Laska and Wootton 1998, Berlow et al. 2004). Similarly the strength of a TIM can be considered from a range of perspectives and with different valid methods (Terry et al. (2017). Metrics applicable to the equilibrium systems studied here are:

TIM Slope parameter (c_{ijk}): The parameter in the model that relates the modifier species density to the functional response relating the interactors.

Flux of Modified Interaction: The flow rate of biomass between the interactor species.

Direct Effect of modifier on interactors attributable to TIM: The derivative of the change in each of the interactor growth rates with respect to the modifier density when using the full model, minus the same value calculated without the presence of the TIM.

Derivatives of Jacobian elements representing the interaction with respect to the modifier: Corresponds to the modifier's effect on the direct effect of the consumer on the resource at equilibrium and vice versa.

Derivatives of the net-effects matrix elements representing the consumer-resource interaction with respect to the modifier: Corresponds to the modifier's effect on the net- effect of the consumer on the resource at equilibrium and vice versa.

Topology of TIMs

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, they link nodes to 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). Multi-layer networks (Pilosof et al. 2017) may also be used to analyse these 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 dynamic differences between interaction modifications and pairwise interactions (Terry et al. 2017). Here we introduce analogues of conventional network metrics that can describe how individual interaction modifications sit within the wider trophic network illustrated in Fig. 1. Aggregate metrics and approaches to consider the relationships of TIMs with each other are discussed in SI 4.

Range of modification: The mean number of trophic links from the modifying species to each interactor by the shortest route.

Trophic direction of modification: How the trophic level of the modifier compares to the trophic level interactors. The direction of a TIM is calculated as the mean trophic level of the interactors minus the trophic level of the modifier. Therefore, positive values imply modifications to interactions higher in the web than the modifier, negative values imply that species higher in the food web are modifying the interactions of those lower down.

Centrality of modifier and interactor species: The centrality of a species within a network can be measured by a diversity of algorithms (Newman 2010) and be applied to TIMs by calculating the centrality of the modifier species or the mean centrality of the interactors in terms of the their trophic linkages. Two common measures for how central a node is within a web are 'betweenness', which assess how many shortest paths between nodes go through a given node and PageRank, the 'Google algorithm' which assesses how much each node is linked to, weighted by the importance of each linked node.

Betweenness of modified interaction: The centrality of the modified interaction can be assessed by the edge-betweenness of the interaction – how often the shortest path between nodes goes via a given edge.

Assessment of predictability

Predictability (Novak et al. 2011, Iles and Novak 2016) is defined as the directional consistency in how species population changes in response to press perturbations (Yodzis 1988). Predictability was calculated as the fraction of matching signs of the net effects matrix ($-\mathbf{J}^{-1}$) between the 'Full' model and the 'Reduced' model. Ten systems were found to be uninvertible – these were removed from further consideration. To standardise across webs we calculated

204 the predictability when using the 'No TIM' model and report the difference in predictability
205 between the 'Reduced' model and the 'No TIM' model. The statistical significance of a metric's
206 ability to identify important TIMs differently to a random draw was tested with a Wilcoxon
207 signed rank test paired by underlying web.

208 **Assessment of TIM metrics for stability**

209 Local stability, whether the system will return to its previous equilibrium after a small
210 perturbation, can be determined from the sign of the real part of the largest eigenvalue of a
211 system's Jacobian matrix. Where this is negative the system can be considered locally stable.
212 Stability was assessed for each 'Full' and 'Reduced' Model. If the sign of the dominant
213 eigenvalue of the 'Reduced' model matched the 'Full' model it was deemed to successfully
214 categorise local stability. The ability of each metric to identify valuable sets of TIMs was
215 assessed with a binomial test with an expected value 0.82, the fraction correctly identified by
216 random draws of included TIMs

217 **Alternative Network structures**

218 To isolate TIM topology from other attributes, we repeated the predictability analysis using
219 underlying networks more restricted structure. Species body masses, parameters and
220 equilibrium densities were set to fixed values to equalise trophic direct effects (SI 5). Web
221 topologies (S=20, n=500) were created using either the niche model (C=0.1) or a simple 'grid'
222 model. The grid model consisted of four trophic levels each with 5 species, where each had 'in'
223 and 'out' degree of 2 as appropriate to its trophic level. Parameters were chosen to either

maintain the asymmetry between resource effect on consumer and consumer effect on resources, or with all direct interactions fixed to a constant value regardless of direction.

