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Interaction Modifications Disrupt The Structure And Stability Of Ecological Communities

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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 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 could significantly alter the overall structure of community interactions. Analyses of the stability of ecological systems based solely on trophic interactions are therefore unreliable, making empirical distributions of interaction modifications essential.

Introduction

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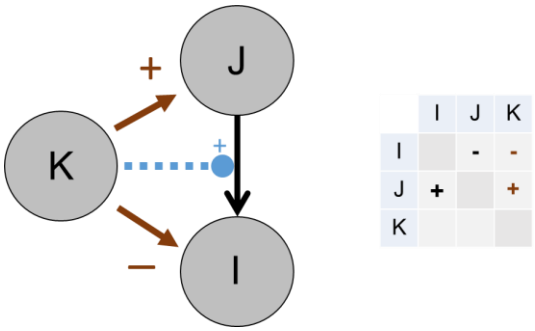
Understanding how large and diverse ecosystems persist is a core challenge in ecology. Theoretical expectations that large random complex systems are unlikely to be locally stable[1], indicate that the interactions within ecological communities are structured in important ways[2]. A growing body of work has demonstrated features of trophic networks that can stabilise communities - including the distribution of weak links[3,4], pairwise correlations[5], modularity[6], row structure[7] and trophic level coherence[8]. However, ecological communities contain complex networks of interactions beyond trophic interactions[9], and there is an emerging appreciation of the value in studying the full spectrum of interaction types[10–16].

Interaction modifications[17], where a pairwise interaction is dependent on a third species, are pervasive within ecological networks[18] and capable of exerting impacts as strong as direct trophic interactions[19]. They are increasingly recognised as having the potential to be of considerable importance in the dynamics of ecological systems [20–22]. Interaction modifications are higher-order interactions that induce non-trophic effects (NTEs, also termed trait-mediated indirect interactions) from the modifier species onto a pair of interactors (Figure 1). This additional source of interactions and dynamic connectance introduces emergent pairwise relationships between species that do not otherwise directly interact, potentially greatly increasing the dynamic connectance of the system [23].



	I	J	K
I		-	-
J	+		+
K			

Figure 1. Schematic representation of the relationship between a trophic interaction modification (blue dashed line), resultant non-trophic effects (brown solid lines) and consequent community matrix. An interaction modification results in two non-trophic effects from the modifier. Here a modifier acts to strengthen a trophic interaction. This results in a positive effect on the consumer (J) and a negative effect on the resource (I).

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The ubiquity and diversity of non-trophic interactions poses a considerable problem for ecologists. Previous theoretical studies have introduced independently distributed higher-order interactions and demonstrated they can have significant influence on stability[24,25]. However, it is known that non-trophic interactions are not randomly distributed[26] and it is expected that the distribution of interaction modifications (and consequent NTEs) will be structured, both internally and with respect to the underlying trophic interactions[27]. This relationship offers an opportunity to build upon the understanding of the structure of trophic networks[28] to inform the likely distribution and consequences of NTEs[13] and move beyond random distributions of non-trophic effects[14,15].

Here, we examine the impact trophic interaction modifications (TIMs)[29,30] can have on the equilibrium dynamics of simple models of the interactions between species in artificial and empirical networks. We combine trophic interaction matrices with NTE matrices generated through distinct distributions, designed to span the range of possibilities for distributions of interaction modifications. 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. Until the empirical distribution of interaction modifications is understood, suggested resolutions of the stability-complexity paradox are premature.

Results

Introducing TIMs to artificial trophic networks

We specified the interactions within artificial communities with a Jacobian matrix **A** from the combination of two matrices specifying the trophic (**B)** and non-trophic (**C**) interactions (Figure 2). Trophic interactions topologies were generated using the niche model[31] and parameterised with draws from a bivariate normal distribution with pairwise correlation[32]. We tested 16 different distribution models for the specification of non-trophic effects caused by TIMs, detailed in Table S1 and depicted in Figure 3, which varied in topology, distribution of modification strengths and

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translation from TIM to NTEs. Each of the resultant non-trophic interaction distributions had distinct structural properties, detailed in Table S2.

