UNIVERSIDADE FEDERAL DE LAVRAS

ANGELO BARBOSA MONTEIRO

Dynamical stability and complex topologies: patterns and mechanisms in food webs

LAVRAS – MG

2018

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para obtenção do título de Doutor.

Orientador

Dr. Lucas Del Bianco Faria

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APROVADA em 16 de março de 2018
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A minha mãe Dilza Maria Barbosa
A minha esposa Nhielma Araújo

DEDICO

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"A ciência exercita a capacidade, não o saber: O valor de praticar com rigor, por algum tempo, uma ciência rigorosa não está propriamente em seus resultados: pois eles sempre serão uma gota ínfima, ante o mar das coisas dignas de saber. Mas isso produz um aumento de energia, de capacidade dedutiva, de tenacidade; aprende-se a alcançar um fim de modo pertinente. Neste sentido é valioso, em vista de tudo o que se fará depois, ter sido homem de ciência."

- Friedrich Nietzsche, 1978

RESUMO

O estudo de interações tróficas aborda as interações de predador e presa em comunidades naturais, e tem sido reconhecido como um dos princípios fundamentais em ecologia. Entretanto, a complexidade como essas interações ocorrem em comunidades naturais impõe abstrações aos estudos, os quais focam em padrões populacionais dinâmicos de poucas espécies ou padrões estruturais (topológicos) de toda a comunidade. Além disso, o processo de coleta de interações tróficas em comunidades naturais requer extensos trabalhos de campo, e a consistência das informações varia com os objetivos do estudo, grau de identificação das espécies e metodologias de inferência. Dessa forma, estudos utilizam modelos teóricos capazes de reproduzir o comportamento de forrageio de predadores, e gerarem grande volume de dados para análises teóricas. O presente trabalho teve como objetivo avaliar padrões e mecanismos em redes tróficas, especificamente as relações entre a complexidade de comunidades naturais e sua estabilidade à perturbações. As análises procuraram combinar aspectos teóricos e empíricos do estudo de comunidades naturais, utilizando inferências de análises dinâmicas, padrões topológicos, modelos probabilísticos e inferências estatísticas. De forma específica, avaliou-se como a ocorrência de módulos estáveis em comunidades naturais (subcomponentes das redes resilientes à perturbações) relaciona-se com as características topológicas. Avaliou-se também a capacidade de modelos teóricos reproduzirem o comportamento de forrageamento do predador e como ele relaciona-se com atributos da presa. Os resultados sugerem que, de maneira geral, a estabilidade esperada para os diferentes módulos de interações de três e quatro espécies, influenciam na sua probabilidade e frequência de ocorrência. Sugere-se um processo barreira, onde módulos com maior estabilidade dinâmica possuem maior probabilidade e frequência de ocorrência. Além disso, observou-se que a causalidade da relação entre dinâmica e topologia ocorre através da presença de módulos estáveis, os quais moldam a ocorrência de determinados padrões topológicos observados em dados empíricos. Por fim, os resultados também sugerem a complexidade na relação entre o comportamento de forrageio dos predadores e os atributos das presas, mas demonstra que modelos que assumem poucas dimensões de nicho são capazes de reproduzir padrões empíricos, além de demonstrarem as melhores associação entre diferentes comportamento de forrageio de predadores e os atributos das presas.

Palavras-chave: Ecological networks. Food-web structure. Complexity/stability. Local stability.

ABSTRACT

Food-web theory evaluates feeding relations between species, and has been recognized as one of the fundamental principals in ecology. However, in order to account for the complexity in which these interactions occur in natural communities, studies either emphasizes topological aspects of food-webs, or the mechanisms for stability of population dynamics. Furthermore, collecting high-quality food-web data involves extensive field works, while the consistency of the final data is conditioned to the objectives of the study, species identification and methods for inferring interactions. Thus, studies usually design theoretical models for the feeding behavior of consumers, in order to generate enough data for theoretical analyses. This work aimed to assess patterns and mechanisms of food webs, specifically the relationship between the complexity of natural communities, and their stability to endure perturbations. In general, the analyses combined theory and practice, using dynamical stability, probabilistic models, statistical inferences, and empirical data. Specifically, this work evaluated the causal relationship between the occurrence of dynamically stable modules (components of th food-web resilient to small perturbations) and statistical patterns of food-web topology. This work also evaluated the ability of food-web models to reproduce observable patterns of association between the feeding behavior of consumers and resources traits. The results suggest that dynamical stability of three and four-species modules allows the occurrence of complex food-web topology. This stability, however, is conditioned to a *hurdle* effect, which favors the probability and frequency of occurrence of modules with higher expected stability. Further, the causal relationship between dynamics and topology occurs through these stable modules, which allow the occurrence of observable topological patterns. Finally, the results contribute to the understanding of the adequacy of inferences under theoretical models to empirical patterns, and the ability of models that assume few dimensions of the niche space to reproduce the complex matching patterns between predators feeding behavior with their resources traits.

Keywords: Ecological networks. Food-web structure. Complexity/stability. Local stability.

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PRIMEIRA PARTE

1 APRESENTAÇÃO

Interações tróficas são aspectos universais na ecologia das espécies, e a complexidade como apresentam-se em comunidades naturais têm fascinado ecólogos desde os primeiros estudos (DARWIN, 1859; DUNNE, 2006). Em um trabalho clássico, Elton (1927) define as cadeias tróficas como as interações entre espécie de uma comunidade em relação às espécies produtoras, e as redes tróficas como o conjunto de todas as cadeias tróficas em uma comunidade; e determina que esses aspectos compõem os princípios fundamentais da regulação de comunidades naturais. Décadas de pesquisas têm, desde então, sido capazes de integrar dinâmica de populações, estabilidade de comunidades, biodiversidade e produtividade de ecossistemas em um sólido arcabouço teórico: a teoria de redes tróficas (DUNNE, 2006; SAINT-BÉAT et al., 2015).

Grande interesse nos estudos têm sido em determinar como esses sistemas complexos de interações são capazes manter-se de forma estável na natureza (JACQUET et al., 2016; MACARTHUR, 1955; MAY, 1972; MCCANN, 2000). Estabilidade refere-se à capacidade desses sistemas sustentarem perturbações externas (resistência), a quantidade de perturbações necessárias para alterá-los (robustez), o tempo necessário para essa alteração ocorrer em um sistema estável (persistência), e o tempo necessário para os sistemas retornarem a um estado inicia após perturbações externas (resiliência) (DEANGELIS, 1980; GRIMM; WISSEL, 1997; SAINT-BÉAT et al., 2015). Na década de 50, havia um consenso de que a própria complexidade, seja através da diversidade de espécies ou do número de interações entre as espécies, era capaz de promover a estabilidade (ELTON, 1958; HUTCHINSON, 1959; MACARTHUR, 1955; ODUM, 1959). Ecólogos acreditavam que as interações tróficas eram capazes de dissipar a energia do sistema, o que regularia os ciclos populacionais e impediria explosões populacionais (MACARTHUR, 1955). A diversidade, por sua vez, dificultaria espécies invasoras a ocuparem nichos não explorados e desestabilizarem a comunidade (ELTON, 1958; HUTCHINSON, 1959). Entretanto, May (1972) demonstrou através de análises matemáticas que sistemas complexos deveriam diminuir a estabilidade a medida que se tornam mais complexos. Esse aparente paradoxo levou diversos trabalhos, tanto teóricos (ALLESINA; TANG, 2015; MCCANN; HASTINGS; HUXEL, 1998), quanto empíricos (JACQUET et al., 2016; POLIS, 1991), à avaliarem as condições biológicas que promovem estabilidade nesses sistemas.

A própria complexidade da rede de interações impõe limitações aos estudos, os quais necessitam de abstrações para avaliar os padrões e mecanismos de comunidades naturais (SCHAFFER, 1981). Por exemplo, estudos de dinâmicas populacionais procuram modelar o efeito das interações ao longo do tempo, reproduzindo ciclos populacionais (GAMARRA; JAVIER; SOLÉ, 2000; TYSON; HAINES; HODGES, 2010), modelando efeitos de controle biológico (MILLS; GETZ, 1996) e espécies invasoras (LEWIS; PETROVSKII; POTTS, 2016), ou inferindo efeitos indiretos de perturbações populacionais, - *i.e.* cascatas tróficas (COURCHAMP; LANGLAIS; SUGIHARA, 1999; RIPPLE et al., 2016). Entretanto, a intratabilidade matemática impõe aos estudos compreender apenas pequenos componentes de interações dentro do emaranhado de interações possíveis na comunidade (MCCANN, 2012). Esses componentes, definidos como módulos, atuam como unidades funcionais dentro da rede e são capazes de produzir padrões reprodutíveis e persistentes (PAINE, 1980).

Por outro lado, uma visão holística de todas as interações da comunidade impõe uma perda na perspectiva dinâmica, como variações na abundância e distribuição das espécies, variações temporais, ou variações na intensidade das interações (PAINE, 1980; POISOT; STOUFFER; GRAVEL, 2015). Logo, esses estudos procuram por padrões estruturais, como padrões estatísticos na estrutura da rede (número de interações, ou proporção de espécies em diferentes níveis tróficos) (JORDÁN; SCHEURING, 2004); ou reproduzir comportamentos de forrageio de predadores durante a escolha de suas presas (ROHR et al., 2016; STOUFFER, 2010; WILLIAMS; MARTINEZ, 2000).

De forma a desenvolver inferências mais robustas, estudos vêm reconhecendo a importância de avaliar estruturas complexas em análises dinâmicas, ou, por outro lado, considerar dinâmicas populacionais em redes complexas (JACQUET et al., 2016; LAWLOR, 1978; TANG; PAWAR; ALLESINA, 2014; YODZIS, 1981). Neste trabalho, procuramos contribuir para o estudo de estabilidade de redes complexas, avaliando os padrões e mecanismos para a ocorrência de estruturas estáveis. Nossas análises baseiam-se principalmente na inferência que chamamos de abordagem de comunidades (PIMM, 1982), a qual sacrifica o formalismo matemático para avaliar estabilidade dinâmica entre diferentes estruturas.

Redes tróficas podem ser representadas por matrizes de predação, na qual cada entrada em uma matriz A_{ij} representa uma interação entre o predador *j* e a presa *i* (abordagem qualitativa), ou a intensidade da interação (abordagem quantitativa). A abordagem dinâmica considera um modelo subjacente para as interações entre as espécies, e a derivação desse modelo produz uma matriz de predação referida como Jacobiana. As entradas da matriz Jacobiana são interpretadas como o efeito do aumento da espécie *j* na taxa de crescimento da espécie *i*, assumindo que as populações estão no equilíbrio (taxa de variação igual a zero na ausência de perturbações). Os autovalores dessa matriz indicam a estabilidade do sistema: se todos os autovalores possuírem partes reais negativas, o sistema é estável, ou seja, perturbações a esse sistema retornarão ao equilíbrio. Por outro lado, se a matriz possuir algum autovalor positivo, o sistema possui um equilíbrio instável, e perturbações podem afastá-lo do ponto de equilíbrio (MCCANN, 2012). A abordagem de comunidades, por outro lado, ignora o modelo subjacente, assume determinada estrutura para matrizes de predação e realiza a parametrização da matriz Jacobiana através de amostras de distribuições de probabilidades (ALLESINA; TANG, 2015).

No Capítulo 1, utilizamos a abordagem de comunidades para avaliar a estabilidade esperada na estrutura de diferentes módulos de três e quatro espécies. Ao total, existem 13 estruturas de módulos de três espécies e 199 estruturas de módulos de quatro espécies (Apêndice A). Amostrando as entradas da matriz Jacobiana por distribuições de probabilidade, avaliamos para cada simulação um valor de estabilidade referente aos parâmetros amostrados. A média das simulações indicou o valor esperado de estabilidade considerando diferentes cenários de interação. Utilizamos um modelo barreira (*hurdle model*) para avaliar a ocorrência desses módulos em redes empíricas. Esse modelo considera que existe uma barreira para a ocorrência de módulos, e que módulos com maior estabilidade esperada, possuem maior probabilidade de ocorrência. Uma vez que ocorreram, o modelo avalia a quantidade de módulos em uma rede em função da sua estabilidade. Além disso, para cada rede, avaliamos a proporção de módulos estáveis em função das suas métricas estruturais. Escolhemos as métricas baseado na literatura, às quais acredita-se que influenciam na estabilidade das comunidades. Foram elas: conectância (MAY, 1972), modularidade (STOUFFER; BASCOMPTE, 2011) e onivoria (MCCANN; HASTINGS, 1997).

Assumimos subjetivamente que a estrutura da rede promove a ocorrência de módulos estáveis. Entretanto, ainda não é claro na literatura se a estrutura da comunidade promove a estabilidade, ou se a estabilidade permite a ocorrência de determinadas estruturas. Dessa forma, no Capítulo 2, utilizamos três modelos teóricos, cada um com diferentes pressupostos biológicos para a seleção de presas por predadores, para amostrar redes tróficas. O uso de modelos teóricos nos permitiu amostrar, de forma consistente, milhares de redes; o que não seria possível com dados empíricos, uma vez que a coleta dos dados sofre inconsistências nos métodos e tempo de coleta, desenho experimental, nível de identificação das espécies e critérios para a inferência de interações (MORALES-CASTILLA et al., 2015). Para cada modelo, avaliamos, entre as simulações, como se correlacionavam a proporção de módulos de três e quatro espécies, a proporção de redes estáveis, considerando a abordagem de comunidades na estrutura da rede completa (*i.e.* métricas de estabilidade); e a modularidade e onívora (*i.e.* métricas de estrutura). Para todos os modelos, a conectância foi um parâmetro fixo, e portanto não foi avaliada. Determinamos, então, diagramas de causalidades, assumindo duas hipóteses: (i) as métricas de estrutura causaram os padrões de estabilidade, ou (ii) as métricas de estabilidade causaram a estrutura observada. Utilizamos a análise de trilha para avaliar qual hipótese possui maior probabilidade de ocorrência, dada as observações, e se essa probabilidade é significativamente diferente do acaso.

Entretanto, precisamos avaliar até que ponto inferências sobre modelos teóricos reproduzem dados empíricos. De fato, a literatura tem proposto diversos modelos para o comportamento de forrageio de predadores que sejam capazes de reproduzir a estrutura de redes empíricas (STOUFFER, 2010). Esses modelos consideram, por exemplo, a ocorrência da presa em uma dimensão do nicho do predador (WILLIAMS; MARTINEZ, 2000), ou sobre a interseção de múltiplos nichos (ALLESINA; ALONSO; PASCUAL, 2008), filogenia (CATTIN et al., 2004; ROHR et al., 2010), formação de grupos (ALLESINA; PASCUAL, 2009), ou relações alométricas (COHEN et al., 1990; WILLIAMS; ANANDANADESAN; PURVES, 2010). Resultados indicam que considerar apenas uma dimensão do nicho do predador possa ser suficiente para reproduzir estruturas de redes empíricas (STOUFFER et al., 2005). Entretanto, o uso de apenas uma dimensão de nicho pode gerar modelos incapazes de reproduzir dados empíricos, uma vez que as interações podem ocorrer fora do intervalo estimado pelos parâmetros (ALLESINA; ALONSO; PASCUAL, 2008). Estudos mais recentes, portanto, sugerem utilizar mais de uma dimensão, além de considerar, não apenas o comportamento do predador, mas também os atributos das presas (EKLÖF et al., 2013; WARTON et al., 2015). No Capítulo 3, utilizamos análises multivariadas para avaliar o quão complexa é a estrutura de associação entre predadores e presas. Utilizamos dois atributos dos predadores e três atributos das presas em uma base de dados de mais de 16 mil interações para comparar diferentes hipóteses para a associação entre as variáveis. Uma vez encontrada a melhor hipótese, reduzimos essa estrutura complexa para algumas variáveis latentes, as quais podem ser interpretadas como diferentes dimensões do nicho das espécies. Avaliamos, assim, o quanto essas variáveis latentes eram capazes de reproduzir a estrutura de associação entre predadores e presas, e reproduzir os complexos padrões de comunidades naturais.

Como resultados, foi observado que poucos módulos são estáveis, ou sejam são resilientes a pequenas perturbações. Houve estabilidade em apenas 27% dos 13 tipos de módulos de três espécies, e em 7% dos 199 tipos de módulos de quatro espécies. Apesar disso, esses módulos estáveis foram os que mais ocorreram nos dados empíricos utilizados. Esse padrão foi independente do tipo de hábitat reproduzido pela rede trófica. Infere-se, portanto, que a estabilidade atua na ocorrência dos módulos através de um processo barreira, em que módulos possuem baixa probabilidade, mas maior chance de ocorrência quando apresentam maior estabilidade esperada. Uma vez que ocorreu, a frequência de ocorrência também relacionou à estabilidade esperada, sendo aqueles mais estáveis com maior ocorrência. Além disso, a presença de módulos estáveis configura a comunidade, permitindo a ocorrência de padrões topológicos como por exemplo a modularidade (grupo de espécies que interagem mais entre si, do que com o resto da rede) e frequência de onivoria (proporção de espécies que se alimentam em mais de um nível trófico). Esses resultados refletem um processo de seleção não adaptativo para sistemas complexos, no qual a seleção de um determinado atributo (no caso, estabilidade), converge diferentes comunidades para um mesmo padrão topológico (BORRELLI et al., 2015). Por fim, foi observado uma complexa relação entre o hábito de forrageamento do predador e os atributos da presa. Entretanto, essa complexidade pode ser reduzida quando utilizadas variáveis latentes que resumem a informação de vários atributos em uma dimensão de nicho. Quando consideradas cinco dimensões de nicho, os resultados sugerem que cerca de 90% da informação de associação entre predadores e presas pode ser reproduzida. Isso sugere que modelos teóricos podem, de fato, reproduzir os padrões de interações tróficas e inferir sobre padrões ecológicos com poucos pressupostos.

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ARTIGO 1 - The interplay between population stability and food-web topology predicts the occurrence of motifs in complex food-webs

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ABSTRACT:

In this paper, we analyzed the occurrence of motifs (modules) in empirical food-webs from different ecosystem types. Differently from previous studies, our analysis did not relied on randomized networks with specific a priori assumptions, which has been demonstrated to produce inconsistent patterns. We aimed to evaluate the interplay between population dynamics and food-web topology, and its consequences to module occurrences in complex food-webs. We evaluated 13 arrangements of three-species modules and 199 arrangements of four-species modules. For each module, we assembled, a corresponding Jacobian predation matrix, and evaluated the arrangements expected to persist after a disturbance in the equilibrium of the populations dynamics (local stability). Our general results were that (1) a limited set of stable arrangements occurs most frequently; (2) the omnivory module is the only three-species module expected to occur both in the stable and unstable regions; (3) connectance and omnivory affects the proportion of stable modules; and (4) the type of ecosystem influences the proportion of stable modules. Further, we demonstrated that food-web topology and population dynamics influenced module occurrences in natural communities; presented a function for the ways that local stability increases the probability of module occurrence; and highlighted the use of omnivory degree to access the effect of feeding at more than one trophic level on food-web stability.

INTRODUCTION

Food-web theory approaches natural communities through species trophic interactions, and has been fundamental to describe energy fluxes between species, evaluate mechanisms that maintain stability in population dynamics, and predict population persistence after species loss (Rooney and McCann, 2012). Given the complexity of species interactions within a community, studies generally abstract biological details to assess major processes (Schaffer, 1981).

Earlier concepts in population dynamics studies (henceforth termed the Community Approach), for example, abstracted complex topologies to assume population modules - functional units producing predictable and persistent patterns (sensu Paine, 1980). In this concept, interaction strengths between species were evaluated as samples from probabilistic distributions. They aimed to depict arrangements capable of persisting after a disturbance on the equilibrium of its population's dynamics – i.e local stability (Dunne et al., 2005). General results suggested that modules tended toward stability in topologies with fewer interactions, small variance of interaction strengths, and self-damping processes (Haydon, 1994; May, 1972; Sterner et al., 1997).

Conversely, network studies usually abstract temporal variation in interaction strengths to evaluate systemic topological patterns emerging from the complexity of interactions within a community (Schoener, 1989). In this perspective, population modules are termed *motifs*; and to "uncover the structural design principles" behind food web topology, studies search for arrangements appearing significantly more in complex communities than in null models (Milo et al., 2002). However, the underlying assumptions adopted in the null models have been shown to influence the patterns of module occurrences and to promote inconsistency in the results (Bascompte and Melian, 2005).