Results

Predictability

Non-topological metrics

The capacity of all of the metrics to identify TIMs that are important for predictability was significantly different from random draws (Fig. 2, results of significance tests given in SI 6) although the divergence varied greatly. The variability in changes to predictability was related to the median improvement – where a metric tended to give a larger improvement in predictability, there was also a greater chance that including those TIMs would result in a reduced model that was considerably worse than the No TIM model. Combinations of metrics were not particularly valuable - trying to optimise over multiple measures simultaneously did not bring additional information. There were strong correlations between a number of the metrics (see SI 7), clustering into topological and non-topological groups, although the two groups are linked by a correlation between interactor trophic level and trophic interaction strength (Spearman's $\rho = -0.58$).

Interaction flux was the best method for identifying the size of the underlying interaction, better than the direct effects between the interactor species. Measures of the dependence on the modifier species density of the interaction itself or the interactor species growth rate gave amongst the greatest improvements in predictability. Dependence on the net-effects between the interactors on the modifier density was less successful. The density of the modifier was

more valuable than the magnitude of the slope parameter c_{ijk} at providing useful information about the TIM function specification. There was no significant difference between selecting TIMs by the most positive or most negative c_{ijk} values (paired Wilcoxon signed-rank test p=0.0651, n=787).

Topological Metrics

The most valuable topological metric in the main set was the 'direction' of the TIM (Fig. 2). Those TIMs 'down' the network, where the modifier had a higher trophic level than the interactors, were particularly important. As lower interactions were likely to have a larger flux and higher trophic level species were likely to be rarer, the measure of direction is correlated with both the modifier biomass and interaction flux (Spearman's ρ: 0.31 and -0.31 respectively). Measures of centrality generally had poor comparative performance. The two measures of centrality (node-betweenness and PageRank) were relatively uncorrelated with each other (Spearman's ρ for modifiers: 0.33, for interactors -0.08). Approaches that identified TIMs involving high centrality modifiers or low-centrality interactions were generally better than random. However, effect size is weak in all sets of webs and effects are attributable to other correlated aspects of TIMs that have stronger impacts. TIMs where the modifier and interactor were widely trophically separated were more valuable than near TIMs, but difference in the median predictability change was smaller than other metrics.

Results for the sets with fixed direct interaction strengths and species density are detailed in Fig. 3. The four sets of networks each show different metrics as being able to identify distinct and important groups of TIMs. In general, as the networks become more rigidly structured,

266 fewer topological metrics were able to identify subsets of TIMs consistently better than
267 random. Downwards acting TIMs from high trophic level modifier species were more impactful
268 in set B whereas upwards TIMs were more valuable in sets A and C. Distributional changes of
269 net effects with trophic level are shown in SI 1. TIM range was able to identify valuable TIMs in
270 the niche model topology case but not in the grid topology case.

271 **Local Stability**

272 Metrics varied considerably in their ability to identify a subset of TIMs that accurately
273 determined local stability by the sign of the dominant eigenvalue (Fig. 4, statistical significance
274 tests in SI 6). Metrics that were better at identifying stability gained the most by increasing the
275 proportion of unstable full systems that were correctly categorised as unstable with the
276 reduced model. Metrics that performed well at identifying important TIMs for predictability
277 were also valuable for identifying those that were important for categorising local stability
278 (Spearman's $\rho = 0.96$, SI 6).

279 Nonetheless there were some notable differences. Selecting TIMs for inclusion that reached
280 further across the web was significantly worse than selecting TIMs at random. There was also a
281 sharp difference between selecting TIMs of differing signs: including the 'most negative' TIMs
282 was better than random draws, successfully identifying more of the unstable systems, while
283 including the 'most positive' was less successful than random.

284 **<u>Discussion</u>**

285 We have presented methods to quantify the structure of interaction modifications within a
286 trophic network and shown that it is possible to identify properties of trophic interaction

287 modifications that are particularly influential in the dynamics of model ecosystems. This is
288 informative both on a theoretical level in helping to discern how TIMs affect dynamics, but also
289 from a practical perspective in highlighting which TIMs are most valuable to study empirically.

290 TIMs introduce a high level of complexity to ecosystem dynamics. It is therefore reassuring to
291 note that relatively simple measures are able to identify TIMs that are important for dynamics.
292 Similar sets of TIMs were identified as being important in two distinct types of dynamics –
293 response to press perturbations (predictability) and response to pulse perturbations (local
294 stability). By identifying relatively high-impact TIMs we can make progress despite the present
295 dearth of empirical distributional data. Below we focus our discussion on specific results and
296 their implications, before looking forward to developing this approach in future work.