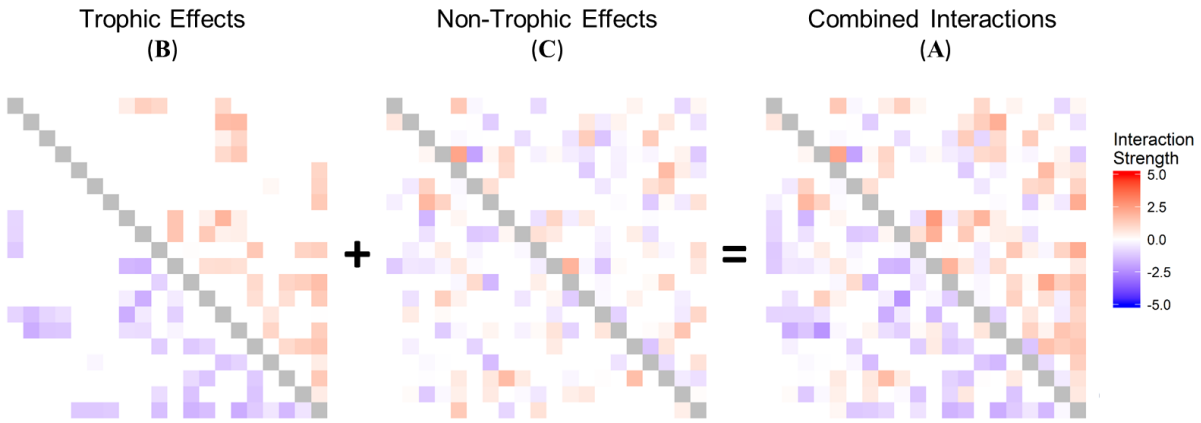

*Figure 2. Illustration of construction of interaction matrices. At an assumed equilibrium, a combined interaction matrix (**A**) can be split into the impact of trophic (**B**) and non-trophic effects (**C**). The species are arranged approximately in trophic height order, with basal species top/left and top predators at the bottom/right. The underlying trophic network was generated by a 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.*

Figure 3: Illustration of the distributions of TIMs and their impacts tested in this study, with representative non-trophic interaction matrices for a 20 species trophic network and a TIM density of 5 per species. Full specification of the distributions are given in Table S1. Mean magnitude of

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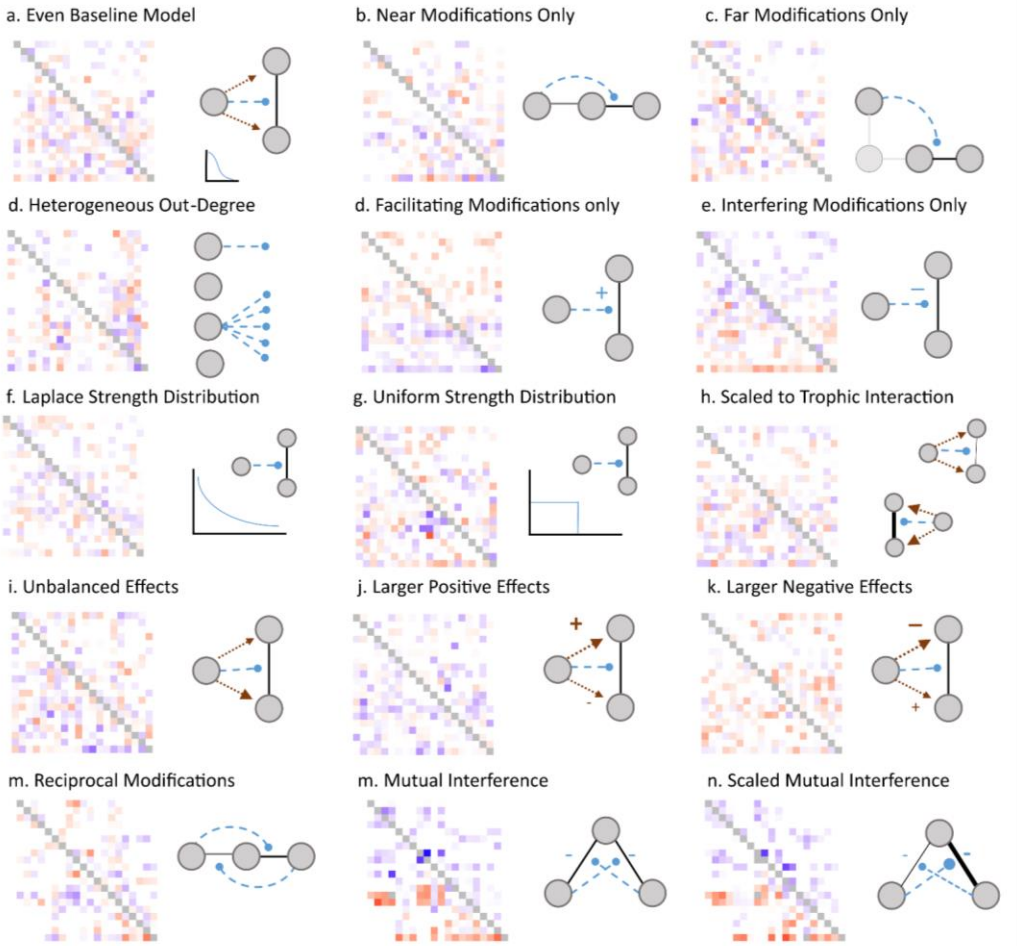
individual non-trophic effects was held constant at 0.5.