Recent studies, however, found that the most occurring modules are those with higher expected stability (Borrelli, 2015; Prill et al., 2005). This suggests that population dynamics and food-web topology interplay to produce a consistent pattern. While biological constraints during prey selection produce over- and under-represented modules, population dynamics select unstable modules, and increase the relative abundance of stable ones (Borrelli, 2015;

Camacho et al., 2007).

In this paper, we stress the interplay among population stability and food-web topology and the consequences to motif occurrences. We aim to elucidate the mechanisms that regulate both the community approach and network analyses. We counted the occurrence of motifs (henceforth modules) in complex food-webs from different environments. We extended the usual 13 three-species-module of previous studies (Bascompte and Melian, 2005; Borrelli, 2015; Dunne et al., 2013; Stouffer et al., 2007) to additionally 199 four-species-module (Prill et al., 2005). We used Jacobian analysis to evaluate the expected stability of each arrangement and we tested the probability of occurrence of a module and its frequency in relation to its expected stability using a Hurdle Model. We also used multivariate regressions to depict the effects of food-web topology and its constraint on the expected module stability. Our results address few inconsistent patterns in food-web literature and advocate the use of this combined approach between population stability and food-web topology in future studies.

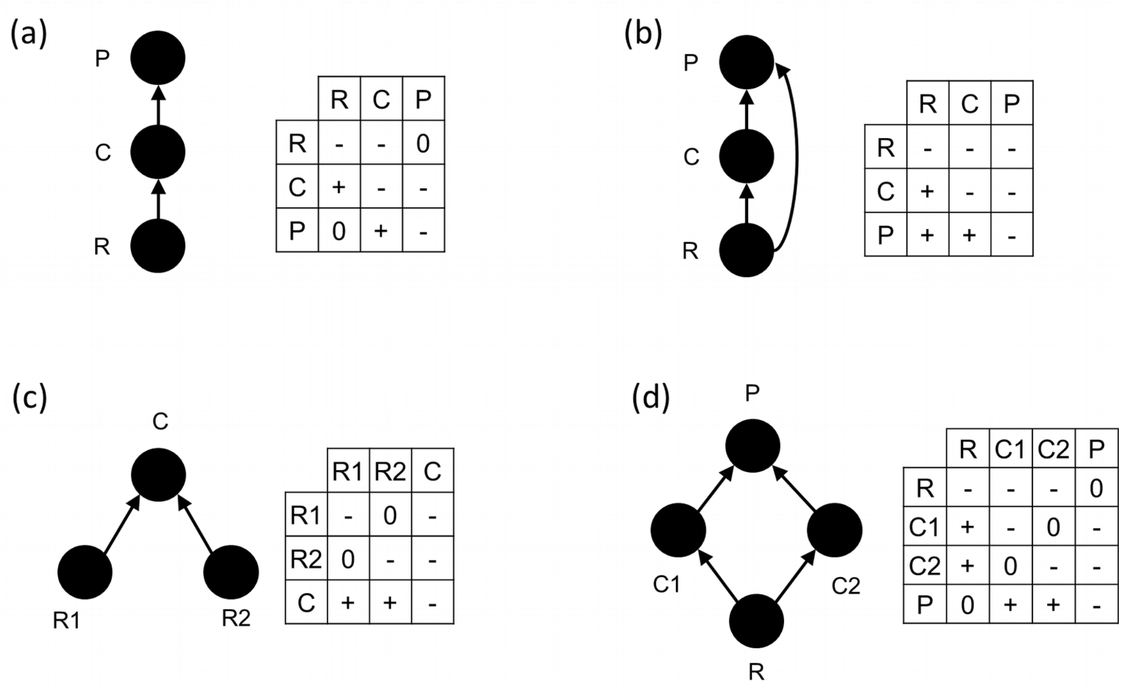
METHODS

Module occurrence and expected population stability

We analyzed the occurrence of 13 types of three-species modules and 199 types of four-species modules (see Appendix for module configurations) in 34 empirical food-webs from different ecosystem types: five terrestrial ecosystems, twelve estuarine ecosystems, seven freshwater systems, and ten closed habitats associated with phytotelmata (Table S1 in Supplementary Material). For each module, we assembled a corresponding Jacobian predation matrix S x S, where S is the number of species (3 or 4) and each entry is the effect of the species in the column on the species in the row. Jacobian matrices assume interaction strength as partial differential equations that describe the population’s growth of a given species with respect to another species' abundance, and each entry as the linearized value of interactions at equilibrium for the two populations:

$$\frac{dX_i}{dt} = X_i \left(b_i + \sum_{j=1}^{n} a_{ij} X_j \right) \tag{I}$$

where X_i is the population density of species *i*, *b* is the instantaneous growth rate of species *i*, *a* is the per-capita effect of species *j* on species *i*, and *n* is the number of species interacting with species *i* (Figure 1).



(a)

	R	C	P
R	-	-	0
C	+	-	-
P	0	+	-

(b)

	R	C	P
R	-	-	-
C	+	-	-
P	+	+	-

(c)

	R1	R2	C
R1	-	0	-
R2	0	-	-
C	+	+	-

(d)

	R	C1	C2	P
R	-	-	-	0
C1	+	-	0	-
C2	+	0	-	-
P	0	+	+	-

Figure 1: Food-web diagram showing how Jacobian predation matrices were assembled from a module arrangement using a classical resource-consumer example. (a) Food chain, (b) Omnivory, (c) Apparent competition, and (d) Bi-parallel.

We assumed that predators exert a negative effect on prey, prey exert a positive effect on predators, and each species may possess a self-damping effect (matrix diagonal), such as limitations on food availability, nesting sites, and intraspecific behavioral responses (Sterner et al., 1997). We followed previous analyses and sampled matrix entries using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 0.1 for the prey-predator interaction, and from 0 to -1 for the self-damping effect. This parameterization implies that the predator affects the prey with a greater magnitude than the prey affects the predator; and that the self-damping effect scales the dynamic's return time (Pimm, 1979; Pimm and Lawton, 1977).

We simulated 10^3 Jacobian matrices for each three- and four-species module, and calculated the mean value of eigenvalues with the most positive real part, Re(λ), which represents the growth rate of a perturbation in the population dynamics close to equilibrium (i.e., local stability). If lower than zero, the perturbation extinguishes and the population dynamics are expect to be stable; otherwise, it leads to an unstable state (Haydon, 1994). Therefore, we interpreted each module as its expected stability, Re(λ), to evaluate the occurrence of stable and unstable modules in food-web data. We estimated 95% confidence intervals to confirm the estimation reliability of Re(λ).

We modeled the occurrence of each module arrangement as a function of Re(λ) with a Hurdle model. The Hurdle model is a two-component model formulation that first applies a binomial probability to predict the binary outcome of a module (since we expect many modules not to occur); and then models the non-zero counts with a truncated negative binomial model, with the modules' expected stability as predictor (Mullahy, 1986; Zuur et al., 2009). However, larger food-webs produce a higher number of modules, and modules' count between food-webs of different size are not comparable. To attend this, we inserted an offset term using the total number of modules of three or four species separately. This offset term in a Hurdle Model formulation permits the count of module occurrence to be interpreted as relative frequency of occurrence, while still using a formulation for count data (Supplementary Material).

Food web topology and ecosystem constraint

We modeled the proportion of stable three- and four-species modules for the whole food-web as a function of food-web topology constraint and ecosystem type. We used a multivariate regression with arcsine transformation to correct for overdispersion, which is preferable to the standard logit transformation in multivariate studies with proportion data (Zuur et al., 2007). We computed three food-web topological properties that have been suggested to influence food-web stability: connectance, modularity, and omnivory degree (May, 1972; McCann and Hastings, 1997; Stouffer and Bascompte, 2011). Connectance counts the realized proportion of possible links. Modularity computes the compartmentalization, and measures the fraction of interactions within compartments minus the expected fraction if interactions were randomly distributed:

$$Q=\frac{1}{2m}\sum_{ij} A_{ij}-\frac{k_i k_j}{2m}\delta\left(c_i c_j\right) \tag{II}$$

where m is the number of edges, A_{ij} is the element of the adjacency matrix A in row i, and the column j ($A_{ij}=1$ if there is an interaction between species i and j, $A_{ij}=0$ otherwise), k_i is the number of interactions of species i, k_j is the number of interactions of species j, c_i and c_j are the compartments of species i and j respectively, and $\delta(c_i c_j) = 1$ if $c_i = c_j$ and 0 otherwise (Newman and Girvan, 2004; Pons and Latapy, 2005). We used the Walktrap Community Finding Algorithm to assign the compartments (Pons and Latapy, 2005). Omnivory degree evaluates the fraction of species that consume two or more species and have a nonadjacent trophic level, considering the mean trophic level of the prey as a measure of trophic position (Levine, 1980; Williams and Martinez, 2004).

RESULTS

Module occurrence and expected population stability

Only 27% of the three-species modules depicted population dynamics capable of returning to a stable state after a perturbation, i.e., had a negative Re(λ) (Figure 2). The stable three-species modules were: apparent competition (M3.1), tri-trophic chain (M3.2), shared prey (M3.4), and omnivory (M3.7, the only module that ranged from both stable to unstable regions) (Figure 2a). The baseline odds of occurrence of three-species modules were 0.05, with a significant increase of 0.27 for stable modules (Z= -16.84, p<0.001). Given that a module occurred, the expected stability affected positively its frequency (Slope= 0.45, Z= -

24.68, p<0.001). Therefore, although only a small proportion of three-species modules are expected to be stable, we found that these modules occurred more frequently than unstable modules in all empirical food-webs (Figure 3).

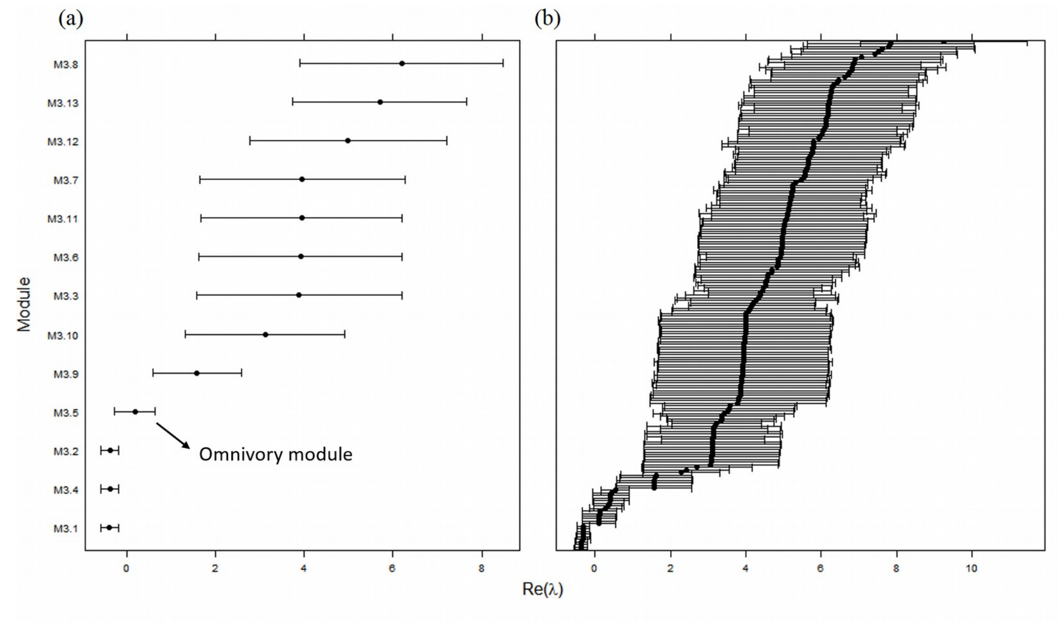


Figure 2: Mean and standard deviation of eigenvalues with the most positive real part – Re(λ) for (a) three-species modules and (b) four-species modules (For module configuration see Supplementary Material).

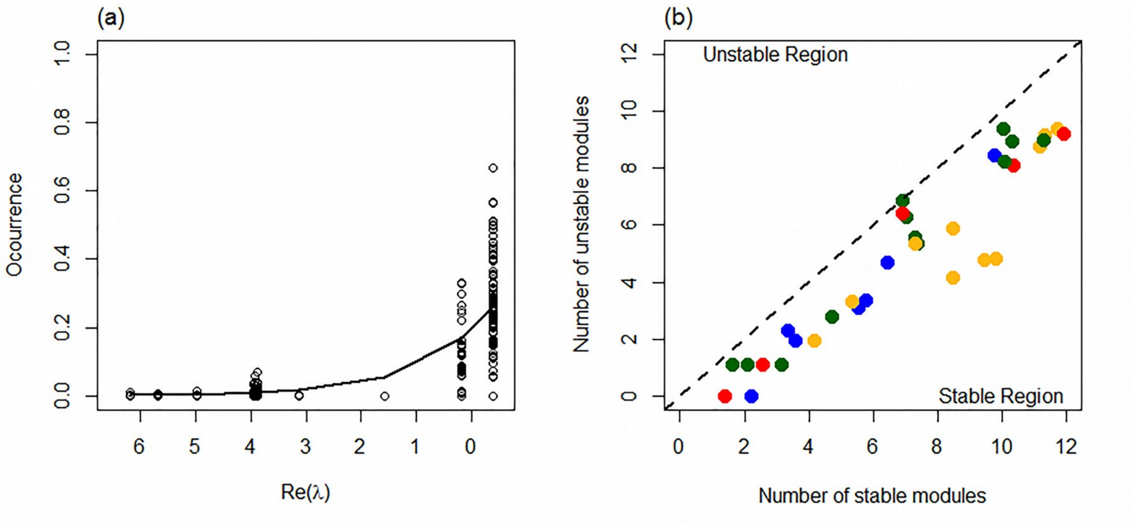


Figure 3: (a) Hurdle model of the relative three-species module occurrence in 34 empirical food-webs as a function of expected stability - Re(λ). (b) Number of stable and unstable three-species modules in empirical food-webs The line indicates the equal proportion and separates the stable and unstable regions in the graph. Axis as *log(n+1)*. Stability is measured as the mean of eigenvalues with the most positive real part in a large number of simulations; and represents the response of population dynamics to small perturbations. Green are estuarine food-webs, blue are freshwater food-webs, yellow are mesocosms food-webs and red are terrestrial food-webs.

Likewise, only 7% of the four-species modules had a negative Re(λ). We found that, four-species modules also related to expected stability, although weakly compared to three-species modules. Stable four-species module were M4.1, M4.2, M4.4, M4.5, M4.10, M4.13, M4.16, M4.25, M4.49 and M4.59 (Supplementary Material). The base-line odds of occurrence of four-species modules were 0.0004, with an increase of 0.31 for stable modules (Z= -45.95, p<0.001). Given that a four-species module occurred, its frequency related positively with its expected stability (Slope= 0.42, Z= -48.21, p<0.001). As a result, six food-webs (17%) occurred in the four-species modules unstable region, encompassing all ecosystems types: one from Freshwater (Skipwith Pond), two from Estuarine (Benguela and NE USA Continental Shelf), one from Terrestrial (Coachella Valley), and two from Phytotelmata (pitcher plants *Nepenthes distillatoria* and *Sarracenia purpurea*) (Figure 4).

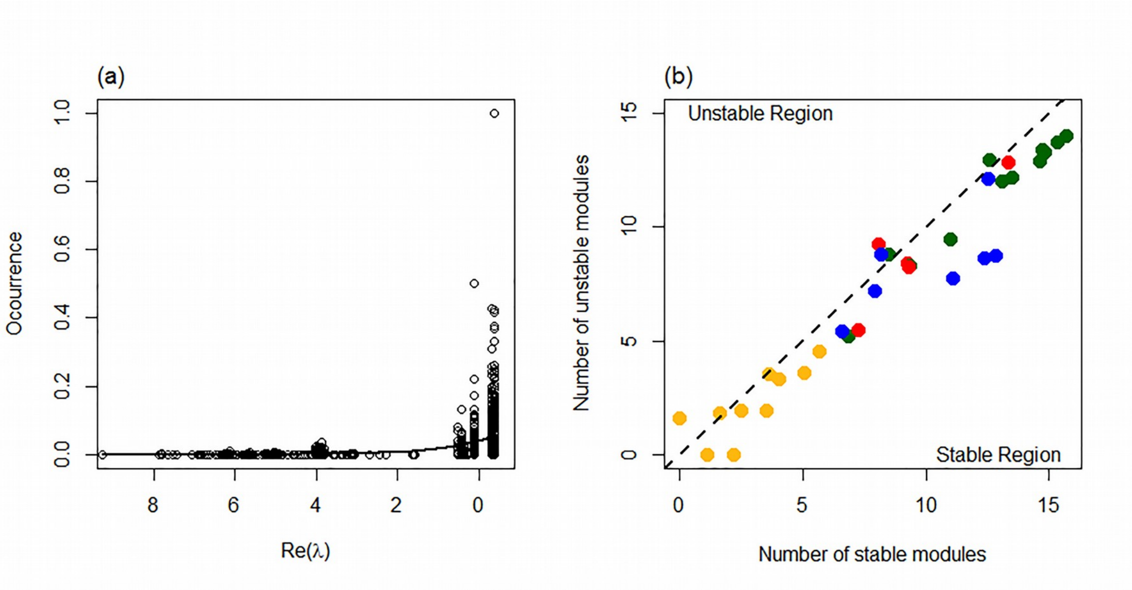


Figure 4: (a) Hurdle model of the relative four-species module occurrence in 34 empirical food-webs as a function of expected stability - Re(λ). (b) Number of stable and unstable four-species modules in empirical food-webs The line indicates the equal proportion and separates the stable and unstable regions in the graph. Axis as *log(n+1)*. Stability is measured as the mean of eigenvalues with the most positive real part in a large number of simulations; and represents the response of population dynamics to small perturbations. Green are estuarine food-webs, blue are freshwater food-webs, yellow are mesocosms food-webs and red are terrestrial food-webs.

Food web topology and ecosystem constraint

In a global model, considering all the variables, we found that connectance and omnivory negatively affected both the occurrence of stable three-species modules and four-species modules. We also observed a significant difference between terrestrial and estuarine ecosystems in three-species modules. Modularity did not significantly affect module occurrence (Table 1). Thus, we found that a model containing connectance, omnivory and ecosystem type significantly predicts the proportion of stable three-species modules: F=17.28, DF=28, R^2=0.71, p-value <0.01; while a model containing connectance and omnivory significantly predicts the proportion of stable four-species module: F=19.8 DF=31, R^2=0.52, p-value <0.01.

Table 1: Food-web expected occurrences of stable modules as a function of food-web topology. Values are with arcsine transformation to correct for overdispersion. Only significant results are showed for the ecosystem categorical variable.

Three-species module				
	Estimate	Std. Error	t value	p value
Intercept	101.51	5.78	17.57	<0.001
Connectance	-72.57	17.76	-4.09	<0.001
Omnivory	-33.26	8.14	-4.09	<0.001
Modularity	-16.21	9.52	-1.70	0.10
Terrestrial*Estuarine	-9.89	3.30	-3.00	0.01
Four-species module				
Intercept	105.97	12.81	8.27	<0.001
Connectance	-109.75	39.36	-2.79	<0.001
Omnivory	-49.49	18.04	-2.74	0.01
Modularity	-12.63	21.10	-0.60	0.55

DISCUSSION

We found that population dynamics and food-web topology influence module occurrences in natural communities. The energy flux in consumer-resource interactions governs species-specific mechanisms of growth rate, resource allocation, prey defense, behavioral responses and chemical composition (Chase, 2000; Rip and McCann, 2011; Shurin et al., 2006). Therefore, studies suggest that estimating interaction strengths are essential to depict stability patterns in modules of interacting species (Aufderheide et al., 2013; McCann et al., 1998; Yodzis, 1988). Others, in contrast, argue that the interplay between weak and strong interaction strengths is secondary when analyzing community stability (Allesina and Pascual, 2008; Allesina and Tang, 2015; Barabas and Allesina, 2015). In this study, we demonstrated a defined function for the ways that local stability increases the probability of a module occurrence; and the ways food-web topology and ecosystem type constrain the occurrence of stable modules. Our results depict new mechanisms to count module occurrences, and extends previous findings using randomized networks with specific a priori assumptions - which have been demonstrated to produce variable patterns (Bascompte and Melian, 2005). Further, our results are robust to increasing interaction strengths variation, predator-prey interaction asymmetry and absence of self-damping processes (for more information, please see the Supplementary Material).