297 Selecting TIMs by interaction flux was a better method than assessing the direct effects
298 between the interactors. This is a helpful result for experimentally identifying TIMs since
299 interaction flux is easier to estimate than dependence of the interactors on each other as it can
300 be directly observed rather than requiring experimental manipulation (Wootton and Emmerson
301 2005). The need to contextualise TIMs in the wider community is reiterated by some of the
302 greatest improvements in predictability deriving from measures of the dependence on the
303 modifier species density of the interaction itself or the interactor species growth rate. Both are
304 measures of instantaneous effect, the first from a TIM perspective (dependence of the
305 interaction on the modifier), the second taking a pairwise non-trophic approach (dependence
306 of the interactors on the modifier through trait-mediated indirect interactions (Abrams 2008,
307 Okuyama and Bolker 2012)).

The importance of the rarity of the modifier in our study can be traced back to dependence of the modification function on the logarithm of modifier density. This has the effect that a change in the density of a rare modifier will result in a greater modification than the same absolute change in a more common modifier. Nonetheless, this dependence on relative changes seems a reasonable assumption and this result shows that TIMs can greatly increase the importance of species that might otherwise be neglected or dismissed. Furthermore, even in this linearised system it can be seen that a simple description of the relationship between the modifier species density and the interaction depends on both the starting density and a slope parameter.

Interpretation of the value of topological measures in the main set of webs is more challenging as a significant part of their effect can be attributed to correlations with strength-based metrics. The most valuable topological metric in the main set was the 'direction' of the TIM. Those TIMs acting 'down' the network were particularly important, although trophic height is correlated with both interaction flux and equilibrium density. However, a 'direction' effect can also be observed in web sets A and B (where interaction flux and equilibrium is fixed) demonstrating a distinct mechanism by which the direction of TIM can identify its importance. The low improvement when selecting TIMs by centrality and the opposing effect direction in sets A and B (with identical trophic topology), suggests the mechanism is not due to pure network topological effects.

An explanation can be found from differences in the trophic net-effects affecting species at different trophic heights. Although direct effects were held constant, the self-limitation terms (Jacobian matrix diagonals) still vary between species. These are composed of contributions from intrinsic rates of change (which differ between producers and consumers) as well as terms

330 from density-dependent predation rates leading to structural patterns in net-effects (SI 1.3).
331 Where mean net-effects increase with trophic height (Set B and the 'realistic' main set),
332 'downwards' TIMs can be seen to have a greater impact, driven by trophic height of the
333 modifier. Greater sensitivity of higher trophic level species to extinction provides some support
334 that this is a common natural relationship. Where the modifier species is more sensitive to
335 other species, the TIM can act as a stronger conduit for other species to spread their impact
336 indirectly through the modification. When mean net-effects decrease with trophic height (set
337 A) the reverse is true –TIMs from low trophic level modifiers have more of an impact.

338 Trophic net-effects tend to decline with the number of trophic links between the interactors
339 (Neutel 2002). Where the trophic net effect is weak, there is a greater potential for a TIM to
340 dominate the pairwise net-effect between those species and therefore be important for
341 predictability. This can be seen in the effect of range in the fixed webs. The comparatively poor
342 indicative potential of TIM range in the main set suggests that other significant features of TIMs
343 (discussed above) may be able to override this expectation, as there is a strong net-effects –
344 distance relationship. Although TIMs have the potential to greatly reduce the dynamic breadth
345 of food webs, given that it is estimated that the majority of species are no more than two
346 trophic links apart (Williams et al. 2002) the extent of this effect may be limited in practice.

347 In two particular cases the results from the stability estimation test diverged from those of
348 predictability. Range of TIM was notably poor at the estimation of stability – including just the
349 long-range TIMs lead to a preponderance of stable web estimates. This is surprising given that
350 long-range TIMs would be expected to contribute more to increasing dynamic connectivity and
351 consequent instability (May 1973). Selecting negative TIMs (that benefit the resource to the

352 detriment of the consumer) result in more stable estimates of systems, while selecting positive
353 TIMs lead to more estimates that the resultant system would be unstable. This is a distinct
354 effect to that caused by mutualism or competitive direct interactions e.g. (Mougi and Kondoh
355 2012, Coyte et al. 2015) since every TIM exerts both a negative and a positive influence and
356 should be investigated further.