As the density of TIMs (the expected number of TIMs per species) was increased, the degree of self-regulation that would be necessary for local asymptotic stability ($\Re(\lambda_1^{\mathbf{A}})$, henceforth 'stability') always decreased while reactivity (the size of the initial response to perturbation, $\lambda_1^{\mathbf{H}}$, $\mathbf{H}=\frac{\mathbf{A}+\mathbf{A}^T}{2}$) 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 and Reciprocal modifications models) led to a higher

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reactivity than those that had a more even effect distribution (Baseline, Scaled, Random NTE, Far TIMs, Uniform strength distribution).

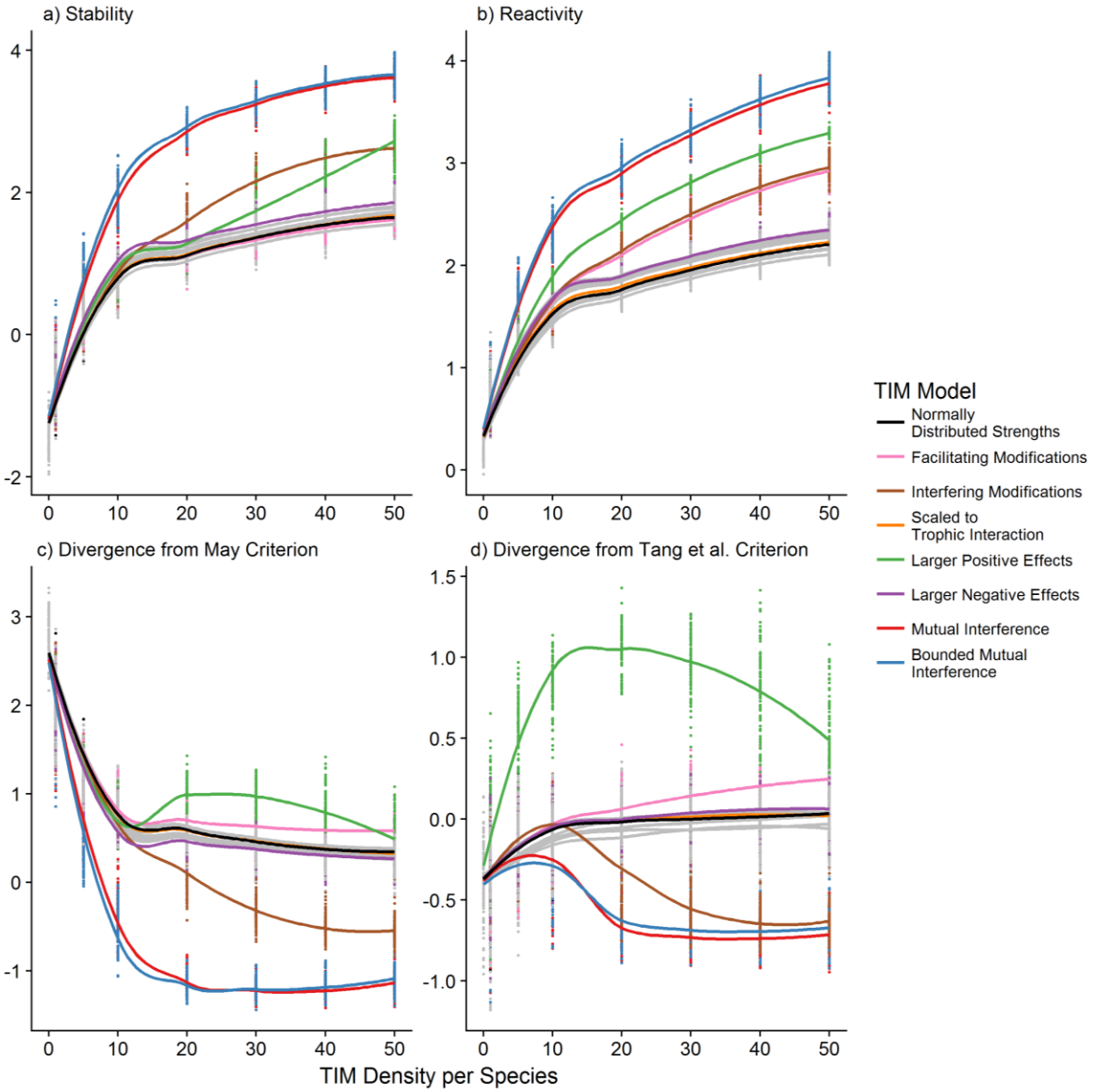

Figure 4. Effect of increasing density of TIMs on (a) stability $\log(\Re(\lambda_1^{\mathbf{A}}))$*, the degree of self-regulation necessary for local asymptotic stability, (b) system reactivity* $\log(\lambda_1^{\mathbf{H}})$*, (c) the log-ratio of the May stability criterion and the observed stability and (d) the log-ratio of the Tang et al stability criterion and the observed stability. TIM distribution models with distinctive responses are highlighted, the*

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remainder are coloured grey and are plotted in Figure S1. Loess fitted lines have been added to highlight differences.

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).

To assess the extent to which the interspecific interactions were non-randomly structured we examined the performance of two analytic criteria for local stability (That of May [1]: $\lambda_1 = \max\left((S-1)\mu, \sqrt{SV} - \mu\right)$ and Tang et al.[33]: $\lambda_1 = max((S - 1)\,\mu,\ \sqrt{SV}(1-\rho)\ - \mu)$, where S is the number of species, V is the variance in interaction strength, μ is the mean interaction strength and ρ is the pairwise correlation between interaction terms). Many of the TIM distributions we tested showed a reduced divergence of the true stability from that estimated by the stability criteria (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[34,35], 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,

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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[36] 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 **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 over the May criterion (Figure 4c-d), although pairwise correlation, ρ, was a less good predictor of stability at weak (near zero) levels of correlation.

Our results contrast with those of Bairey et al.[25], who found that the classic negative relationship between complexity and diversity can be reversed with higher order interactions. Using unstructured random matrices, their findings were driven by a decrease in the variance of the resulting NTE matrices due to an increasing central tendency of the strength of resultant pairwise interactions when composed of an increased number of random elements drawn from higher-order array. It is clear from our results that non-random distribution of NTEs can have a considerable impact by introducing additional variance and structure to the overall interaction network.

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[1]. This effect is driven largely by emergent pairwise mutualism, long-recognised as destabilising for interaction matrices[37]. The NTEs induced by these TIMs are very efficient at breaking down the negative correlation between pairwise elements (Figure S4), inducing mutualistic effects between resources that share a

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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 **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 **B** and **C** have a low covariance, and the resultant variance of **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[38], adaptive foraging[39] and associational defence[40]. These effects are widespread[41] and are regularly included in general models of population dynamics[42] through multi-species functional responses[43], 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[44–46], 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 sign pattern observable in Figure 3e and 3f. Since there are distinct patterns in the underlying trophic

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interaction distributions (Figure 2) the covariance between matrices **B** and **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 **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[47,48] is dependent on the eigenvalues of $(\mathbf{A} + \mathbf{A}^T)/2$, 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 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.