Regarding food-web topological constraints, we found that connectance and omnivory degree affects the occurrence of stable modules in food-webs. The negative relationship between connectance (a straightforward measure of food-web complexity) and stability is one of the classical debates in food-web theory (McCann, 2000). The seminal results of May (1972) argues that a module's expected stability decays with increasing connectance. Further studies have demonstrated that topologies with biologically feasible interactions of consumer-resource interactions and self-damping processes - rather than the number of random interactions used originally by May, enhance the biological robustness and promotes stabilization (Allesina and Pascual, 2008; Yodzis, 1981). Still, our results demonstrated that connectance reduces the probability of occurrences of stable modules, although we also used topologies with biologically feasible interactions (for more information please see Figure S1 on the supplementary material).

The effects of omnivory on food-web stability have been unclear for a long time mainly due to inconsistencies between food-web dynamics and structural approaches (Gellner and McCann, 2012). Pimm and Lawton (1978) observed the lack of omnivory modules in empirical data, and argued for their destabilizing role in the structural context. This pattern agrees with the recent results of Milo et al. (2002), which suggested that omnivory modules are selected against. In contrast, studies have found highly variable occurrences of omnivory modules due to different search algorithms, null models adopted, and methodologies used to set up empirical food-webs (i.e. using consistent methods at a single spatial and temporal time, or using cumulative information on species diet) (Bascompte and Melian, 2005; Stouffer et al., 2007). Given the link between module occurrences that we have demonstrated, these contradictory results – apart from the use of null models in previous analysis – could be explained by the fact that the three-species module for omnivory was the only module that ranged from both stable to unstable regions.

McCann and Hastings (1997) long argued that it is important to evaluate the effect of interaction strengths on the stabilizing processes of the omnivory module. Only recently, however, Gellner and McCann (2012) linked population stability and topological aspects to propose the specific conditions for stability. We, on the other hand, found that the degree of omnivory negatively relates to stability. This result agrees with the findings of Johnson et al. (2014) that evaluated food-webs' "trophic coherence". Trophic coherence measures the degree of homogeneity between the difference of prey and predators trophic positions. Johnson et al. (2014), also using local stability, found that a perfect coherent food-web (i.e a food-web with zero omnivory degree) are more easily stabilized by self-damping effects (Sterner et al., 1997). Therefore, we highlight the use of omnivory degree as an alternative tool to the use of omnivory module, in order to predict local stability patterns. Using degree of omnivory does not presume estimation of interaction strengths, and prevents motif search algorithms from confounding omnivory module with intraguild predation module (a widespread interaction that may misinterpret the actual role of omnivory) (Arim and Marquet, 2004; Stouffer et al., 2007).

We found that compartmentalization does not relate to the occurrence of stable modules in food-webs. Early studies by Pimm (1979), also using the Community Approach, suggested that compartments would lead to food-web instability. However, population dynamics shown that dynamic asynchrony within different compartments is a key factor for stabilization (Teng and McCann, 2004); while structural analysis suggested that compartmentalization affects species-deletion stability, damping the propagation of extinctions throughout the community after species loss (Stouffer and Bascompte, 2011). Our results, however, contradicts this pattern. This may be a consequence of our use of local stability, that neither account for dynamic asynchrony nor global stability (stability after species loss). It remains for future studies, however, to attend the differences in local stability, global stability and temporal variation of interaction strengths.

Finally, we found that stable three-species module occurrences on estuarine habitats were significantly lower than on terrestrial ecosystems. This result may indicate different stabilization mechanisms between ecosystems. Generally, aquatic ecosystems present stronger impacts of consumers on primary producers, with larger indirect effects of predators; while, terrestrial ecosystems present weaker consumer-resource interactions and lesser top-down control (Cebrian and Lartigue, 2004). For example, studies have found that the loss of primary predators produce more pronounced impacts on aquatic ecosystems than terrestrial ecosystems (Shurin et al., 2006). However, it should be emphasized that terrestrial and marine environments have traditionally been investigated separately, which have created barriers to infer about more general ecological patterns (Webb, 2012).

In conclusion, we found four general results: 1) Although only a limited set of arrangements have an expected stable state, they occurred most frequently in the empirical food-web; 2) the omnivory module is the only three-species module expected to occur both in the stable and unstable region; 3) topological constraints of connectance and omnivory relates to the proportion of stable modules; and 4) the type of ecosystem influence the proportion of stable three-species modules. However, it is still unclear the causality between population dynamics and food-web topology. Borrelli et al. (2015) suggest that a non-adaptive selection process rules motif occurrences, based on intrinsic system properties that do not act to adapt species, but rather, to produce a similar topological pattern among systems. Therefore, population stability would drive food web topology. Cohen et al. (2009), on the contrary, argued that a food-web topology is more than its constituent modules and properties emerge at progressively higher levels of structure. In order to attend these divergences and depict the causal relation between population stability and food-web topology, future studies should consider new ways to integrate complex dynamic responses, and evaluate the extent to which local stability relates to food-web topology.

SUPLEMENTARY MATERIAL

Food-web database

Table S1: Food-web database.

Dataset name	Ecosystem type	Number of species	Reference
Chesapeake Bay	Estuarine	29	Baird and Ulanowicz (1989)
St. Marks	Estuarine	48	Christian and Luczkovich (1999)
Ythan Estuary	Estuarine	79	Hall and Raffaelli (1991)
Bahía San Quintín	Estuarine	180	Hechinger et al. (2011)
Carpinteria Salt Marsh	Estuarine	198	Hechinger et al. (2011)
Estero de Punta Banda	Estuarine	226	Hechinger et al. (2011)
NE USA Continental Shelf	Estuarine	79	Link (2002)
Otago Harbour	Estuarine	136	Mouritsen et al. (2011)
Caribbean reef	Estuarine	245	Opitz (1996)
Sylt tidal basin	Estuarine	189	Thieltges et al. (2011)
Benguela	Estuarine	29	Yodzis (1998)
Flensburg Fjord	Estuarine	143	Zander et al. (2011)
Tuesday Lake	Freshwater	21	Carpenter and Kitchell (1996)
Bridge Brook Lake	Freshwater	25	Havens (1992)
Little Rock Lake	Freshwater	93	Martinez (1991)
Blackrock stream	Freshwater	85	Townsend et al. (1998)
Canton stream	Freshwater	103	Townsend et al. (1998)
Stony stream	Freshwater	110	Townsend et al. (1998)
Skipwith Pond	Freshwater	27	Warren (1989)
Pitcher plant (*Nepenthes albomarginata*)	Phytotelmata	15	Beaver (1985)
Pitcher plant (*N. ampullaria*)	Phytotelmata	11	Beaver (1985)
Pitcher plant (*N. distillatoria*)	Phytotelmata	7	Beaver (1985)
Pitcher plant (*N. madagascarensis*)	Phytotelmata	8	Beaver (1985)
Pitcher plant (*N. pervillei*)	Phytotelmata	5	Beaver (1985)
Pitcher plant (*Sarracenia purpurea*)	Phytotelmata	6	Bradshaw (1983)
Pitcher plant (*N. mirabilis*)	Phytotelmata	11	Corker (1984)
Treeholes Australia	Phytotelmata	11	Kitching (1983)
Treeholes England	Phytotelmata	7	Kitching (1983)
Treeholes Papua	Phytotelmata	18	Kitching (1990)
St. Martin	Terrestrial	42	Goldwasser and Roughgarden (1993)
UK Grassland	Terrestrial	62	Martinez et al. (1999)
Scotch Broom	Terrestrial	83	Memmott et al. (2000)
Coachella Valley	Terrestrial	58	Polis (1991)
El Verde	Terrestrial	155	Reagan and Waide (1996)

Offset term in the Hurdle Model formulation

During a modelling procedure, the offset term does not consider an estimated parameter to the selected variable. Suppose we have the following model in the non-zero counts formulation of the Hurdle Model:

$$y = a + b * x_1 + offset(x_2)$$

where *y* in the number of occurrence of each module arrangement, *a* and *b* are the parameters to be estimated, x_1 is the predictor variable - Re(λ) - and x_2 is the reference with an offset term. With a truncated negative binomial family distribution, the model becomes:

$$\log(y) = a + b * \log(x_1) + \log(x_2)$$

Since, $log(x_2)$ does not have a parameter, we can pass it to the left side, and the model becomes:

$$\log(y) - \log(x_2) = a + b * \log(x_1)$$

which is the same as:

$$\log\left(\frac{y}{x_2}\right) = a + b * \log(x_1)$$

Therefore, when we introduce the offset term in the non-zero count formulation of the Hurdle Model, we are modelling the number of occurrences of stable modules balanced by the total number of modules in the food web – of three or four species separately –, using a modelling procedure for truncated count data.

Confidence intervals of modules expected stability

The 95% confidence intervals demonstrated a robust estimation of the expected stability of three- and four-species modules (Figure S1). We observed small intervals, and we did not observed intervals varying between stable and unstable regions. Thus, the 95% confidence intervals confirmed that only a small subset of modules are expected to be stable - 27% of the three-species modules and 7% of four-species modules.

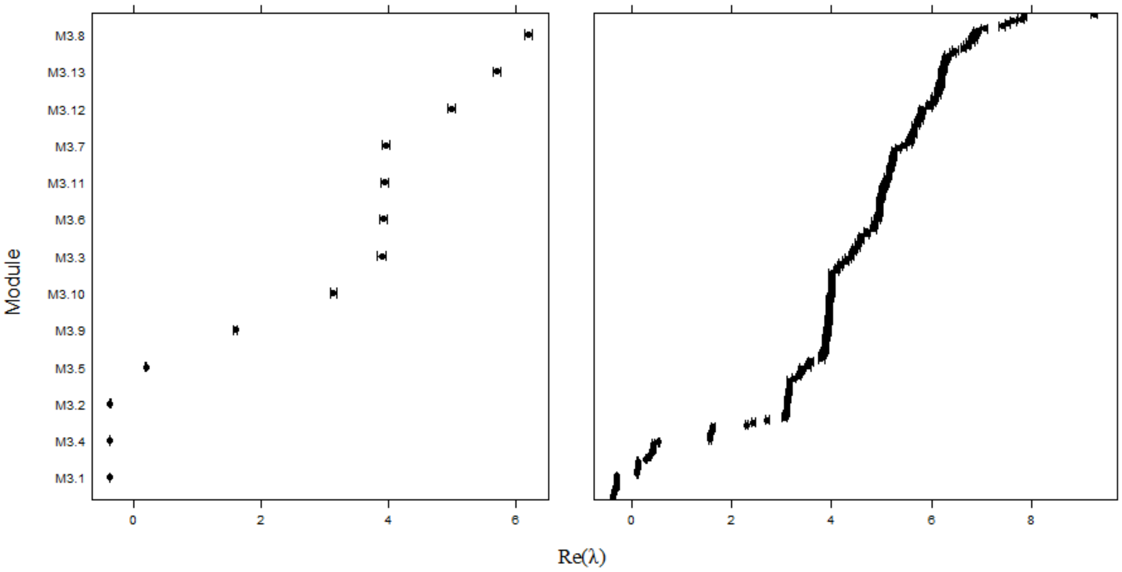


Figure S1: Mean and 95% confidence intervals of eigenvalues with the most positive real part – Re(λ) for (a) three-species modules and (b) four-species modules.

Sensitivity analysis

For every predation matrix, there are as many eigenvalues as the number of species. For random predation matrices, these eigenvalues spread uniformly on circles in a complex plane (i.e. with real values on the x-axis and imaginary values on the y-axis). Each circle has its center at one diagonal coefficient (self-damping processes) and radii ruled by the number of species, connectance and variance of interactions strengths. The eigenvalue with the most positive real part - Re(λ) - represent the underlying equilibrium and estimate the return time to an initial condition after a perturbation. Negative Re(λ) depict an stable equilibrium, while positive Re(λ) depict instability. In cases where all species have the same self-damping processes coefficient, all the circles superimpose, and Re(λ) will have higher probability of being negative if (May 1972):

$$\sigma \sqrt{SC} < d \tag{SI}$$

where, σ is the standard deviation of interaction strengths, S is the number of species, C is the connectance and d is self-damping processes. This is called the circular law (Figure S2a).

Conversely, in a predator-prey structure where a negative predator-prey interaction correlates with a positive prey-predator interaction, coefficients are sampled from a bivariate distribution. In this scenario, and when species have the same self-damping processes coefficient, stability is achieved by:

$$max\left\{\sqrt{SV}\left(1+\rho\right)-E,\left(S-1\right)E\right\}<d \tag{SII}$$

where, ρ is the correlation between pairs of coefficients, *S* is the number of species, *d* is self-damping processes and $V=C(\sigma^2+(1-C)\mu^2)$, in which *C* is the connectance, σ is the variance of interaction strengths and μ is the mean of the bivariate distribution (Tang *et al* 2014, Allesina & Tang 2015). This criterion of stability is called the elliptical law, for it produces eigenvalue distributions with smaller variations of real part values than its random counterpart (Allesina & Tang 2015) (Figure S2b). These generalizations occur on predation matrices with $S\rightarrow\infty$, but holds for finite S in conditions of small variance in self-damping processes (see results from Haydon 1994 with 6x6 matrices; Allesina et al 2015).

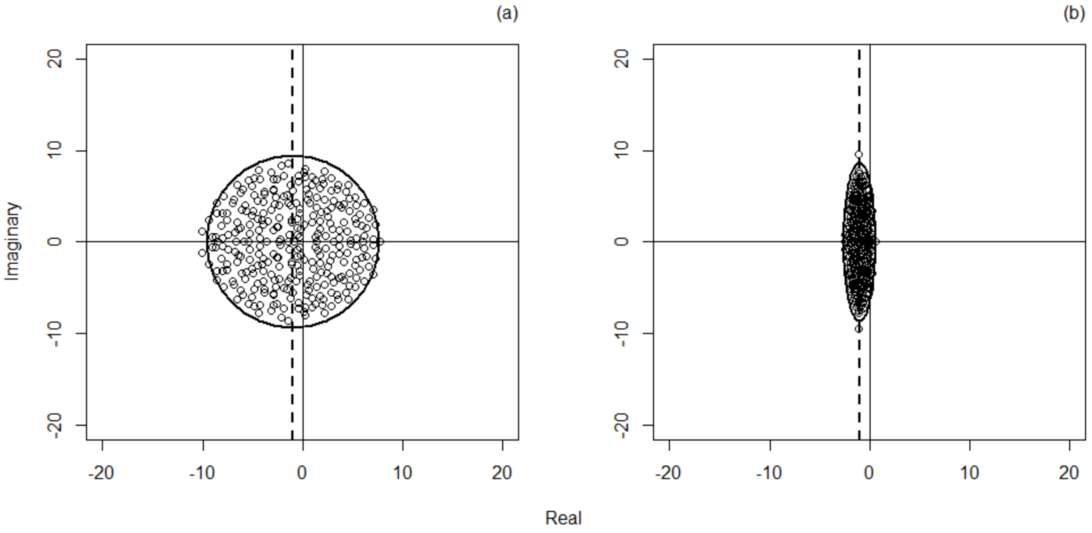


Figure S2: Eigenvalues distribution in a complex plane for matrices with (a) random interactions: circular law; and (b) with predator-prey interactions: elliptical law. Values from a matrix with *S*=500, *C*=0.25 and interaction strengths sampled from a uniform distribution ranging from -1 to 1. All self-damping processes were set to -1, thus, eigenvalues distributions superimpose within the same circle/ellipse. There are as many eigenvalues as species, and the eigenvalue with the most positive real part represent the growth rate of a perturbation in the population dynamics close to the equilibrium.

In our analysis, the modules produced matrices with predator-prey structure and with small variation of self-damping processes. Thus, we expect eigenvalue distribution with small variation of real values. We sampled the entries using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 0.1 for the prey-predator interaction, and from 0 to -1 for self-damping processes. This parameterization has been used in several other studies (Pimm & Lawton 1977; Gellener & McCann 2012; Borrelli 2015) and biologically implies that predators populations affects prey populations with a greater magnitude than prey populations affects predators populations; and that a perturbation's return time to equilibrium scales by the time it takes to species produce one new individual (self-damping processes) (Pimm 1979). Thus, the eigenvalues depend only on interaction strengths coefficients (since the number of species and connectance are constant within the modules). In this section, we discuss the implications of alternative parameterizations to our results.

Essentially, our results rely on distributions of Re(λ) for each module (Figure 2 of main document). These distributions depict the expected stability value of a give module, but also provide the stability variations. To perform the parameter sensitivity analysis, we increased interaction strengths variations by a factor of 10: ranging predator-prey interactions from -100 to 0 and prey-predator interactions from to 0 to 1. We also altered predator-prey and prey-predator asymmetry, setting ranging them from -10 to 0 and from 0 to 10, respectively. We simulated 5000 matrices for each module and evaluated the distributions of Re(λ). As discussed above, interactions strengths relates to the radii of the circle/ellipse. Thus, we expect that, with increasing interaction strength variations, we would achieve an unstable condition.

In Figure S3 we demonstrate the effect of variations on interaction strengths coefficients to the Re(λ) distribution for the trophic chain module (M3.1), the omnivory module (M3.5) and for an unstable module (M3.9). We discuss only the results for these three-species modules, but the results for the trophic chain module holds for every other stable module; and the results from M3.9 holds for every other unstable module.

We found that increased interaction strengths produced unstable conditions for the omnivory module (Figure S3b mid) and for the unstable module (Figure S3c middle). However, for a stable module we did not observed occurrences of positive Re(λ) (Figure S3a middle). This consistency maintained for stable four-species modules and even for increased interaction strengths variations with a factor of 100 (results not shown).

Conversely, decreased interaction asymmetry produced a stable condition for the omnivory module and the unstable module, but, again, did not produced positive Re(λ) on stable modules (Figure S3 right). Prill et al. (2005) used random predation matrices with lower interaction asymmetry and found stability-occurrence results similar to ours. These authors set self-damping processes from a uniform distribution ranging from 0 to -1 – in accordance to our parameterization – but set both predator-prey and prey-predator interactions from an uniform distribution ranging from -1 to 1.