357 **Outlook**

358 For this study we had to make a number of assumptions about the form, distribution and
359 strength of TIMs. The lack of empirical data at a community level is a particular challenge,
360 although identifying non-trophic effects at the network level is possible (Pocock et al. 2012, Kéfi
361 et al. 2015) and shows that networks of pairwise non-trophic interactions have considerable
362 structure (Kéfi et al. 2016). Our study emphasises the tight relationship between the underlying
363 trophic network and the consequences of interaction modifications. Isolating an interaction
364 modification from its context will result in the loss of valuable information. The five properties
365 of TIMs identified here (Fig. 5) build up a profile that could be used to identify processes that
366 are more likely to have a considerable effect on dynamics in response to perturbations.

367 One avenue that will need particular work is the degree of accuracy to which interaction
368 modifications must be known in order to contribute to improving ecological forecasts (Petchey
369 et al. 2015). Our assumption that all pairwise interaction strengths are known, and that
370 included TIMs are perfectly quantified, constitutes rather wishful thinking for any system of
371 realistic size. For small systems, qualitative analyses (Dambacher et al. 2003, Dambacher and
372 Ramos-Jiliberto 2007) can be useful for mapping out the potential responses of systems

although for larger systems they can rapidly become indeterminate. As a testament to the importance of quantifying TIMs we conducted a randomisation study (SI 8) which showed randomising slope parameter values while maintaining the sign yielded an average directional predictability of 0.57, barely better than chance. Without empirical estimates for the distribution of TIMs it is difficult to assess the potential impact on overall predictability in the manner of Novak et al. (2011) but it is clear that there is the potential for a significant impact. Future work should 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. The balance of the impact of exogenous impacts on a system compared to 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.

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Table 1: Parameters used in the main set of simulations.

Parameter	Value	Meaning and source
B_i	(from integration)	Species Density
K	5	Producer carrying capacity
e	0.45 (herbivory) 0.85 (carnivory)	Assimilation efficiencies (Brose et al. 2006b)
y	10	Maximum ingestion rate (Boit et al. 2012)
B_0	1	Half-saturation density
x_i	$a_i M_i^{-0.25}$	Species-specific metabolic rate following ¼ power-law (Brown et al. 2004)
a_i	Producers: 1 Trophic Level 2: 0.314 Trophic Level 3+: 0.88	Allometric constant (Brose et al. 2006b)
r	1	Producer growth rate
M_{max}	10	Greatest increasing modification
M_0	0	Greatest reducing modification
c_{ijk}	-0.3 : 0.3	TIM slope parameter. Impact of modifier *k* on the consumption of *i* by *j*.
B_k^*	(from integration)	Modifier equilibrium density

552 Table 2: Metrics used to rank TIMs to determine inclusion in reduced model.

	Metric to Rank by	**Ranking Method**
Strength	TIM parameter c_{ijk}	Magnitude, most +, most -
	Interaction flux	Largest
	Direct effect of modifier on interactors, due to TIM	Largest magnitude , effect on prey & effect on predator
	Derivative of direct effect between interactors w.r.t modifier	Largest magnitude. Effect of prey on predator and vice-versa
	Derivative of net- effect between interactors w.r.t modifier	Largest magnitude. Effect of prey on predator and vice-versa.
	Equilibrium density of modifier	Highest, Lowest
Topological	Distance	Largest (furthest), smallest (nearest)
	Direction of TIMs	Most upwards, most downwards
	Mean PageRank of interactors	Highest, Lowest
	Mean betweenness of interactors	Highest, Lowest
	PageRank centrality of modifier	Highest, Lowest
	Betweenness centrality of modifier	Highest, Lowest
	Betweenness of interaction	Highest, Lowest
	Mean trophic level of interactors	Highest, Lowest
	Trophic level of modifier	Highest, Lowest
Combinations	Largest flux & modifier rarity	Average rank across metrics
	Largest flux, modifier rarity & downwardsness	Average rank across metrics

553 Figure 1. Example of metrics to describe the topology of trophic interaction modifications
554 relative to the underlying trophic network.

555 Figure 2. Change in directional predictability when 30% of trophic interaction modifications
556 (TIMs) selected by different methods are included in a reduced model compared to a No-TIM
557 model. Red line demarks median predictability increase when drawing TIMs at random. All
558 metrics gave predictability results significantly different to random draws (paired Wilcoxon test,
559 $p<0.05$, n= 787. See SI 6 for full results).