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TIMs and Row Structuring

It has been suggested that row-structuring (where the rows of **A** having markedly different means) is key for stability of empirical networks[49], although the effects may be greater on the rate of return to equilibrium than the sign of the eigenvalue [50]. 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 [51,52]) 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.[49] 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

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(the 'Mid-Atlantic Bight' network), many of the TIM models led to a small increase in stability, with the largest effect from facilitating modifications.

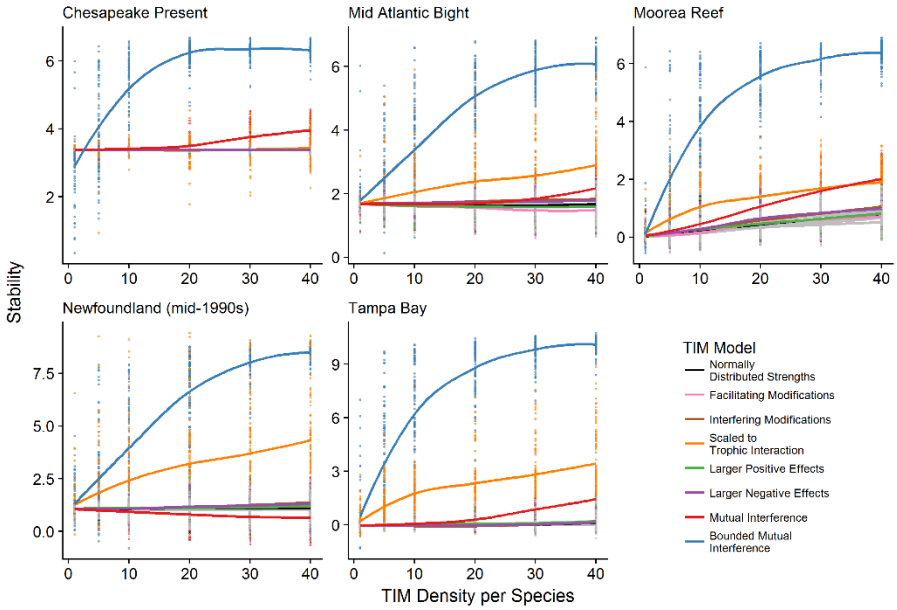

Figure 5. Stability, $\Re(\lambda_1^{\mathbf{A}})$, of five empirically parameterised food webs with increasing density of TIMs. TIM distribution models with distinctive responses are highlighted, the remainder are coloured grey and are plotted in Figure S5. Loess fitted lines have been added.

The empirical networks studied here differ significantly from randomly generated networks (see Jacquet et al.[49] 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 ('fat-tailed') 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 effectively only add noise.

Consequently, the introduction of TIMs hardly changed the overall pairwise correlation - the largest value of ρ across all TIM iterations was just -0.016. The NTEs introduced by the scaled models

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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.

Discussion

Our results show that interaction modifications have the potential to cause significant disruptive effects in ecological communities yet the inter-relationship between non-trophic and trophic interactions is critical to understanding their consequences. Our work reiterates the importance of the relationship between superimposed interaction networks [12,26]. 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 trophic cascades, the distribution of interaction motifs in ecological communities [53,54] 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 interaction modifications in real communities is at present essentially unknown beyond a limited number of inter-tidal communities[55,56]. The fraction of interspecific interactions driven by interaction modifications is unknown, but likely to be large[18,57]. The set of TIM models used here attempt 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[25] and empirically parameterised

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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 [22,29]. 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 [58–60], 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. 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.

Methods

Communities as Interaction Matrices

We represent the complete set of interactions in a system as a Jacobian matrix **A**, also termed a community matrix [61], 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 non-trophic (**C**) interactions present in the community (Figure 2). For

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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[31], a network generating algorithm that has been shown to reproduce many of the features of real food webs [62]. We generated 100 networks each with 60 species (S) 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. [63]. This specification maintains an average interaction strength of 0 and an overall symmetry in impacts between consumer and resource. This simplifies analysis but is known to be unrealistic [64]. 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 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 [29]. 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 [24,25] at the system state under consideration (Figure 1). These non-trophic effects (NTEs) can be used to construct a matrix, **C**, of 'direct' 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 **B** already incorporates the consequence of the equilibrium level of the modifier species.