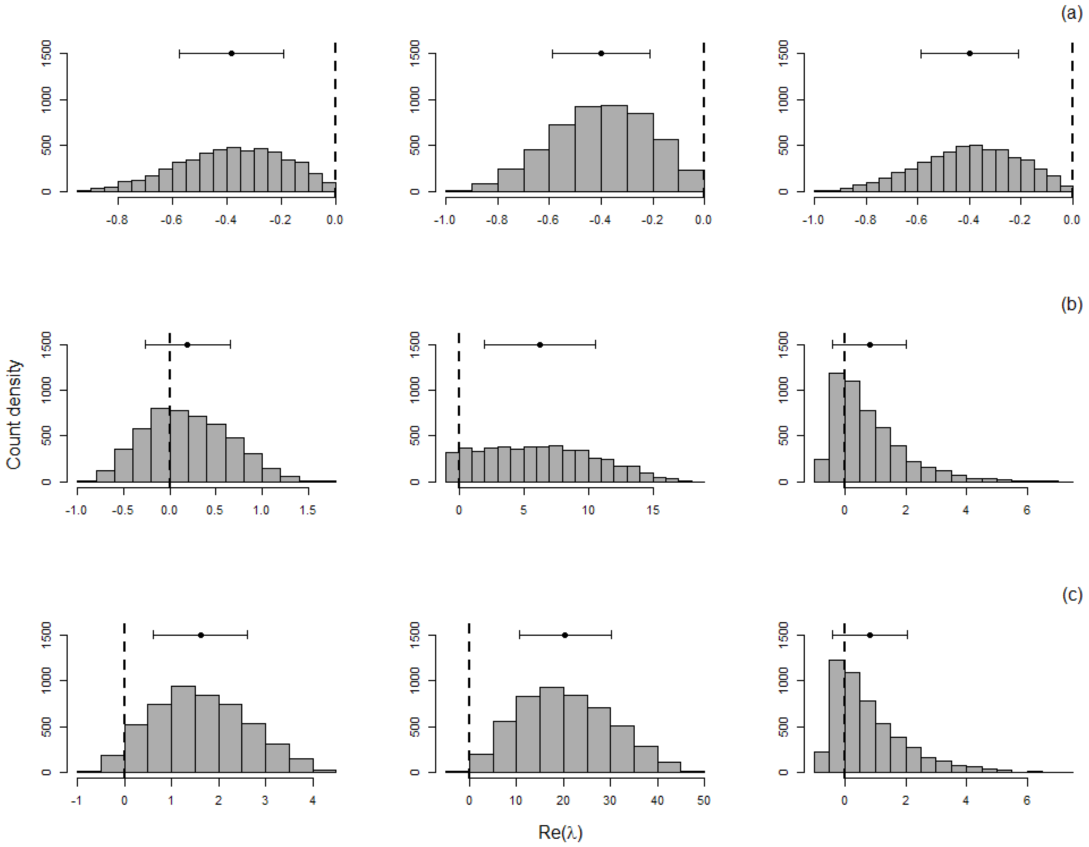


Figure S3: Distribution of eigenvalue with the most positive real part - Re(λ) - from 5000 simulations of (a) trophic-chain modules (M3.1), (b) omnivory module (M3.5) and a (c) unstable module (M3.9). Left side: entries sampled using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 0.1 for the prey-predator interaction, and from 0 to -1 for self-damping processes. Middle: increased interaction strength variation, with entries sampled using a uniform distribution ranging from -100 to 0 for the predator-prey interaction, from 0 to 1 for the prey-predator interaction, and from 0 to -1 for self-damping processes. Right: decreased interaction asymmetry, with entries sampled using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 10 for the prey-predator interaction, and from 0 to -1 for self-damping processes. Above each graphic are the correspondent mean and standard deviations.

Furthermore, we altered self-damping processes, first increasing it to -10 and later removing it by setting to 0. Self-damping processes relates to the circle/ellipse center in the eigenvalue complex plane plot (Figure S2). As demonstrated in Eq (SI) and (SII), we expect that an increase in self-damping processes shifts the eigenvalues circle/ellipse centers to the left and promotes stability. In the same way, setting self-damping processes to 0 places the circle/ellipse center on the origin (0,0) and increases the chance for instability.

This is what we observed for the omnivory module (Figure S4b) and for the unstable module (Figure S4c). If we were to use means and standard deviations to depict stability (Figure 2 from the main document), we would observe these modules in the stable region. In contrast, setting self-damping processes to 0 did not produced positive Re(λ) on previously stable modules, with all eigenvalues being exactly 0 (Figure S4a). In this way, we set self-damping processes ranging from 1^{-10} to 0 and observed results consistent to the interaction strength variation: stable modules maintain its pattern and did not produced positive Re(λ).

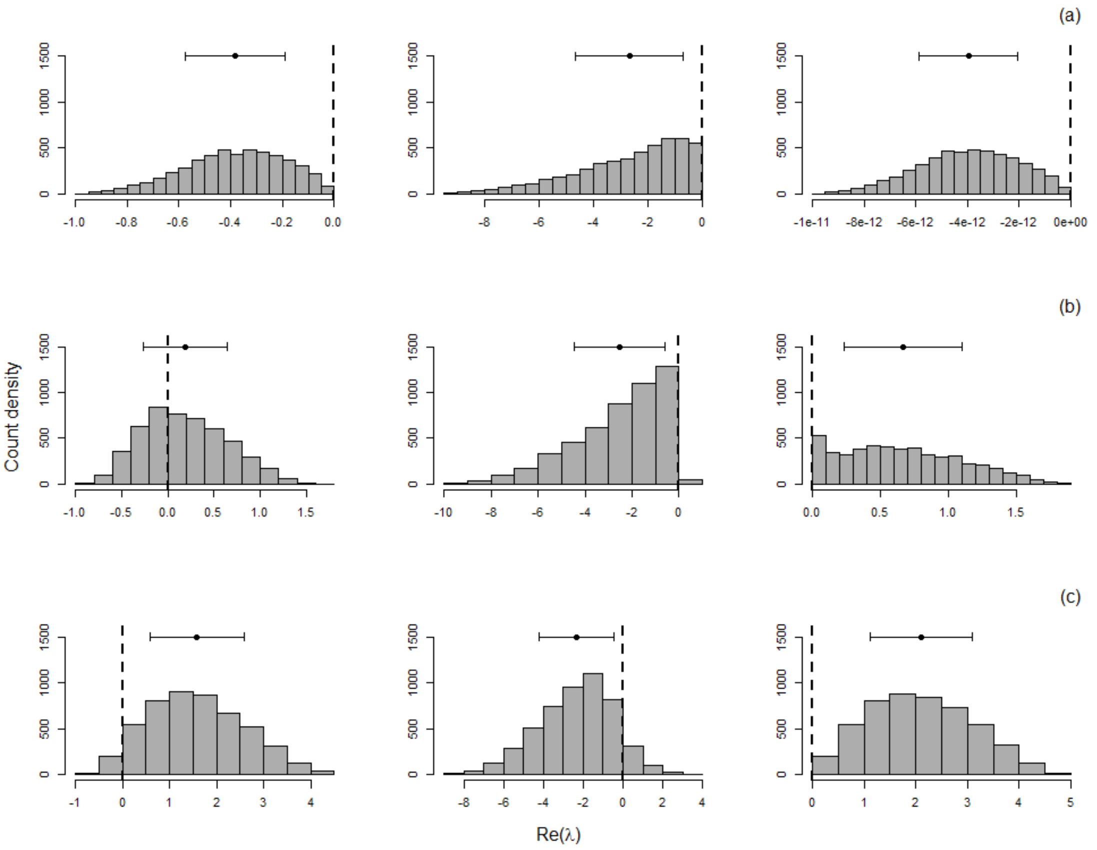


Figure S4: Distribution of eigenvalue with the most positive real part - Re(λ) - from 5000 simulations of (a) trophic-chain modules (M3.1), (b) omnivory module (M3.5) and a (c) unstable module (M3.9). Left side: entries sampled using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 0.1 for the prey-predator interaction, and from 0 to -1 for self-damping processes. Middle: increased self-damping processes, with entries sampled using a uniform distribution ranging from -100 to 0 for the predator-prey interaction, from 0 to 1 for the prey-predator interaction, and from 0 to -10 for self-damping processes. Right: absence of self-damping processes, with entries sampled using a uniform distribution ranging from -10 to 0 for the predator-prey interaction, from 0 to 10 for the prey-predator interaction, and 0 for self-damping processes. Trophic-chain modules with absence of self-damping processes – top-right graphic - were generated from a uniform distribution ranging from 1-10 to 0 (see text). Above each graphic are the correspondent mean and standard deviations.

In conclusion, we found that increasing interaction strengths, predator-prey interaction asymmetry and absence of self-damping processes produced instability on previously unstable modules in our original parameterization. However, we found that previously stable modules were robust and maintained stability despite every scenario.

This consistency depict robustness on our results and validate the parameter we used to future studies.

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ARTIGO 2 - Causal Relationships Between Population Stability and Food-Web Topology

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ABSTRACT

1. Historically, food-web theory has examined the aspects of natural communities that are responsible for maintaining stability in complex communities. The two main lines of research emphasize either topological aspects damping the propagation of perturbations, or population-stability mechanisms that regulate population outbreaks and prevent a total system destabilization. Recent studies, however, have demonstrated that these two aspects act synergistically to produce a single conceptual framework.

2. Nevertheless, causal relationships are still unexplored: it remains uncertain if topological patterns maintain population stability, or alternatively, if population stability promotes food-web topology.

3. In this contribution, we explored the causal relationships between food-web topology and population stability within complex communities. We generated food webs using three models with specific biological assumptions, and measured three population-stability variables, i.e. the proportion of locally stable three-species and four-species modules and the proportion of stable matrices; and two topological variables, i.e. modularity and degree of omnivory. We then used path analysis to evaluate two causality hypotheses, in which (i) topology promotes population stability, and (ii) population stability promotes food-web topology.

4. We found that population stability promoted food-web topology for all models, despite the different biological assumptions. We also observed consistent causal relationships between variables, in accordance with recent literature.

5. These results suggest that studies that intend to discuss the appearance of omnivorous behavior or the stabilization aspect of compartmentalization, should first consider the stability of population dynamics. Additionally, they strongly support a recently proposed theory of an intrinsic mechanism to natural communities, selecting topologies capable of producing an equilibrium point where all species could coexist, and shaping natural communities to a similar and consistent pattern.

INTRODUCTION

In a seminal paper, May (1972) demonstrated that randomly assembled communities are inherently unstable; and that complexity (e.g. diversity, number of interactions and energy flows) would further increase this instability. These results contrasted with the established scientific paradigm, which postulated that stability was maintained by complexity (Elton 1927; MacArthur 1955); and stimulated empirical studies to stress that natural communities are extremely diverse, are far from being randomly assembled, and possess a high degree of complexity (Lawlor 1978; Polis 1991).

Food-web theory involves evaluating species trophic interactions to depict the mechanisms by which natural communities maintain stability in view of this observed complexity (De Angelis 1975; McCann, Hastings & Huxel 1998; Stouffer & Bascompte 2011). One main line of research emphasizes topological aspects of food-webs, such as recurrent patterns, the presence of compartments, the importance of omnivory, and the mechanisms that reproduce species interactions (Dunne 2006; Stouffer 2010). These findings relate to early assumptions that multiple interactive paths regulate the energy channels within a community, damping the propagation of perturbations, while optimizing energy transfer (MacArthur 1955). An alternative line of research emphasizes the importance of population stability, and the mechanisms that regulate population outbreaks and prevent a total system destabilization (Elton 1927; McCann 2000; Dunne et al. 2005).

Only recently have investigators begun to explore the synergism between these two perspectives, suggesting that food-web topology and population stability combine to produce a single conceptual framework (Rooney & McCann 2012; Borrelli et al. 2015). These studies have suggested that species assemble in ways that maximize energy transfer (Milo et al. 2002), that topologies may be consequences of dynamic relationships between species (Tunney et al. 2012), and that topologies may guarantee the persistence of food webs after perturbations (Stouffer & Bascompte 2011). Further, recent studies have explored patterns of small topological components, and have demonstrated that, although a limited set of these components are expected to be stable, these are the components that occur most often in natural communities (Prill, Iglesias &

Levchenko 2005; Borrelli 2015; Monteiro & Faria 2016)

Although studies recognize the interplay between population dynamics and food-web topology, it is still uncertain if topologies maintain population stability or, conversely, if population stability promotes food-web topologies. Borrelli et al. (2015), for example, suggested a non-adaptive selection process governing the occurrence of modules (small topological components of communities). This process would act on intrinsic properties of population stability to produce a single consistent topological pattern. In contrast, Cohen et al. (2009) argued that in the same way that an organ is more than its constituent cells, patterns within fewer species modules would not account for the properties of progressively higher levels of structure; i.e., a food-web topology is more than its constituent modules.

In the present study, we investigated the causal relationship between population dynamics and topological patterns of complex food webs. We measured three population-stability variables and two topological variables. We simulated food webs with three different models with specific biological assumptions: the Niche Model, the Probabilistic Niche Model, and the Minimal Potential Niche Model. We then used path analysis to evaluate two causality hypotheses, in which (i) topology promotes population stability, and (ii) population stability promotes food-web topology. We evaluated the hypothesis that best fit each model, and discussed the pattern of causal relationships among the variables.

METHODS

Food-web models

The process of collecting high-quality food-web data involves many practical problems: extensive fieldwork, sampling design, refined species identification, and estimation of interaction strengths (Cohen *et al.* 1993; Morales-Castilla *et al.* 2015). Although empirical food-web databases have been valuable to depict patterns of natural communities (Milo *et al.* 2002; Stouffer & Bascompte 2011; Jacquet *et al.* 2016), analyses using these databases may suffer from inconsistencies, due to differences in levels of taxonomic detail, interaction-assembling criteria, and the objectives of the original study (Woodward 2010). Food-web modeling permits phenomenological models to reproduce the biological patterns of a predator’s prey-selection behavior and to depict recurring patterns of food webs with similar diversity and complexity (Williams & Martinez 2008; Stouffer 2010).

The most recognized model is the **Niche Model**, which assumes prey-selecting behavior conditioned to a single niche dimension, and with each species having a specific exponentially decaying probability of preying on species with lower niche values (Williams & Martinez 2000). The Niche model uses the Number of Species (*S*) and Connectance (the proportion of realized interactions; *C*) as input parameters; and employs a single niche dimension from 0 to 1, with each species having a single niche position (*n*). A consumer *i* consumes all prey within an interval of length $r_i=xn_i$, where x is a random variable from a Beta-distribution with a probability density function of $p(x) = \beta\ (1-x)^{(1-\beta)}$ and with $\beta = (1/2C) - 1$. The interval center (*c*) is sampled from a uniform distribution between $r_i/2$ and $\min(n_i, 1- r_i/2)$.

Although the Niche Model was able to reproduce empirical observed data with a single niche dimension (Williams & Martinez 2008), studies suggested that food webs have a certain degree of nonintervality (Cattin *et al.* 2004; but see Stouffer, Camacho & Amaral 2006). The **Probabilistic Niche Model** modified the original Niche Model to introduce a scenario with gaps in the species-feeding interval, while still considering a single niche dimension (Williams, Anandanadesan & Purves 2010). The Probabilistic Niche Model also employs *S* and *C* as input parameters, but inserts a Gaussian formulation to the Niche Model, in which consumers have a higher probability of eating prey that are close to the interval center (*c*), and have a lower probability of eating prey at the ends of the interval. Specifically, a consumer *j* eats each prey *i* with a probability:

$$P(i,j) = \alpha \exp\left\{ -\left(\frac{n_{i-c_j}}{r_i/2} \right)^2 \right\} \qquad (1)$$

where *P(i,j)* is the probability that *j* eats *i*, n_i is the scaled niche position of prey *i*, *c* is the interval center, and r_i is the interval length.

The **Minimal Potential Niche Model** assumes that a single niche dimension interval for a predator's diet is only a smaller subset of all intervals produced by the combination of multidimensional niches. Disregarding higher dimensions of the niche would produce irreproducible interactions, observed to occur outside a single niche dimension. Thus, nonintervality occurs when wider multidimensional intervals are combined (Allesina, Alonso & Pascual 2008). The Minimal Potential Niche Model sets niche values and niche intervals for all species in the same way as the original Niche Model. However, this model automatically considers the first and last species in the interval as prey, while the other species falling within the interval are consumed with probability ($1–f$), where f is a measure of food-web intervality and represents the “forbidden links” (Allesina, Alonso & Pascual 2008).

These models were originally designed to approximate food-web topologies. However, none of them explicitly includes parameters to adjust the topology. Rather, each model uses specific biological assumptions to reproduce species-specific interactions, given a defined community size (number of species), a number of interactions, and a defined mechanism for prey selection. Although topology was, for decades, the criterion to evaluate model adjustments, recent studies have evaluated the performance of models based on the likelihood that they reproduce observed interactions (Allesina, Alonso & Pascual 2008; Staniczenko, Smith & Allesina 2014). Therefore, for the purpose of this study, we considered food-web models as hypotheses for the mechanisms of prey selection, which aim to reproduce species-specific interactions, rather than as tools to deliberately generate topologies.

Modeling procedures and food-web variables

We generated 3000 food webs for each model described above. We used ranges of S from 10 to 100, C from 0.05 to 0.30, and f from 0.1 to 0.9 (for an analysis of the sensitivity of these parameters please see the Supplementary Material). For each food web, we computed two topology variables that are suggested to influence food-web stability, i.e. modularity and degree of omnivory; and three population-stability variables, i.e. the proportion of stable three-species modules (M3), proportion of four three-species modules (M4), and proportion of stable communities (Monteiro & Faria 2016).

Modularity is a measure of compartmentalization, and evaluates the fraction of interactions within compartments minus the expected fraction if the interactions were randomly distributed. Stouffer and Bascompte (2011) suggested that modularity dampens the propagation of extinctions throughout the community after species loss.

We assigned modules using the Walktrap Community Finding Algorithm (Pons & Latapy 2005) and evaluated modularity as:

$$Q=\frac{1}{2m}\sum_{ij} A_{ij}-\frac{k_i k_j}{2m}\delta\left(c_i c_j\right) \tag{II}$$

where, m is the number of edges, A_{ij} is the element of the adjacency matrix A in row i and column j (A_{ij}=1 if there is an interaction between species i and j, $A_{ij}=0$ otherwise), k_i is the number of interactions of species i, k_j is the number of interactions of species j, c_i and c_j are the compartments of species i and j respectively, and $\delta(c_i c_j) = 1$ if $c_i = c_j$ and 0 otherwise (Newman & Girvan 2004).

While the effects of omnivory on food-web stability have been extensively debated, Gellner and McCann (2012) suggested that food-web stabilization is achieved only under specific conditions of omnivory. The degree of omnivory evaluates the fraction of species that consume two or more prey species with a nonadjacent mean trophic level, and has been suggested as a reliable measure to evaluate the stabilization role of omnivory (Williams & Martinez 2004; Monteiro & Faria 2016).

We evaluated the occurrence of 13 types of three-species modules and 199 types of four-species modules. For each module, we assembled a corresponding Jacobian predation matrix S x S, where S is the number of species in the module, i.e. three or four, and each entry is the interaction strength of the consumer in the column on the prey in the row, which represents the linearized value of the feeding interaction at equilibrium of the two populations. We followed previous analyses and sampled matrix entries using a uniform distribution ranging from –10 to 0 for the predator-prey interaction, from 0 to 0.1 for the prey-predator interaction, and from 0 to –1 for the self-damping effect (Pimm 1979). We simulated 10^3 Jacobian matrices for each three- and four-species arrangement, and calculated the mean value of the eigenvalues with the most positive real part. Negative eigenvalues represent the decay of a perturbation in the population dynamics close to equilibrium (local stability), while positive eigenvalues indicate an unstable state. Thus, the mean value of eigenvalues represents the expected stability of a given module arrangement (for more information see Monteiro & Faria 2016). We computed M3 and M4 as the proportion of stable three- and four-species arrangements respectively. To calculate the proportion of stable communities, we sampled the Jacobian matrices considering the entire food-web structure, calculated the eigenvalues with the most positive real part, and evaluated the proportion of stable matrices.

Path analysis

We used a Path analysis to employ causal relationships between food-web topology and population stability. Path analysis modeling forms multi-equation regression models to validate a causality framework for an observed correlation matrix, and tests the hypothesis that best fits an observed co-occurrence pattern (Shipley 2002).

We developed two frameworks (hypothesis) of causal relationships. Both hypotheses are consequence of complexity, i.e. the selected input parameters: *S* and *C* for the Niche Model and the Probabilistic Niche Model; and *S*, *C* and *f* for the Minimal Potential Niche Model. In the first hypothesis, we assumed that complexity, constrained within the biological assumptions of the model, generates a topological pattern of compartmentalization and omnivory, which, in turn, produces population stability (Fig. 1). A second hypothesis, in contrast, assumed that complexity, and the biological assumptions of the models, produce the population-stability patterns, which in turn generate the observed topology (Fig. 2).

Path analysis minimizes the difference between the observed covariances in the data and the covariances predicted by each hypothesis, using maximum-likelihood estimation of the free parameters. Therefore, we evaluated the hypothesis that most likely reproduced the data using the Akaike Information Criteria (Akaike 1974). In addition, path analysis permits testing the null hypothesis of differences between observed and predicted covariances being obtained only by sampling variation using a maximum likelihood chi-squared test. Given multivariate normality, one can show that:

$$\lim_{N \to \infty} (N-1) F_{ML} X^2_{u-(p+q)} \tag{III}$$

where, N is the number of observations, F_{ML} is the maximum-likelihood fitting function, $X^2_{u-(p+q)}$ is a chi-squared distribution with $u-(p+q)$ degrees of freedom, u is the number of unique variables, p is the number of free path coefficients in the model, and q is the number of free variances (Shipley 2002). To test for multivariate normality, we performed Mardia's Multivariate Normality Test.