560 Figure 3. Results from webs with fixed direct interaction strengths and equilibrium densities.
561 Change in directional predictability when 30% of trophic interaction modifications (TIMs)
562 selected by different methods are included in a reduced model compared to a no-TIM model.
563 Each panel is standardised to the median change in predictability when drawing TIMs at
564 random form comparison. Colour indicates significance of difference in predictability compared
565 to the random draws (paired Wilcoxon test, green = $p<0.05$, blue = $p>0.05$, n= 500)

566 Figure 4. Match between estimate of local stability from a reduced model including TIMs
567 selected by different metrics and the stability of the full model. Black line shows which metrics
568 did not correctly estimate local stability (shown in blue) significantly differently to the random
569 draw (Binomial test, expectation = 0.82, n=787, $\alpha = 0.05$. Full results of significance tests are in
570 SI 6.)

571 Figure 5. Properties of trophic interaction modifications that tend to increase their impact on
572 system dynamics.

573

Figure 1.

Metric:	Modification: Blue	Brown
Range	1	2
Direction	-0.5	+1.5
Centrality of Modifier	0	24.5
Centrality of Interactors	19.5	3.75
Modified Interaction Betweenness	17.5	7.5

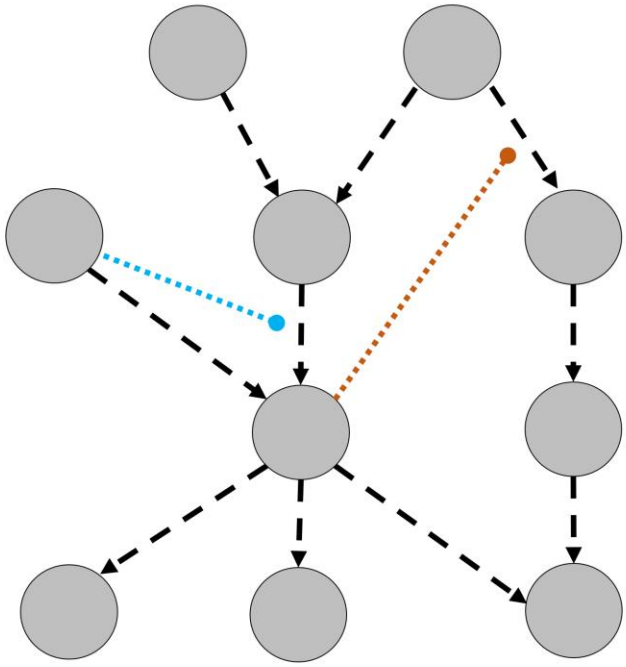
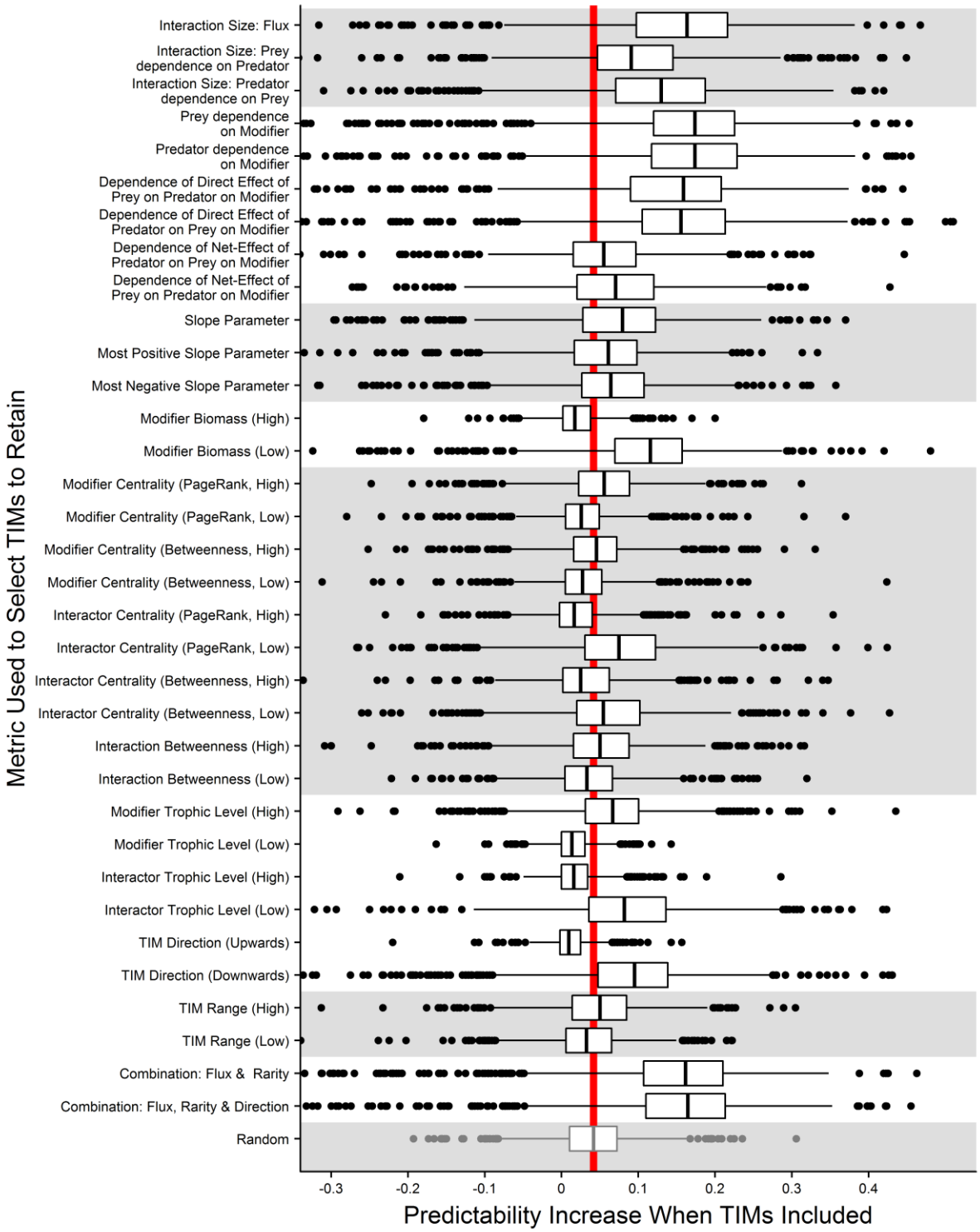
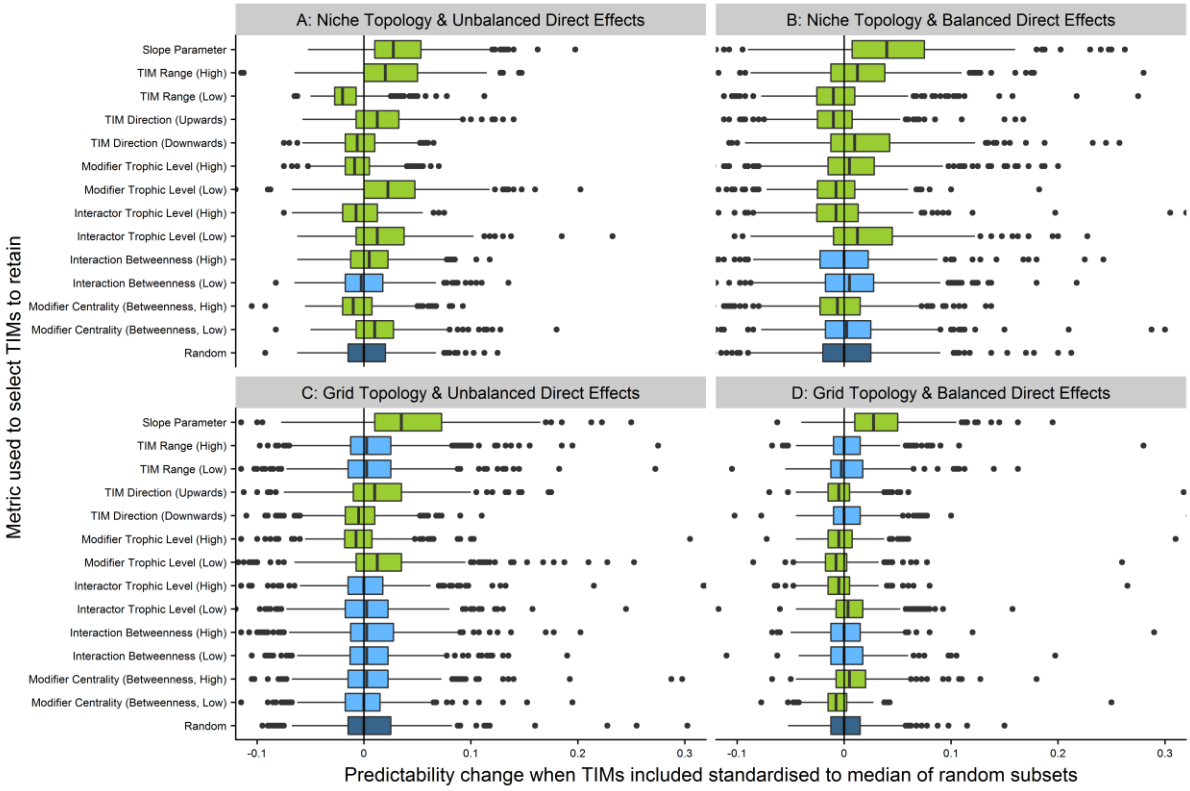