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From the trophic networks, NTE matrices were generated from distributions of TIMs (detailed in Table S1, and summarised in Figure 2) that varied in topology, strength distribution and translation from TIM to NTEs. Since the distribution of interaction modifications in real communities is at present essentially unknown, this large collection of models is an attempt to span the range of potential distributions to identify key features pertinent to dynamics. In addition, we also tested an NTE distribution model where there was no underlying interaction modification structure and NTEs were independently randomly distributed with their strengths drawn from a Normal distribution.

Each TIM was assigned an effect size parameter (c_{ijk}), such that the mean magnitude of individual non-trophic effects (α) incorporated into a community is 0.5, in line with results from meta-analysis that suggests an approximate correspondence between the strength of trophic and non-trophic interactions [19]. A positive c_{ijk} indicates that 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. The c_{ijk} values determined the NTEs of the modifier on the two interactors ($\mathbf{C}_{ik}$, $\mathbf{C}_{jk}$) and were used to construct a TIM effect matrix **C**, Table S1.

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 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

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connectance (the resultant fraction of non-zero elements of the consequent TIM effect matrix **C**, which is dependent on the distribution and overlap of the TIMs).

We applied each of the 16 NTE distribution models at each TIM density across each of the 100 underlying trophic networks for a total set of 11 200 community models including TIMs.

Properties of Interaction Matrices

Structural properties of the resultant interaction matrices were calculated:

- Mean interaction strength (μ) of **A**
- Connectance (fraction non-zero entries) of **A** and **C**,
- Variance (V) of the off-diagonal elements of **A** and of **C,**
- Degree heterogeneity of **A** as the variance of the normalised in and out-degree distribution,
- Correlation (ρ) of the pairwise elements of **A:**, $\frac{\mathrm{E}(\mathrm{a_{ij}a_{ji}})-\mu^2}{\mathrm{V}}$, $(a_{ij}, a_{ji})_{i\neq j}$
- Covariance between **B** and **C**,
- Row structure ζ_{row} as the variance in mean interaction magnitude across rows $Var(\frac{\sum_j|a_{ij}|}{S})$ and likewise:
- Column structure ζ_{col}, $Var(\frac{\sum_i|a_{ij}|}{S})$.

We separately 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 (two-tailed).

Local asymptotic stability is determined by the sign of the real part of the leading (dominant) eigenvalue of **A,** $\Re(\lambda_1^{\mathbf{A}})$, 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 **A** specify the self-regulation of each species. With sufficient self-regulation any community can be stabilised. Although the distribution of self-

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regulation effects can have important consequences [65] we follow previous work[49,66] and set all diagonal elements of **A** to zero to focus on the impact of the inter-specific interactions. Without self-regulation, $\Re(\lambda_1^{\mathbf{A}})$ 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 can use "less stable" to refer to a system farther from stability (a larger $\Re(\lambda_1^{\mathbf{A}})$).

The immediate response of a system to perturbation is described by its reactivity, the maximum instantaneous amplification of a small perturbation [47,48]. This is computed as the leading eigenvalue of the Hermitian part of the community matrix: $\lambda_1^{\mathbf{H}},\ \mathbf{H} = \frac{\mathbf{A}+\mathbf{A}^T}{2}$. Since **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 [1,34,67]. We refer to these as the May criterion: $max((S-1)\,\mu,\ \sqrt{SV}\ -\mu)$ and the Tang et al. criterion: $max((S\ -\ 1)\,\mu,\ \sqrt{SV}(1-\rho)\ -\mu)$. 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, $\frac{E(a_{ij}a_{ji})-\mu^2}{V}$. The first term of each criteria specifies the eigenvalue derived from the expected row-sum [5]. In most trophic networks (where μ<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 [34,35].

Empirical Trophic Networks

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The stability analysis was repeated for the five largest empirical trophic networks in the set compiled by Jacquet et al. [49]. These are models of the trophic interactions in marine fisheries that had been parameterised by the EcoPath modelling approach [68] 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 web (range 0.017-0.18) to be comparable with the artificial networks.

Data and Code Availability

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

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Author contributions

JCDT initiated the research, and JCDT, MBB and RJM contributed to the ideas presented in the manuscript. JCDT conducted the research, facilitated by discussions with RJM and MBB. JCDT wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing Interests

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The authors declare no competing interests.

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