In case of non-normality, but a high number of observations (e.g. 3000), a null hypothesis can be evaluated by Bootstrap estimates. This estimation produces a sampling distribution based on randomizations of the observed data, which do not make parametric assumptions. In this context, we computed the Bollen-Stine bootstrap p-value to test the adjustment of the best model in relation to a null hypothesis (Bollen & Stine 1992).

RESULTS

Our modeling procedure showed a consistent pattern. Between the two conflicting hypotheses, the AIC indicated that the framework of population stability causing food-web topology best adjusted to the data in all three scenarios (Table 1). In addition, p-values from all models showed consistency between this framework and the data, e.g. apart from the biological assumptions in each scenario, the causal hypothesis that population stability promotes the food-web topology performed better than the null hypothesis (Bollen-Stine Bootstrap adjusted p-value<0.001 in all cases). Therefore, we discuss only the pattern of causal relationships among the variables of this framework.

We observed a consistent effect on the causal relationships between the variables. For all models, complexity, e.g. the number of species (*S*) and Connectance (*C*), negatively affected all three population-stability metrics, although the connectance effect was greater. The proportion of stable three-species modules (*M3*) positively affected the topological variables: omnivory (*Omni*) and modularity (*Mod*). Although negative effects were observed for omnivory, they were not statistically significant ($M3 \rightarrow Omni$: Niche Model p=0.08; Minimal Potential Niche Model p=0.86). The proportion of four-species modules (*M4*) and the proportion of stable communities (*PS*), in contrast, negatively affected omnivory and positively affected modularity. As a result, the path analysis indicated a negative covariance between the two topological variables (*Omni* and *Mod*). These results were robust and not dependent on the biological assumptions of each model (Figs 2 to 4).

For the Minimal Potential Niche Model, the forbidden link (*f*) parameter, which dictates the degree of nonintervality in the food-web, negatively affected the population stability (M3, M4 and PS). It also indirectly and negatively affected connectance, whereas it positively affected the number of species.

DISCUSSION

We found that a single consistent pattern reproduced the causal relationship between population stability and food-web topology: apart from the different biological assumptions employed by the three models, population stability promoted food-web topology. Further, our results demonstrated a consistent causal relationship between complexity (*S*, *C* and *f*), the three dynamic variables (*M3*, *M4* and *PS*), and the two topological variables (*Mod* and *Omni*), in concordance with the models and with recent literature.

We found a negative effect of complexity on stability. The negative effect of the number of species and connectance (i.e. complexity) on population stability has long been known (May 1972). On one hand, some researchers on population dynamics argued that this destabilizing effect is compensated by dynamic stability, through the synergism between weak and strong interaction strengths (McCann, Hastings & Huxel 1998). Others, in contrast, argued that interaction strengths are secondary to realistic topologies — using negative and positive effects, with a defined correlation, between consumers and prey (henceforth referred to as species-level topologies). These latter depicted, through the elliptical law (which describes the expected distribution of eigenvalues), that species-level topologies could dampen the strong negative effect of connectance on stability; and that weak interaction strengths could be either stabilizing or destabilizing, depending on the species-level topology (Allesina & Pascual 2008; Allesina *et al.* 2015; Allesina & Tang 2015). Recently, however, Jacquet *et al.* (2016) revisited May’s results, using an extensive food-web database, and employed the diet composition, biomass, production and consumption rates of each species as input parameters for the predation matrix. These authors found that a heavy-tailed interaction-strength distribution (i.e. a high proportion of weak interactions) was the food-web property that most strongly promoted stability in empirical food webs; and that species-level topologies did not significantly affect the complexity-stability relationship.

Our simulations depicted only the expected stability of three- and four-species modules and the proportion of stable communities, ignoring the variance of the most positive eigenvalue, and limiting our inferences on the role of variations in interaction strengths. In this contribution, Monteiro and Faria (2016) demonstrated that three and four-species modules considered stable with our parameterization, are robust to variations of interaction strengths, interaction asymmetry, and variation of the self-damping effect. In contrast, unstable three and four-species modules with our parameterization present variable responses to variation of these coefficients. Although our analysis limited inferences about the mechanisms responsible for compensating for the negative effects of complexity on stability, we found that this effect could scale up to produce network-level topology patterns, such as lower modularity and a higher degree of omnivory.

Some investigators have argued that modularity would either lead to food-web instability (Pimm 1979), or dampen the propagation of perturbations through food webs, preventing secondary extinctions after species loss (Stouffer & Bascompte 2011). Our results suggest, on the contrary, that the causal process begins with population stability. We argue that food webs are able to manifest compartments only because populations are locally stable. Indeed, Monteiro and Faria (2016) found that modularity did not predict the proportion of stable three- and four-species modules, resulting from the fact that many modules are not expected to be stable. Further, Teng and McCann (2004) demonstrated that reticulate food webs would have relatively uniform energy flows, and consequently, unstable dynamics. They found that weak and strong interaction strengths, and increasing the asynchrony of energy flows modifies the topology, compartmentalizing food webs into stable arrangements. Finally, recent findings from Grilli, Rogers and Allesina (2016) demonstrated that modularity has variable effects on stabilization, which depend on the patterns of interaction strengths: a modular structure is stable only with small mean interaction strengths.

This process of population stability causing topology can also inform the long-standing debate in the food-web literature regarding omnivory. Topological analyses have recognized omnivory as a destabilizing agent (Pimm & Lawton 1978; Johnson *et al.* 2014), while dynamic studies discuss specific patterns of interaction strengths in which stabilization should occur (McCann & Hastings 1997; Gellner & McCann 2012; Monteiro & Faria 2016). Regarding the occurrence of the omnivory module, studies have found that omnivory is under-represented in empirical food webs, suggesting they are selected against; while others have found widely variable patterns of occurrence, suggesting that the inferences depend on the level of aggregation and the null models used (Milo *et al.* 2002; Bascompte & Melian 2005). We suggest that modularity and omnivory do not act on population stability, but rather is a consequence of unstable population dynamics. Studies that discuss the appearance of omnivorous behavior should first consider the stabilization of population dynamics. For example, recent studies have demonstrated that an environmental contraction (such as habitat fragmentation) causes mobile higher-order organisms to strongly couple local habitats, which reduces chain lengths, exerts a strong destabilizing effect and favors omnivorous behavior (McCann, Rasmussen & Umbanhowar 2005; Tunney *et al.* 2012). Finally, the omnivory patterns found here also concorded with previous findings, and showed a dualistic behavior, being positive to the proportion of three-species modules; and negative to the proportion of four-species modules and proportion of stable matrices (Bascompte & Melian 2005; Gellner & McCann 2012; Monteiro & Faria 2016).

Path analysis estimates multiple causal inferences for competing hypotheses, and, in consequence, estimates a high number of parameters. For the purpose of simplicity, our analysis considered only a limited set of variables. We suggest that future studies consider different hypotheses and evaluate different variables. Topological variables could include, for example, the number of top predators, proportion of interactions between trophic levels, and keystone species. Further, dynamic variables could benefit from inserting interaction-strength patterns, evaluating how they regulate the observed coefficients.

Patterns in the network of trophic interactions among species are far from random, since they reflect the underlying processes that generated natural communities (Lawlor 1978; Milo *et al. 2002; Stouffer et al. 2005)*. Borrelli *et al.* (2015) suggested that topologies better able to maintain stability - in which all species could coexist -, would be selected by a nonadaptive selection process. Contrary to an adaptive selection process that results in diversification of individual populations adapted to their environment, this nonadaptive mechanism would select feasible and dynamically stable topologies that results in a similar and consistent pattern among communities (Borrelli *et al.* 2015). Our results demonstrated that population stability, in fact, promotes food-web topology; and recent studies, analyzing module occurrences in empirical food webs, demonstrated that arrangements that are expected to be stable occur more frequently than unstable arrangements (Prill, Iglesias & Levchenko 2005; Borrelli 2015; Monteiro & Faria 2016). Therefore, our results strongly support the nonadaptive selection mechanism, and suggest that natural communities are shaped by a single consistent mechanism.

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TABLES

Table 1. The adjustment of two hypotheses for the causal relationships between population stability and food-web topology in three food-web models. We used Path analysis to generate the hypothesis framework and Akaike Information Criteria (AIC) as the selection method. P-value tests the null hypothesis of differences between observed and predicted covariances being obtained only by sampling variation.

		Niche Model	Probabilistic Niche Model	Minimal potential Niche Model
Topology-> Dinamics	df	7	7	10
	Loglikelihood	-2635.15	-1797.43	-1175.71
	AIC	5306.30	3630.86	2391.41
	p-value	<0.01	<0.01	<0.01
Dinamics -> Topology	df	7	7	9
	Loglikelihood	-102.36	547.46	791.24
	AIC	240.72	-1058.92	-1540.48
	p-value	<0.01	<0.01	<0.01

FIGURES

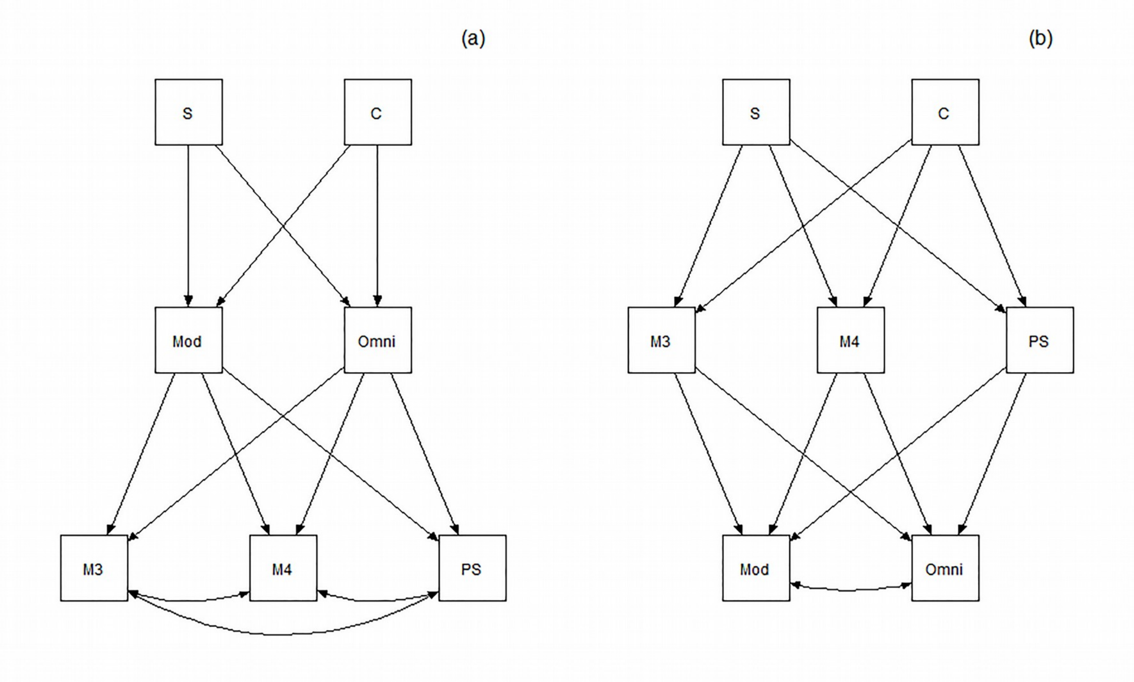

Fig. 1. Path analysis modeling framework for the hypothesis of (a) food-web topology causing local stability and (b) local stability causing food-web topology. Number of species (S) and connectance (C) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. The Minimum Potential Niche Model includes an additional input parameter *f*. One-headed arrows represent causal effect, in which A → B indicates that A causes B, while double-headed arrows represent covariance.

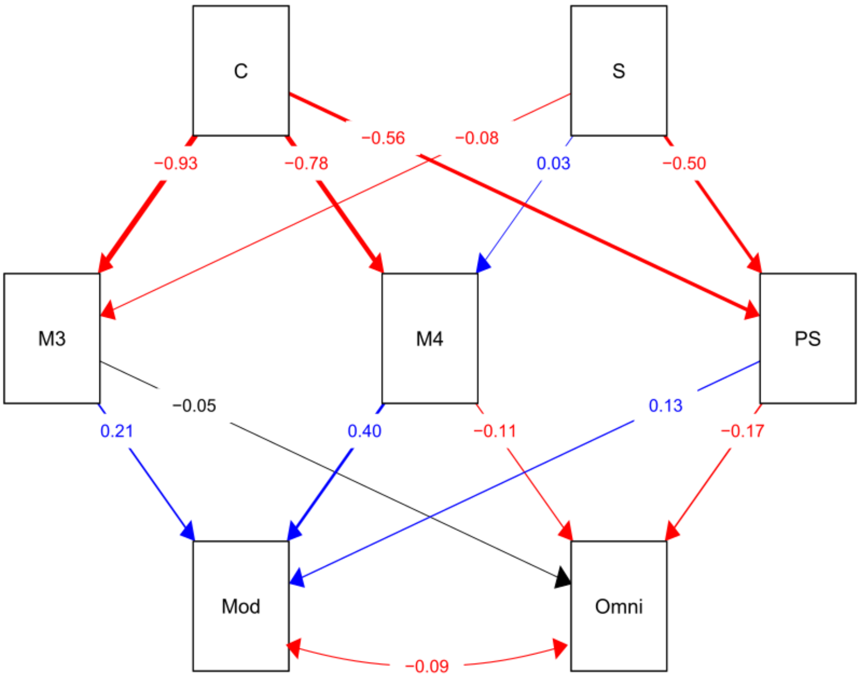

Fig. 2. Causal relationships between variables for a Path analysis that depicts population stability causing food-web topology in data generated by the Niche Model. Number of species (S) and connectance (C) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red lines represent negative effects, blue lines represent positive effects, and black line represents a non-significant relationship. Line width indicates the strength of the relationship. Line labels are standardized parameter estimates.

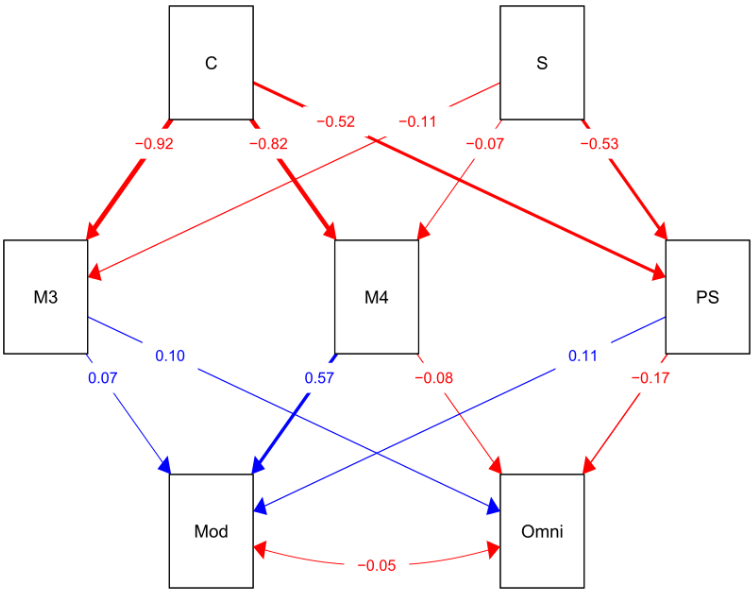

Fig. 3. Causal relationships between variables for a Path analysis that depicts population stability causing food-web topology in data generated by the Probabilistic Niche Model. Number of species (S) and connectance (C) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red lines represent negative effects, while blue lines represent positive effects. Line width indicates the strength of the relationship. Line labels are standardized parameter estimates.

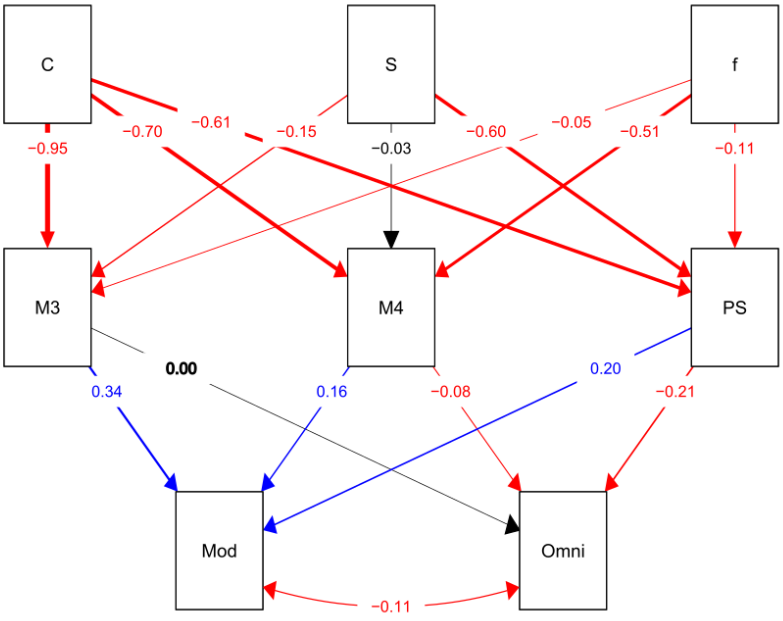

Fig. 4. Causal relationships between variables for a Path analysis that depicts population stability causing food-web topology in data generated by the Minimal Potential Niche Model. Number of species (S), connectance (C) and the “forbidden links” (*f*) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red lines represent negative effects, blue lines represent positive effects, and black lines represent non-significant relationships. Line width indicates the strength of the relationship. Line labels are standardized parameter estimates.

SUPPLEMENTARY MATERIAL

Sensitivity analysis

We performed a sensitivity analysis to evaluate the robustness of our results. We tripled the maximum number of species (S) in each food-web model, varying from 10 to 300 (see section 3.2). We found general results consistent with previous analysis, and robustness for the hypothesis of causal relation from dynamic stability to food web topology better adjusted to the data (see Results section). However, as expected, we observed that larger food-webs are harder to reproduce. Considering only the better hypothesis, we found higher number of non-significant parameter estimations, and different causal relations from previous analysis (Figures S2 to S4). Specifically, we observed that omnivory relations were not significantly estimated for all three models, and a significant negative relation occurred between $M3 \rightarrow Mod$ for the Probabilistic Niche Model. Apart from that, all other values were consistently estimated. This may come from the fact that varying the number of species produce a greater spectrum of interactions, and parameters estimation are more difficult to converge. To produce a consistent distribution of parameters we would have to greatly increase the number of simulations, which, in practice, would be too computationally extensive. From this, we can conclude that the hypothesis of dynamical stability generating food-web topology holds, although the mechanisms that produce this pattern can be better evaluated in smaller food-webs.

Table S1: The adjustment of two hypothesis for the casual relations between population stability and food-web topology in three food-web models with number of species varying from 10 to 300. We used Path analysis to generate the hypothesis framework and Akaike Information Criteria (AIC) as selection method. P-value tests the null hypothesis of differences between observed and predicted covariances being obtained only by sampling variation.