Figure 2.


Interaction Size: Flux
Interaction Size: Prey dependence on Predator
Interaction Size: Predator dependence on Prey
Prey dependence on Modifier
Predator dependence on Modifier
Dependence of Direct Effect of Prey on Predator on Modifier
Dependence of Direct Effect of Predator on Prey on Modifier
Dependence of Net-Effect of Predator on Prey on Modifier
Dependence of Net-Effect of Prey on Predator on Modifier
Slope Parameter
Most Positive Slope Parameter
Most Negative Slope Parameter
Modifier Biomass (High)
Modifier Biomass (Low)
Modifier Centrality (PageRank, High)
Modifier Centrality (PageRank, Low)
Modifier Centrality (Betweenness, High)
Modifier Centrality (Betweenness, Low)
Interactor Centrality (PageRank, High)
Interactor Centrality (PageRank, Low)
Interactor Centrality (Betweenness, High)
Interactor Centrality (Betweenness, Low)
Interaction Betweenness (High)
Interaction Betweenness (Low)
Modifier Trophic Level (High)
Modifier Trophic Level (Low)
Interactor Trophic Level (High)
Interactor Trophic Level (Low)
TIM Direction (Upwards)
TIM Direction (Downwards)
TIM Range (High)
TIM Range (Low)
Combination: Flux & Rarity
Combination: Flux, Rarity & Direction
Random
Metric Used to Select TIMs to Retain
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
Predictability Increase When TIMs Included

580 Figure 3.



581

Figure 4.