		Niche Model	Probabilistic Niche Model	Minimal potetial Niche Model
Topology-> Dinamics	df	7	7	10
	Loglikelihood	-5441.54	-4272.31	-4349.42
	AIC	10919.08	8580.62	8738.84
	pvalue	<0.01	<0.01	<0.01
Dinamics -> Topology	df	7	7	9
	Loglikelihood	-1925.59	-1203.56	-1349.95
	AIC	3887.18	2443.12	2741.90
	pvalue	<0.01	<0.01	<0.01

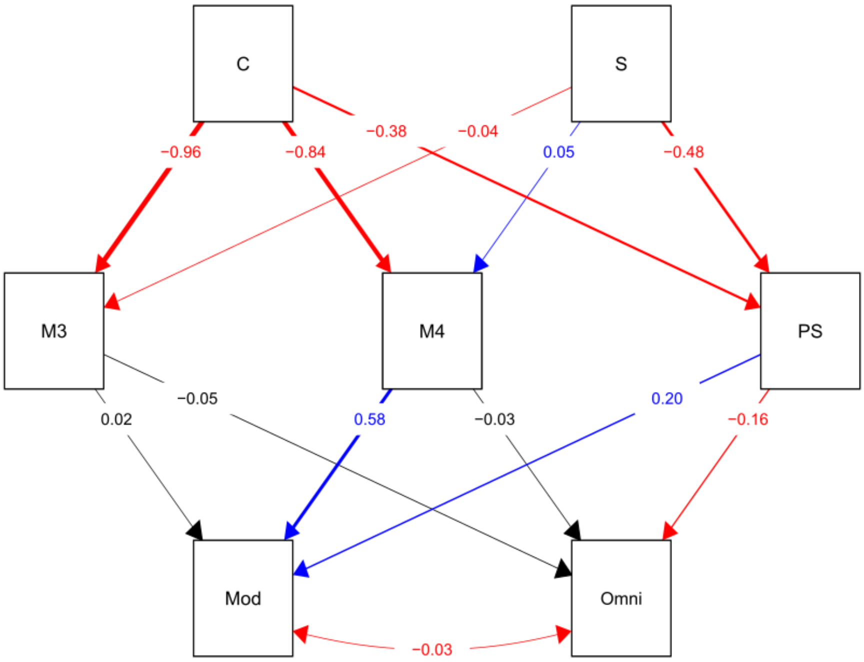

Figure S1: Casual relations between variables for a Path analysis that depict population stability causing food-web topology in data generated by the Niche Model. Number of species (S) and connectance (C) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red edges represent negative effects, blue edges represent positive effects and black edges represent non-significant relations. Edge width indicate the strength of the relation. Edge labels are standardized parameters estimates.

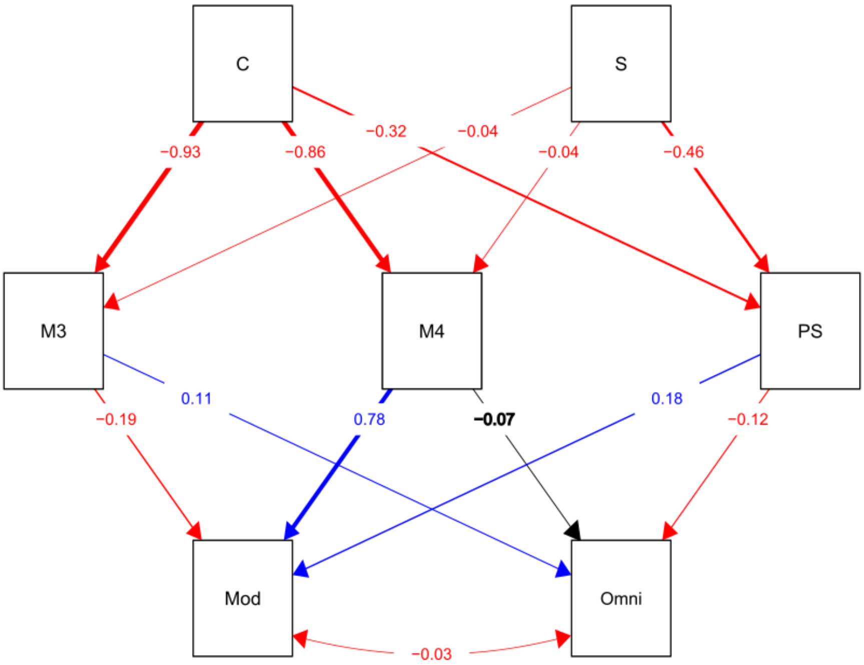

Figure S2: Casual relations between variables for a Path analysis that depict population stability causing food-web topology in data generated by the Probabilistic Niche model. Number of species (S) and connectance (C) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red edges represent negative effects, blue edges represent positive effects and black edges represent non-significant relations. Edge width indicate the strength of the relation. Edge labels are standardized parameters estimates.

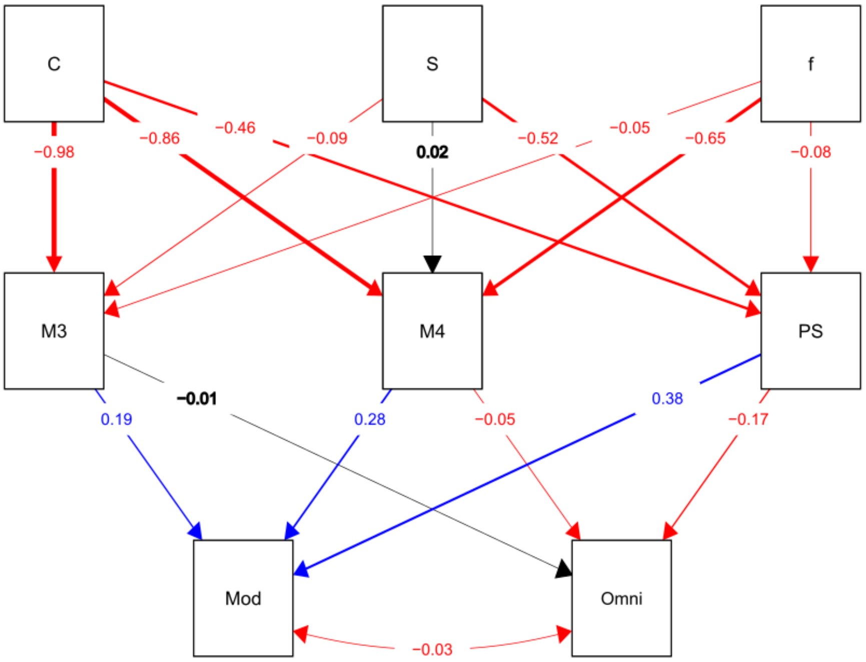

Figure S3: Casual relations between variables for a Path analysis that depict population stability causing food-web topology in data generated by the Minimal potential niche model. Number of species (S), connectance (C) and the “forbidden links” (f) are input parameters; modularity (Mod) and Omnivory (Omni) are topological variables; and the proportion of stable three- and four-species modules (M3 and M4) and the proportion of stable matrices (PS) are local stability variables. Red edges represent negative effects, blue edges represent positive effects and black edges represent non-significant relations. Edge width indicate the strength of the relation. Edge labels are standardized parameters estimates.

Em processo de correção na revista:
Ecology letters

ARITGO 3 - Matching consumer feeding behaviors and resource traits: a fourth-corner problem in food-web theory

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Abstract

For decades, food web theory has proposed phenomenological models for the underlying structure of ecological networks. Generally, these models rely on latent niche variables that match the feeding behavior of consumers with their resource traits. In this paper, we used a comprehensive database to evaluate different hypotheses on the best dependency structure of trait-matching patterns between consumers and resource traits. We found that consumer feeding behaviors had complex interactions with resource traits; however, few dimensions (i.e., latent variables) could reproduce the trait-matching patterns. We discuss our findings in light of three food web models designed to reproduce the multidimensionality of food web data; additionally, we discuss how using species traits clarify food webs beyond species pairwise interactions and enable studies to infer ecological generality at larger scales, despite potential taxonomic differences, variations in ecological conditions, and differences in species abundance between communities.

Introduction

Food webs are an abstraction: a reduction in dimensionally used to understand the underlying complexity of natural communities (Schaffer 1981). One prevalent method in food-web theory is to propose phenomenological models that reproduce consumer feeding behavior and predict topological properties of empirical data with minimum assumptions (Cohen *et al.* 1990; Stouffer 2010). Early studies suggested that food webs were interval, meaning that a single dimension was enough to characterize consumer feeding behavior in a community (Cohen 1977; Stouffer *et al.* 2006; Mouillot *et al.* 2008). Thus, models capable of collapsing food-web structure into a single and ordered dimension, with each species having a specific position and each consumer having an exponentially decaying probability of consuming a fraction of species below its position, would most successfully reproduce the observed patterns (Williams & Martinez 2000; Stouffer *et al.* 2005). Dimensions, in this case, refer to the community niche space, such as a single niche axis (usually body size) (Williams *et al.* 2010), or a hypothetical latent variable that provides information on many traits (Rohr *et al.* 2010; Warton *et al.* 2015).

However, recent results have demonstrated that, although the information within a single dimension may be able to reproduce a relatively large proportion of interactions (Williams *et al.* 2010; Eklöf *et al.* 2013), in most cases, multiple dimensions are required to explain most of the food-web structure (Rohr *et al.* 2010; Warton *et al.* 2015). Additionally, when selecting likelihood criteria to evaluate the probability of models to reproduce observed interactions, single-dimension models may produce *forbidden interactions (sensu* Jordano et al. 2003), which cannot be determined based on the assumptions in single-dimension models; therefore, they must be considered stochastic (Allesina et al. 2008). These studies propose that intervality results from the intersection of feeding patterns that occur in multiple dimensions and that resource traits may play a larger role than previously assumed; finally, these studies assume that models that match both consumer feeding behaviors and resource traits using high-dimensional trophic niche spaces can better reproduce interval food webs (Allesina *et al.* 2008; Rossberg *et al.* 2010; Brännström *et al.* 2011; Poisot *et al.* 2015).

Matching traits through interaction matrices has been addressed before in the ecological literature, and this practice is referred to as the fourth-corner problem (Legendre *et al.* 1997;

Dray *et al.* 2014). The fourth-corner problem originally aimed to evaluate the relationship between species traits and environmental attributes to generalize patterns in ecosystem processes beyond species taxonomy, assuming species diversity as a diversity of ecological functions (Dray & Legendre 2008). Specifically, the fourth-corner analysis is based on finding a matrix, D_{mq}, that maps m habitat characteristics with q species traits. This is done through a matrix C_{mn}, which contains information about m habitat characteristics of n sites; a matrix B_{pq}, which contains q traits of p species; and a matrix A_{pn}, which contain the abundance (or presence) of p species at n sites.

In this study, we proposed a new approach to address food-web dimensionality. Using an extensive database of trophic interactions, a matrix of consumer feeding behavior, and a matrix of resource traits, we evaluated the matchings between consumer feeding behaviors and resource traits as a fourth-corner problem. Specifically, we computed multi-way contingency tables for the number of interactions between consumer feeding behaviors and resource traits, and we evaluated the underlying structure of this table by applying model selection procedures for different dependency hypotheses between traits. Finally, we performed a dimension reduction analysis on the most parsimonious hypothesis to evaluate how hypothetical latent variables accounted for the matching patterns of this complex structure.

Methods

Food web data

We used data on 16,866 trophic interactions, which are available in (Brose *et al.* 2005). This database was originally assembled to address the effects of patterns of consumer-resource body sizes on food-web structure, interaction-strength distributions, population dynamics, and community stability. Further, the database provided information on consumer feeding behaviors, species metabolic groups, and species biomass from different ecosystems (Table 1). Consumer feeding behavior, species metabolic group, and biomass comprise topological traits, which relate to feeding probabilities between consumers and resources (Gravel *et al.* 2016). The type of habitat, on the other hand, relates to demographic patterns and is termed life-history traits. Life-history traits affect equilibrium abundances and provide insights into the neutral principle that, without trait-matching constraints, interactions are driven by random encounters between consumers and resources (Canard *et al.* 2012, 2014; Poisot *et al.* 2015; Gravel *et al.* 2016). It is worth mentioning that Gravel *et al.* (2016) also distinguished and defined consumption traits, which refer to functional and numerical responses of prey and predators, and these traits are related to patterns in population dynamics, such as attack rate and handling time. However, these traits are more difficult to measure than are topological and life-history traits and were outside the scope of our analysis (Gravel *et al.* 2016).

We categorized the logarithm of the biomass of a resource, binning values using the Sturges' formula (Sturges 1926). This guaranteed the formation of contingency tables when performing fourth-corner analysis, preserved the chi-squared distances between variables, and permitted better visualization and inferences on the association patterns between consumer feeding behaviors and resource traits (henceforth: matchings).

Fourth-corner analysis and model selection

Assuming a predation matrix A_{ij}, where $a_{ij}=1$ when consumer j eats resource i, and $a_{ij}=0$ otherwise; a matrix B_{in}, in which $b_{in}=1$ when resource i has trait n, and $b_{in}=0$ otherwise; and a matrix C_{mj}, in which $c_{mj}=1$ when consumer j has feeding behavior m, and $c_{mj}=0$ otherwise; we performed a fourth-corner analysis to produce a contingency table D_{mn}, in which the entries d_{mn} are the number of interaction between a consumer trait m and a resource trait n, calculated as follows:

$$D = CA'B \qquad (1)$$

With matrix D_{mn}, the original fourth-corner analysis evaluates the independence between each consumer and resource trait based on the number of interactions between traits. This is usually done with X^2 or G statistics; however, these tests must be based on randomization of the data since observations are not independent (Legendre *et al.* 1997). Non-binary matrices can also be computed through inflated tables, and these matrices can be tested using correlation coefficients and pseudo-F statistics (Dray & Legendre 2008).

However, different from previous studies, we separately inferred the following: (i) identifying which resource traits were related to the feeding behavior of consumers, and (ii) determining the structure of the dependency matrix between resource traits and consumer traits. We assembled log-linear models, which are a standard tool used to test independence structure in multi-way contingency tables when considering only binary data. Log-linear models evaluate the expected cell frequencies as a function of different interactions between variables, and the goodness-of-fit is computed using a likelihood ratio statistic; furthermore, a general two-dimensional table has the following form:

$$L\left(m \vee D_{mn}\right)=2\sum_{m=1}^{M}\sum_{n=1}^{N} y_{mn}\log\left(\frac{y_{mn}}{\widehat{\mu_{mn}}}\right) \tag{2}$$

where y_{mn} is the number of interactions between traits m and n, and $\widehat{\mu_{mn}}$ is the expected number of interactions between traits m and n. The degrees of freedom were computed as $df=\pi-\delta$, where π is the number of cells and δ is the number of free parameters (Agresti 2003). To find a parsimonious hypothesis, we computed the Akaike information criteria (AIC) (Akaike 1974):

$$AIC=L-2\delta \tag{3}$$

To determine which resource traits were related to consumer feeding behavior, we computed a global model for the feeding behavior of consumers and the three resource traits using only additive terms. Then, we performed an AIC stepwise procedure on the resource traits, removing each trait and computing the change in the AIC, finally selecting the model with the lowest ΔAIC.

To evaluate the dependency structure of the multi-way contingency table between resource traits and consumer feeding behavior, we evaluated different hypotheses and varied the interaction terms between the resource traits. We also considered an additional dimension in the traits of consumers and inserted an interaction term between the feeding behavior of consumers and the metabolic group of consumers. This additional dimension in the traits of consumers was considered only during this later stage because we thoroughly selected which hypothesis to test since not all combinations were biologically feasible (Burnham & Anderson 2003). For example, we assumed that it was not feasible to consider models with an additive term between consumer feeding behavior and consumer metabolic group, since consumer metabolic group alone was not expected to depend on resource traits. We selected the best hypothesis for the dependency structure of the multi-way contingency table based on which computed model had the lowest ΔAIC (Table 2).

Finally, given the multi-dimensional structure of the data, we performed correspondence analysis on the selected hypothesis, which permitted us to visualize patterns between the feeding behavior of consumers and resource traits in a reduced space. Since we assumed only qualitative variables, correspondence analysis preserved the X^2 distances within the selected contingency table. Thus, closer points within this reduced space represented higher matchings between consumer feeding behaviors and resource traits (Legendre & Legendre 2012).

All analyses were conducted in the R environment (R Core Team 2017). Model selection was conducted using the “MASS” package (Venables & Ripley 2002), and correspondence analysis was conducted using the “ca” package (Nenadic & Greenacre 2007).

Results

We found that all resource traits were related to the feeding behavior of the consumer. The AIC stepwise procedure indicated that removing any of the resource trait variables from the global additive model increased the model’s AIC, despite the fact that this model was more complex (Table 3).

However, compared to models that included interaction terms, the additive model had the highest AIC, and consequently, this model also had the least support (Table 4). In this case, we found that the best model was the most complex model, i.e., the model that assumed an interaction term between consumer feeding behavior and consumer metabolic group as well as interaction terms between all resource traits (Model 2.4 in Table 2). Given the complex interactions between the 36 trait-levels that we evaluated, the best model had 424 free parameters. Despite this model being five times more complex than the next best model (that had 76 free parameters), the ΔAIC was 1668.79. By comparison, the best model had a complexity that was 15 times higher than the complexity of the additive model, which had a ΔAIC of 40,987.25.

We performed correspondence analysis using the selected model to match consumer feeding behavior and resource traits in a lower-dimension plot. With two dimensions, our results preserved 57.2% of the multi-way contingency table variance (i.e., 29.7% and 27.5% for the first and second dimension, respectively). The third and fourth dimensions contributed 13.4% and 12.4%, respectively, for a total of 83% of the cumulative explained variance (Figure 1). Overall, the five dimensions accounted for 89.1% of the cumulative explained variance.

We also found consistent patterns between resource traits and consumer feeding behaviors. When considering only two dimensions, the most distinct association was between invertebrate parasitic behavior and terrestrial vertebrates. This feeding behavior did not distinguish between the category of ectotherms and endotherms or the biomass category. Further, we found matchings between consumers with herbivorous, detritivorous and bacterivorous feeding behaviors, and between consumers and detritus, bacteria, and photoautotroph resources with lower biomass. Interestingly, however, was the predominance of aquatic habitats, both marine and freshwater, in these matchings, and the fact that consumers were all in the invertebrate and bacteria metabolic groups. Indeed, we found that ectothermic vertebrates with herbivorous and detritivorous feeding behaviors were in this same axis and were associated with lower biomass invertebrates and detritus from aquatic ecosystems. However, these consumers had lower associations with the resources of the invertebrate consumers described above, suggesting a more specific matching between these consumers and their resources. The remaining matchings, at the center of both axes, had indistinguishable patterns in terms of these two dimensions. These included predators (both invertebrates and vertebrates, and, within the latter, both endotherms and ectotherms), omnivores, parasitoids and parasitic fungi. Since the selected model had interaction terms between all traits, we could not isolate the levels of traits into separate groups, such as habitats, metabolic groups or biomass categories, which suggested a general matching pattern between consumers and resources (Figure 2).

Discussion

When evaluating different hypotheses for the dependency structures of the contingency table between consumer feeding behaviors and resource traits, we found the most support for the most complex hypothesis, which encompassed over 400 matchings. This hypothesis depicted consumer feeding behavior as being dependent from its metabolic group; additionally, it found complex links between consumer feeding behaviors and their resource traits, i.e., the metabolic group, habitat and biomass categories. This identified general matching patterns that did not differentiate specific groups, such as specific patterns for different habitats. We deconstructed this complex structure into fewer dimensions and found that the first dimension accounted for 30% of the trait matching information, while the inclusion of two dimensions further accounted for 57% of the information. Still, many matching patterns were indistinguishable using two dimensions, and only five dimensions accounted for nearly 90% of the information. These results support previous findings that concluded that the use of few dimensions were able to reproduce empirical patterns (Eklöf *et al.* 2013); however, the results also suggested that including more traits and further increasing the complexity of the dependency hypothesis, would result in even more complex structures.

Traits shape ecological communities and provide better inferences about ecosystem functioning. Computing every pairwise trophic interaction in a large community requires extensive sampling effort, and consistency is conditioned based on the objectives of the study, the levels of taxonomic detail or the assembling criteria (Cohen *et al.* 1993). In fact, given the possible number of combinations, many interactions are usually inferred from functional traits, geographical distributions, and phylogenies (Morales-Castilla *et al.* 2015). Further, many studies merge species with the same consumers and resources to compute *trophic species*, which subject the results to small inference errors (Cohen & Briand 1984; Martinez 1991; Sander *et al.* 2015). Food webs are more than their predation matrices, and efforts to compute species traits and biological backgrounds may enable future studies to better infer general patterns (Spitz *et al.* 2014; Gravel *et al.* 2016). Addressing species traits reduces data to a diverse set of ecological functions, which enables studies to infer ecological generality in observed patterns and permits comparisons at larger scales, both in space and time, despite taxonomic differences, variations in ecological conditions and differences in species abundance (McGill *et al.* 2006; Dray & Legendre 2008; Poisot *et al.* 2015).

In this method, fourth-corner analysis provides tools to evaluate matching patterns between consumers and resource traits, which, in turn, permit the development of inferences on ecological processes. Using fourth-corner analysis, Spitz *et al.* (2014) matched consumer-resource traits of a marine mammal community and found that physiological and morphological traits shaped consumer feeding behaviors. On the other hand, Tall *et al.* (2006) found resource partitioning patterns between benthic grazers that were feeding in different levels of the algal canopy.

For decades, studies in food web theory have modeled biological assumptions to predict consumer feeding behaviors (Williams & Martinez 2000, 2008; Stouffer *et al.* 2005; Williams *et al.* 2010). Specifically, recent models have addressed the multidimensionality in food web data, expanding analysis beyond a single dimension, and this approach portrays consumers and resource traits as hypothetical latent variables. The number of dimensions, however, are not always explicit, nor is the biological information behind the latent variables. Thus, in view of our results, we highlight three of these models and propose that the fourth-corner analysis could provide insights into their underlying structure.

Allesina & Pascual (2009) proposed a model based on the ubiquitous biological concept of classifying species into groups. In this model, the number of groups and the membership of each species is computed using a parsimonious solution in a heuristic search that optimizes the within-group and between-group consumption probabilities. Nevertheless, the authors inquire about the biological interpretation found by the optimal solution. Based on our results, we support that the final classification reflects the complex patterns found in trait matching; consequently, higher probabilities are computed for traits with closer matchings, and lower probabilities are computed for traits with distant matchings. For example, when inferring from two dimensions, the optimal solution could produce higher probabilities for invertebrate parasitic consumers that feed on terrestrial vertebrates or for invertebrate herbivorous-detritivorous consumers that feed on basal aquatic resources; in contrast, lower probabilities should be produced for invertebrate predators that feed on basal aquatic species.

Alternatively, Rohr *et al.* (2010) proposed a model that starts from the premise of log differences in body sizes existing between consumers and resources, and the authors model the unexplained residuals with latent variables, reducing the multidimensional matching patterns between consumer feeding behaviors and resource traits into fewer dimensions. The authors found that the first dimension (e.g., optimal body size ratios) predicted between 3% and 46% of the trophic interactions, but the model prediction ability increased to 93% after the addition of two latent variables. The authors termed these latent variables as foraging and vulnerability traits and assumed these traits reproduced similarities between species in their roles as consumers and resources. However, this interpretation of these latent variables is not straightforward, and the authors evaluated three assumptions related to the biological information contained within them. The results demonstrated that, in most food webs, the latent variables were more related to phylogeny than to trophic structure or the residuals of the first dimension (Rohr *et al.* 2010). In comparison, our results suggested these latent variables were, in fact, composed by multiple traits, with complex associations between them (though we did not evaluate the role of phylogeny). Further, this model relied on dimension reduction analysis, and, in this way, fourth-corner analysis could be used to directly evaluate different hypotheses for the biological interpretation of the latent variables since fourth-corner analysis preserves the X^2 distances between traits and calculates higher matchings between consumers and resources.

Finally, Rohr *et al.* (2016) recently proposed a general model for network structure based on latent variables, and this model evaluated the centrality of a species to a certain trait as well as the matchings between traits. The more closely two traits matched, the higher the interaction probability between a consumer and a resource encompassing those traits. Further, as the centrality of species to the trait increased, the species-specific probability of interaction also increased. The parameters and latent trait values for each species were modeled using heuristic approaches (Rohr *et al.* 2016) but can be acquired through experiments (Brousseau *et al.* 2017). In this context, we propose our findings as a third approach for a general and biologically feasible parametrization method; additionally, our method permits testing different *a priori* dependency hypotheses for consumers and resource traits.

We computed contingency tables by counting the number of interactions between consumers and resource traits; as a result, our analyses only considered binary predation matrices. Many studies, however, have stressed the importance of interaction strengths in shaping natural communities and have demonstrated that the results from weighted food webs may differ from their binary counterparts (Bersier *et al.* 2002; Scotti *et al.* 2009; Jacquet *et al.* 2016). Thus, future studies should evaluate how interaction strengths influence trait-matching patterns between consumers and resources, and these studies should evaluate the implications related to these modeling procedures.

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Tables

Table 1: Consumer and resource traits and the respective levels used for formulating dependency hypotheses on the structure of the multi-way table between consumer feeding behaviors and resource traits.

Trait	Levels
Consumer Feeding Behavior	Bacterivorous, Detritivorous, Herbivorous, Omnivorous, Parasitic, Parasitoid, Predator
Consumer Group	Ectotherm Vertebrate, Endotherm Vertebrate, Heterotrophic Bacteria, Heterotrophic Fungi, Invertebrate
Resource Group	Detritus, Ectotherm Vertebrate, Endotherm Vertebrate, Heterotrophic Bacteria, Invertebrate, Photoautotroph
Resource Habitat	Freshwater, Limnic, Marine, Soil, Terrestrial
Resource Biomass Category	B1, B2, B3, B4, B5, B6, B7, B8, B9, B10, B11, B12, B13

Table 2: Dependency hypotheses for the structure of the multi-way table between consumer feeding behaviors and resource traits, assuming all resource traits. Freq is the frequency of interactions between traits, Cs is the strategy of the consumer, Cg is the metabolic group of the consumer, Rg is the resource metabolic group, Rh is the habitat of the resource, and Rb is the biomass category of the resource.

Model	Variables
m1.1	Freq ~ Cs + Rg: Rh + Rb
m1.2	Freq ~ Cs + Rg + Rh: Rb
m1.3	Freq ~ Cs + Rh + Rg: Rb
m1.4	Freq ~ Cs + Rg: Rh: Rb
m2.1	Freq ~ Cs: Cg + Rg: Rh + Rb
m2.2	Freq ~ Cs: Cg + Rg + Rh: Rb
m2.3	Freq ~ Cs: Cg + Rh + Rg: Rb
m2.4	Freq ~ Cs: Cg + Rg: Rh: Rb

Table 3: Variable selection through an AIC stepwise procedure for the resource traits that are related to the consumer feeding behaviors in a dependency structure of trait matching. Freq is the frequency of interactions between traits, Cs is the strategy of the, Cg is the metabolic group of the consumer, Rg is the metabolic group of the resource, Rh is the habitat of the resource, and Rb is the biomass category of the resource. $\mathscr{L}$ is the log likelihood, and δ is the number of free parameters.

Variables	$\mathscr{L}$	δ	**AIC**	**ΔAIC**
Freq ~ Cs + Rg + Rh + Rb	57,694.72	28	57,750.72	0.00
Freq ~ Cs + Rg + Rh	83,783.12	24	83,831.12	26,080.40
Freq ~ Cs + Rg + Rb	100,246.80	23	100,292.80	42,542.08
Freq ~ Cs + Rh + Rb	135,675.02	16	135,707.02	77,956.30

Table 4: Results for the dependency structure of the multi-way table between consumer feeding behaviors and resource traits. Model specifications can be found in Table 2. $\mathscr{L}$ is the log likelihood, and δ is the number of free parameters.

	$\mathscr{L}$	δ	**AIC**	**ΔAIC**
m2.4	15,915.47	424	16,763.47	0.00
m2.1	18,280.26	76	18,432.26	1668.79
m2.3	22,073.45	116	22,305.45	5541.97
m2.2	23,348.08	104	23,556.08	6792.61
m1.4	49,578.08	396	50,370.08	33,606.61
m1.1	51,942.87	48	52,038.87	35,275.40
m1.3	55,736.05	88	55,912.05	39,148.58
m1.2	57,010.69	76	57,162.69	40,399.22
m0	57,694.72	28	57,750.72	40,987.25

Figures

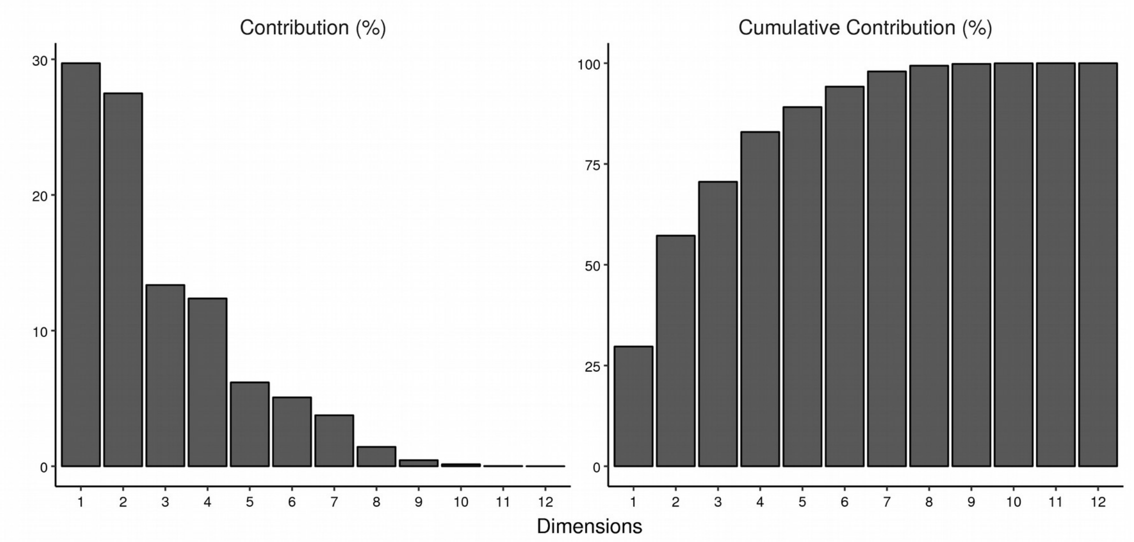

Figure 1: Contribution and cumulative contribution of each dimension in correspondence analysis for reducing the dimensions of the best model depicting the dependency structure of the multi-way table between consumer feeding behaviors and resource traits.

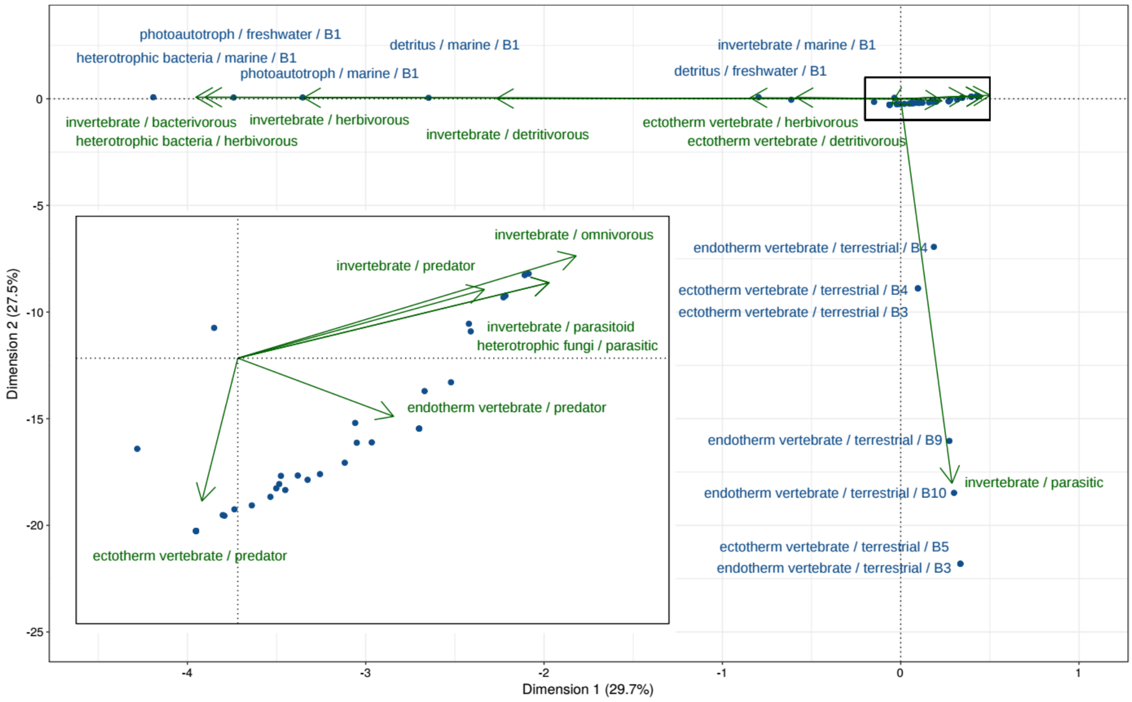

Figure 2: Correspondence analysis for reducing the dimensions of the best model for the dependency structure of the multi-way table between consumer feeding behaviors (red arrows) and resource traits (blue points). Closer points indicate higher matching. The huddled points in the intersection region are detailed in the plot on the bottom left.

APÊNDICE A

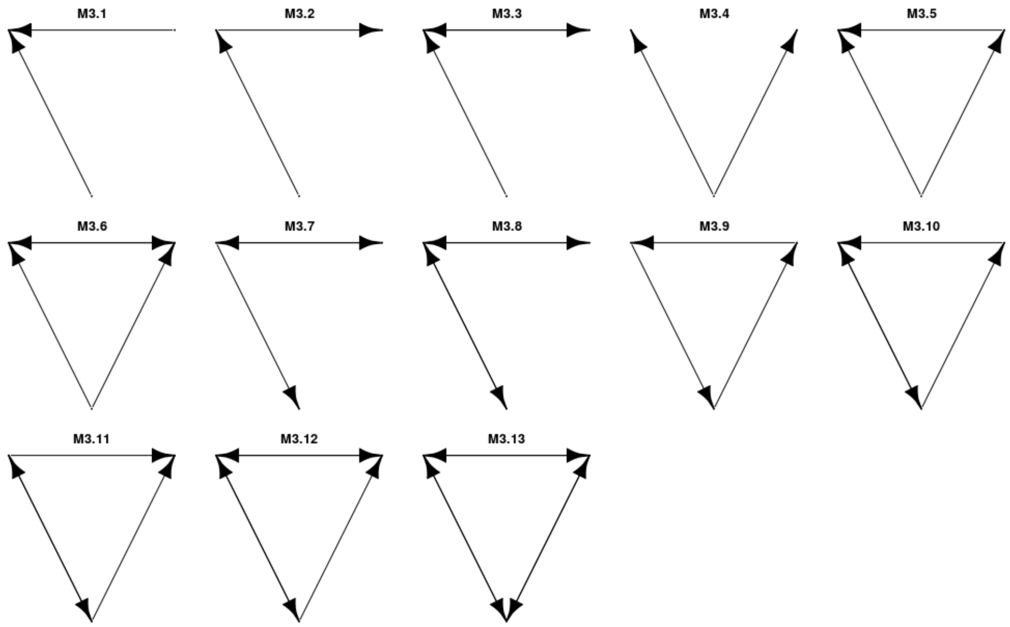

Figure A1: three-species modules arrangements.

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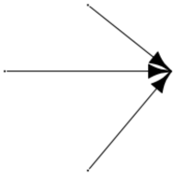

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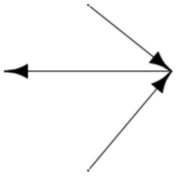

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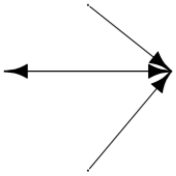

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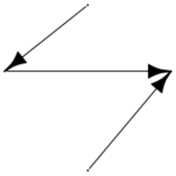

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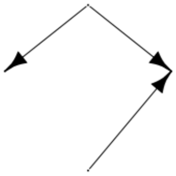

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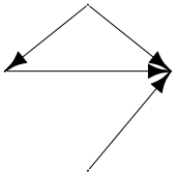

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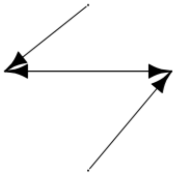

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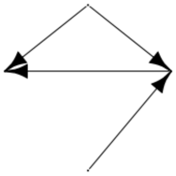

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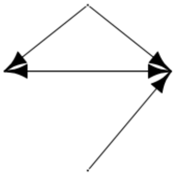

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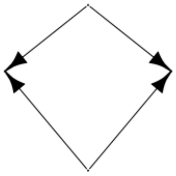

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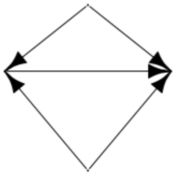

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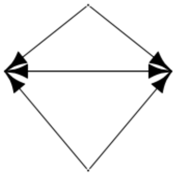

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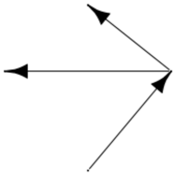

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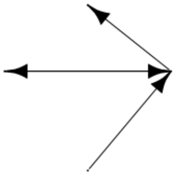

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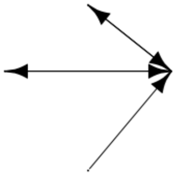

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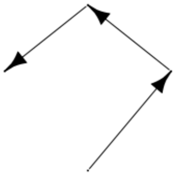

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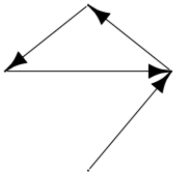

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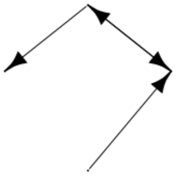

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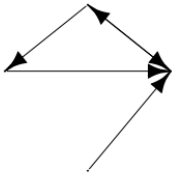

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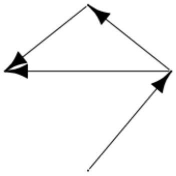

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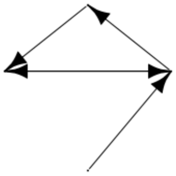

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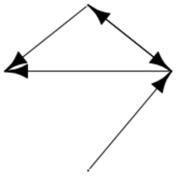

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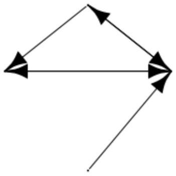

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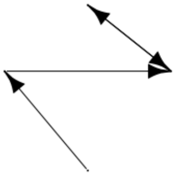

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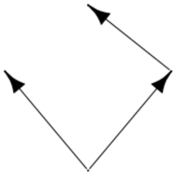

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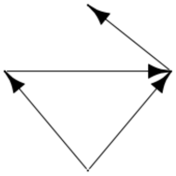

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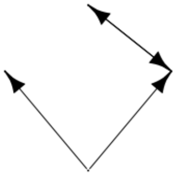

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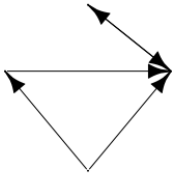

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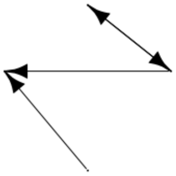

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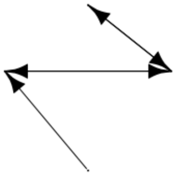

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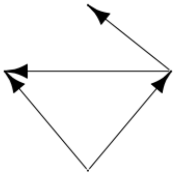

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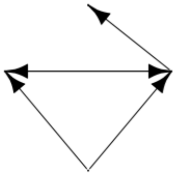

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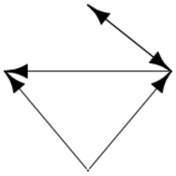

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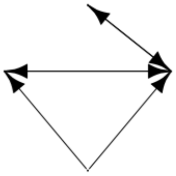

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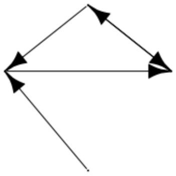

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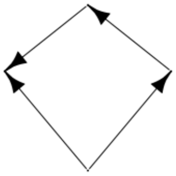

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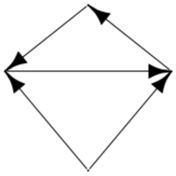

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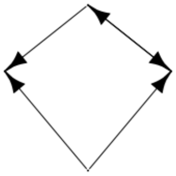

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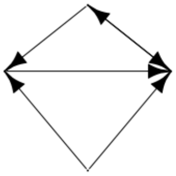

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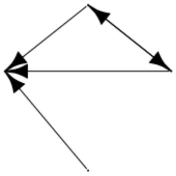

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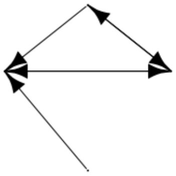

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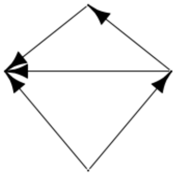

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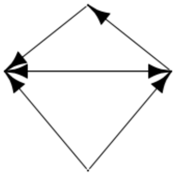

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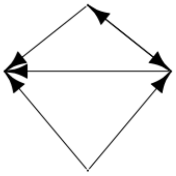