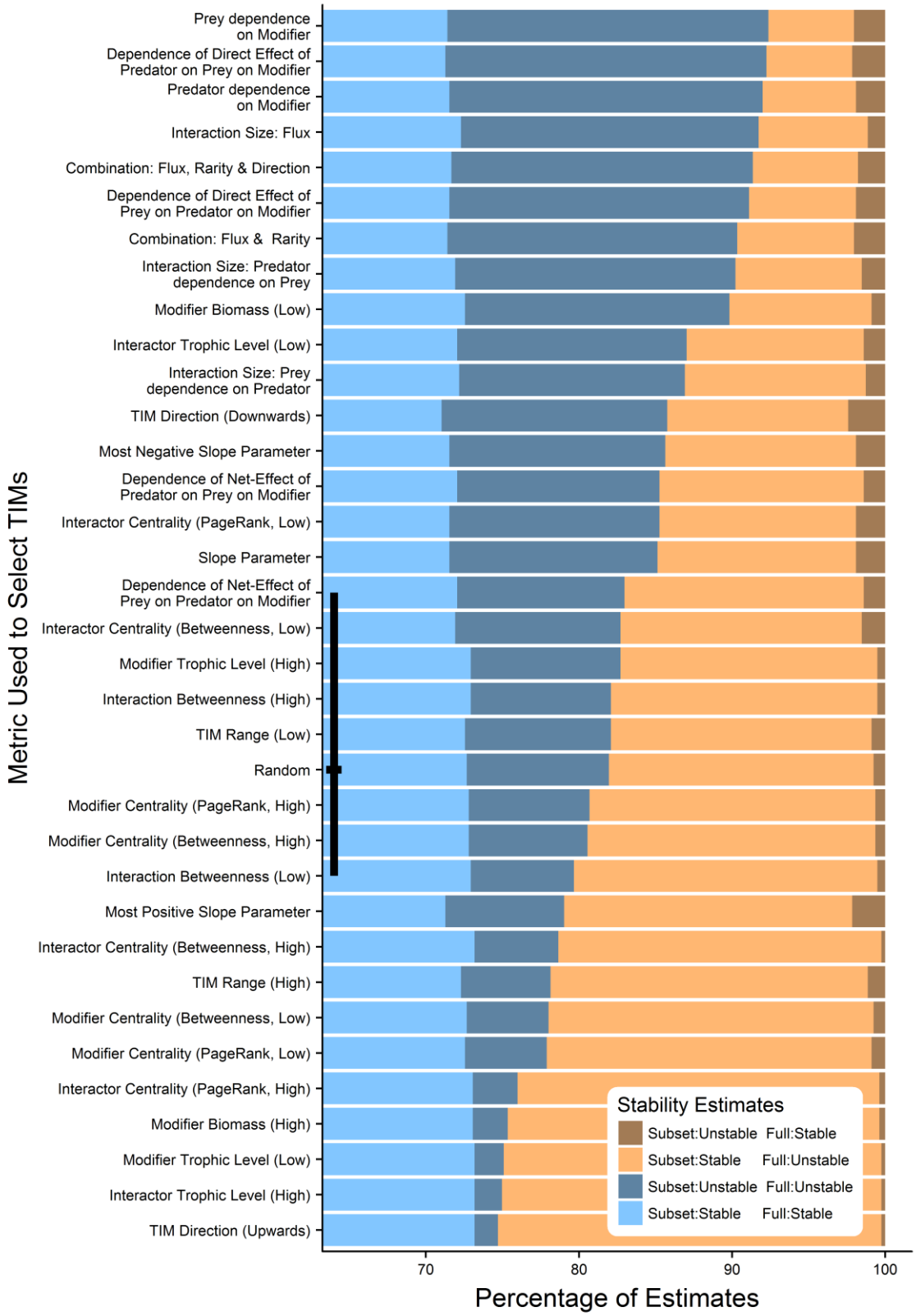
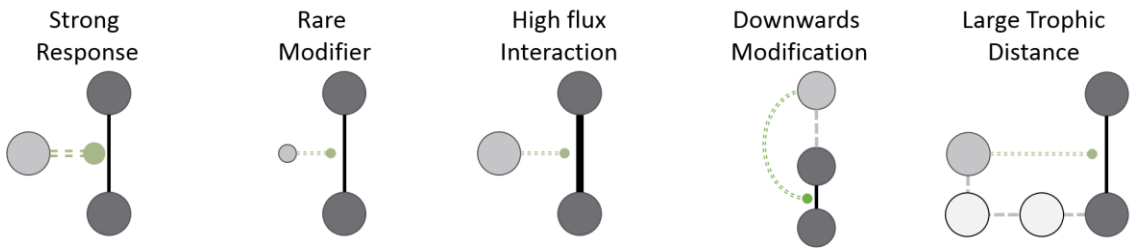

Metric Used to Select TIMs
Prey dependence on Modifier
Dependence of Direct Effect of Predator on Prey on Modifier
Predator dependence on Modifier
Interaction Size: Flux
Combination: Flux, Rarity & Direction
Dependence of Direct Effect of Prey on Predator on Modifier
Combination: Flux & Rarity
Interaction Size: Predator dependence on Prey
Modifier Biomass (Low)
Interactor Trophic Level (Low)
Interaction Size: Prey dependence on Predator
TIM Direction (Downwards)
Most Negative Slope Parameter
Dependence of Net-Effect of Predator on Prey on Modifier
Interactor Centrality (PageRank, Low)
Slope Parameter
Dependence of Net-Effect of Prey on Predator on Modifier
Interactor Centrality (Betweenness, Low)
Modifier Trophic Level (High)
Interaction Betweenness (High)
TIM Range (Low)
Random
Modifier Centrality (PageRank, High)
Modifier Centrality (Betweenness, High)
Interaction Betweenness (Low)
Most Positive Slope Parameter
Interactor Centrality (Betweenness, High)
TIM Range (High)
Modifier Centrality (Betweenness, Low)
Modifier Centrality (PageRank, Low)
Interactor Centrality (PageRank, High)
Modifier Biomass (High)
Modifier Trophic Level (Low)
Interactor Trophic Level (High)
TIM Direction (Upwards)
Stability Estimates
Subset:Unstable Full:Stable
Subset:Stable Full:Unstable
Subset:Unstable Full:Unstable
Subset:Stable Full:Stable
70
80
90
100
Percentage of Estimates

Figure 5


Strong Response
Rare Modifier
High flux Interaction
Downwards Modification
Large Trophic Distance