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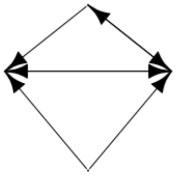

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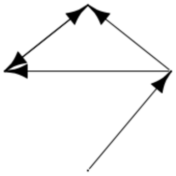

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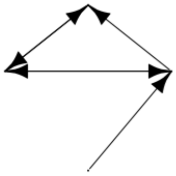

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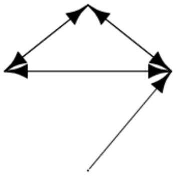

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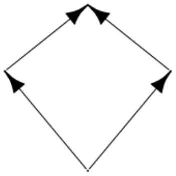

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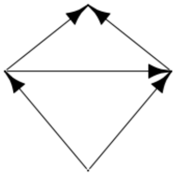

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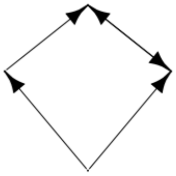

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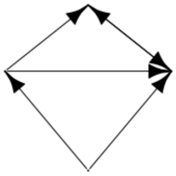

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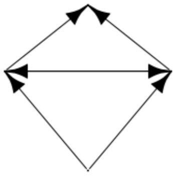

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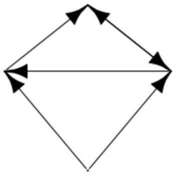

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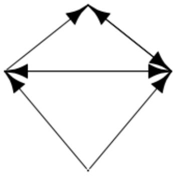

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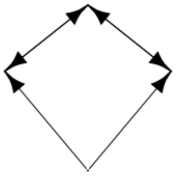

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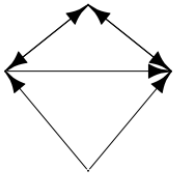

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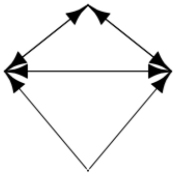

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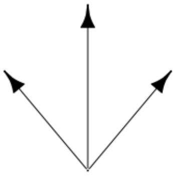

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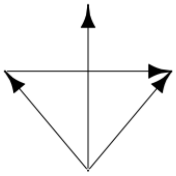

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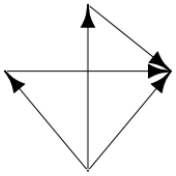

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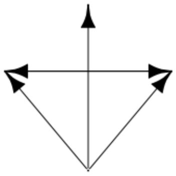

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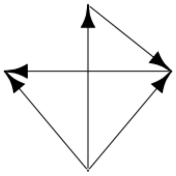

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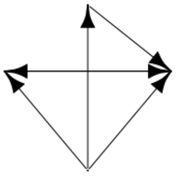

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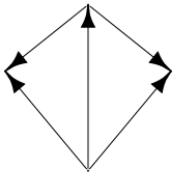

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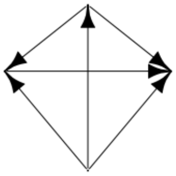

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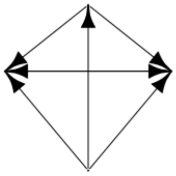

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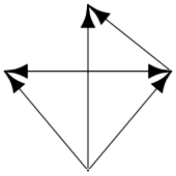

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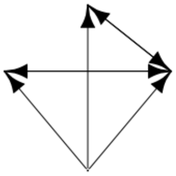

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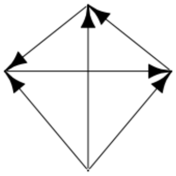

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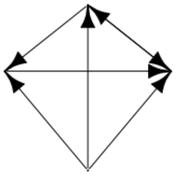

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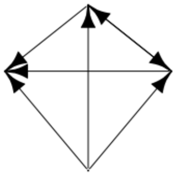

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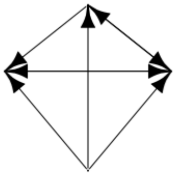

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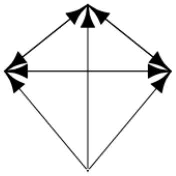

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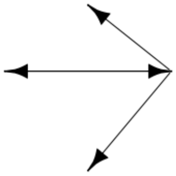

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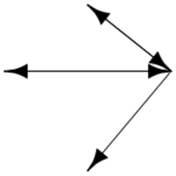

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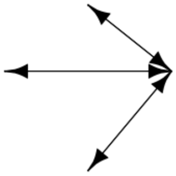

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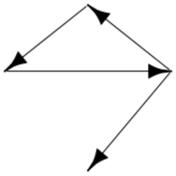

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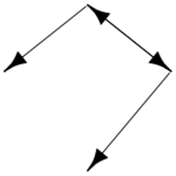

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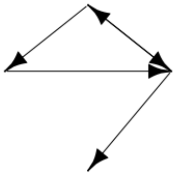

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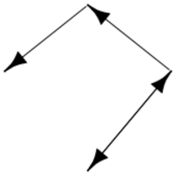

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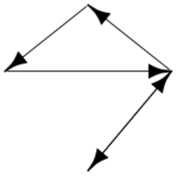

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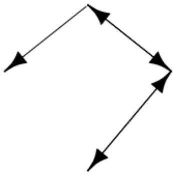

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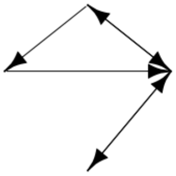

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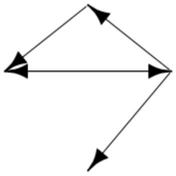

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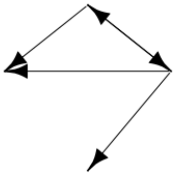

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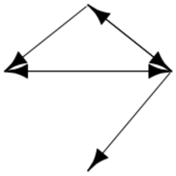

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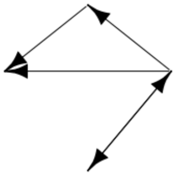

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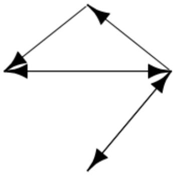

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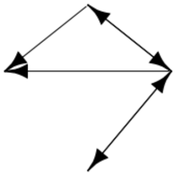

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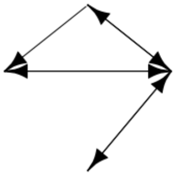

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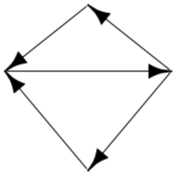

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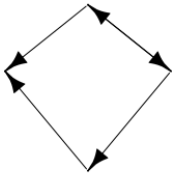

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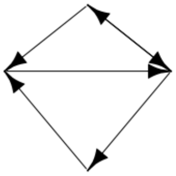

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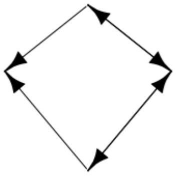

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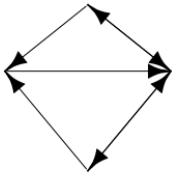

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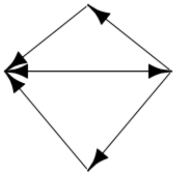

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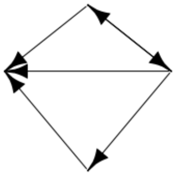

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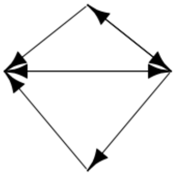

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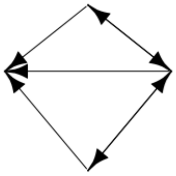

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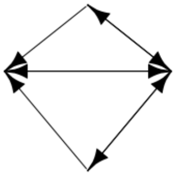

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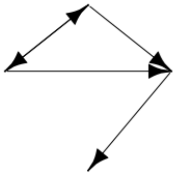

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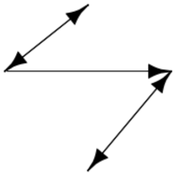

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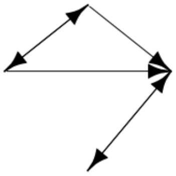

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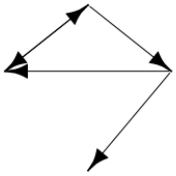

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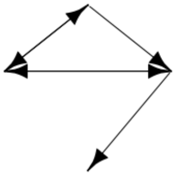

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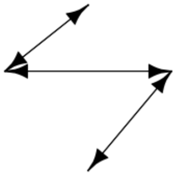

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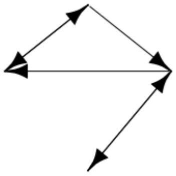

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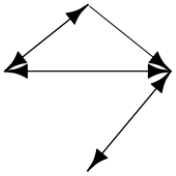

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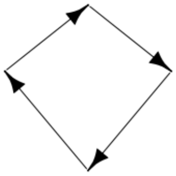

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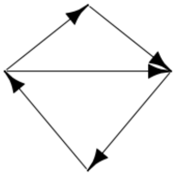

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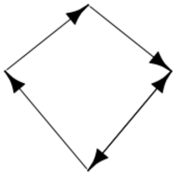

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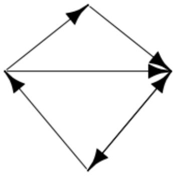

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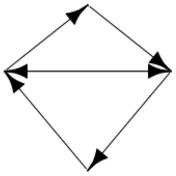

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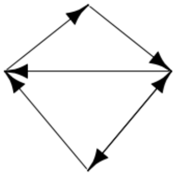

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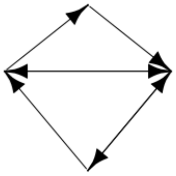

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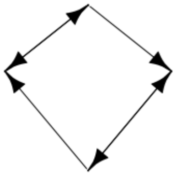

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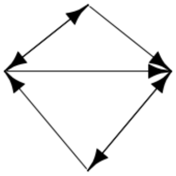

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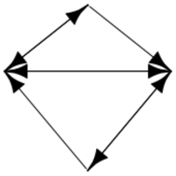

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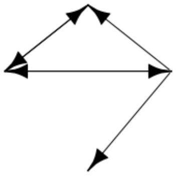

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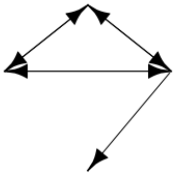

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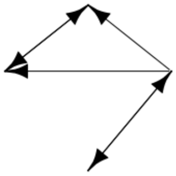

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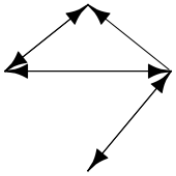

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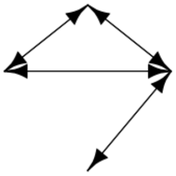

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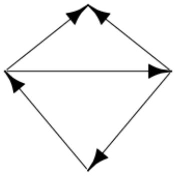

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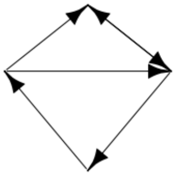

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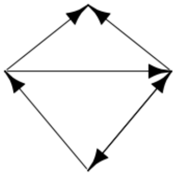

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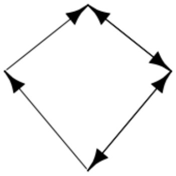

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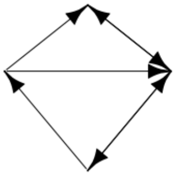

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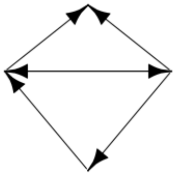

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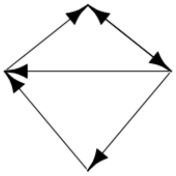

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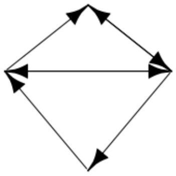

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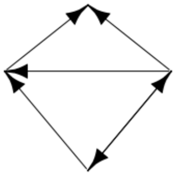

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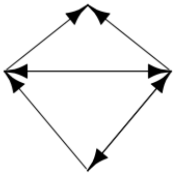

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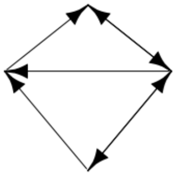

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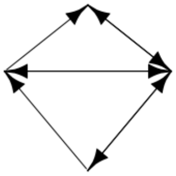

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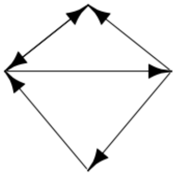

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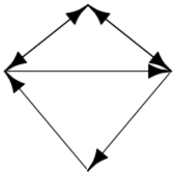

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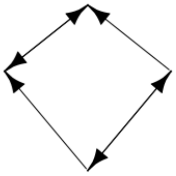

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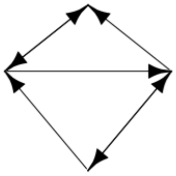

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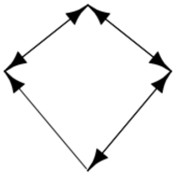

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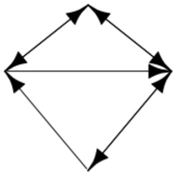

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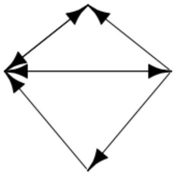

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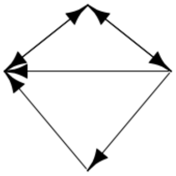

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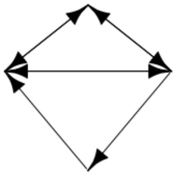

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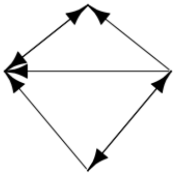

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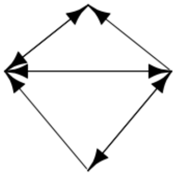

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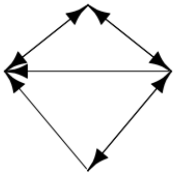

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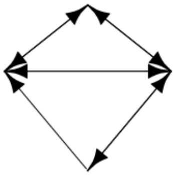

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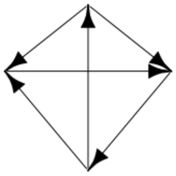

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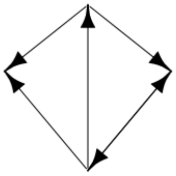

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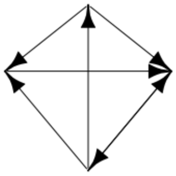

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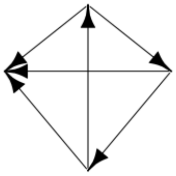

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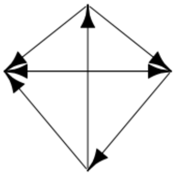

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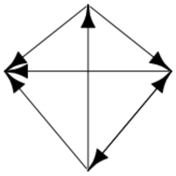

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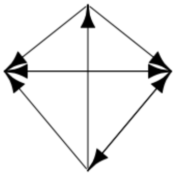

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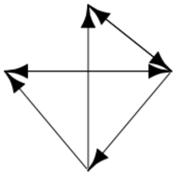

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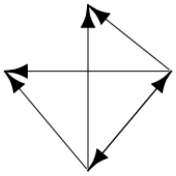

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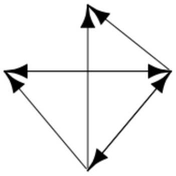

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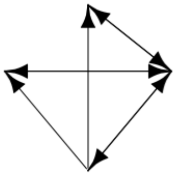

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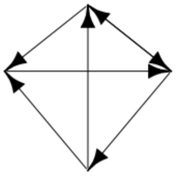

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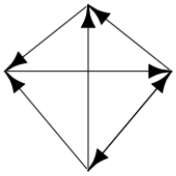

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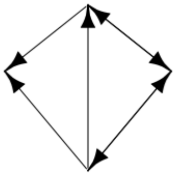

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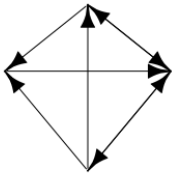

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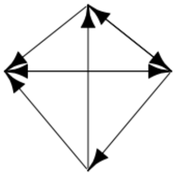

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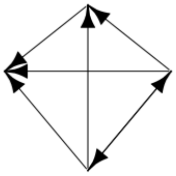

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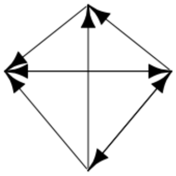

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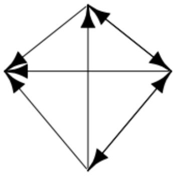

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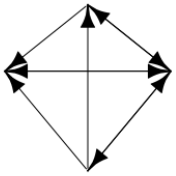

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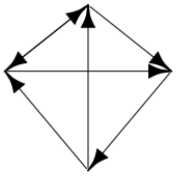

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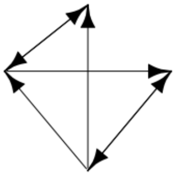

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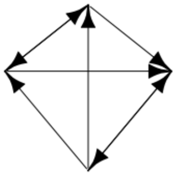

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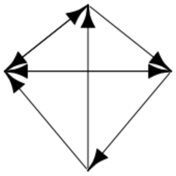

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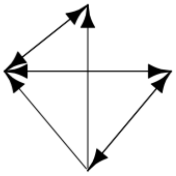

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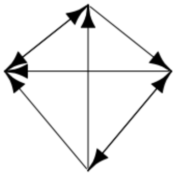

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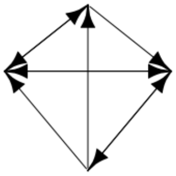

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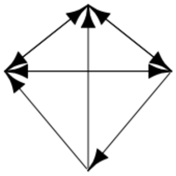

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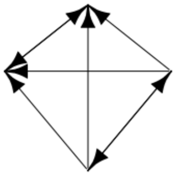

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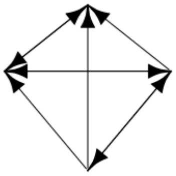

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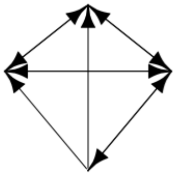

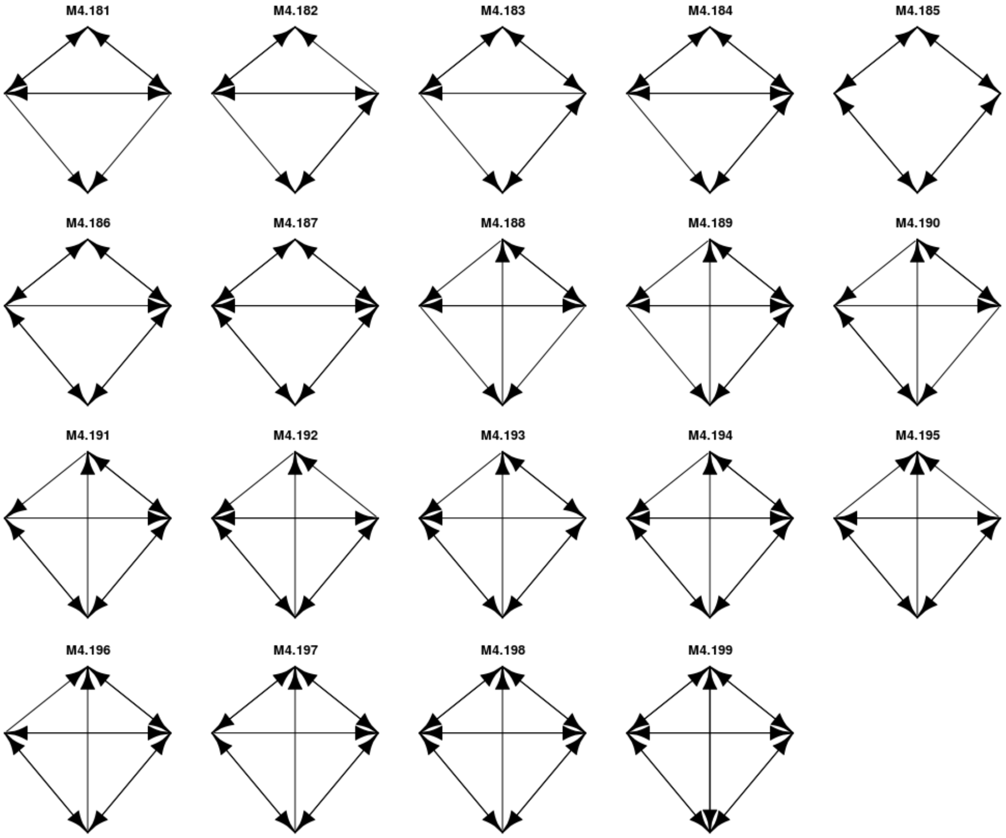

Figure A2: four-species modules arrangements.