

LETTER

Understanding food-web persistence from local to global scales

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Abstract

Understanding food-web persistence is an important long-term objective of ecology because of its relevance in maintaining biodiversity. To date, many dynamic studies of food-web behaviour—both empirical and theoretical—have focused on smaller sub-webs, called trophic modules, because these modules are more tractable experimentally and analytically than whole food webs. The question remains to what degree studies of trophic modules are relevant to infer the persistence of entire food webs. Four trophic modules have received particular attention in the literature: tri-trophic food chains, omnivory, exploitative competition, and apparent competition. Here, we integrate analysis of these modules' dynamics in isolation with those of whole food webs to directly assess the appropriateness of scaling from modules to food webs. We find that there is not a direct, one-to-one, relationship between the relative persistence of modules in isolation and their effect on persistence of an entire food web. Nevertheless, we observe that those modules which are most commonly found in empirical food webs are those that confer the greatest community persistence. As a consequence, we demonstrate that there may be significant dynamic justifications for empirically-observed food-web structure.

Keywords

Apparent competition, dynamics, ecological networks, exploitative competition, food chain, network motif, omnivory, trophic module.

Ecology Letters (2010) 13: 154–161

INTRODUCTION

Food webs, the network of who-eats-whom in an ecosystem, provide a representation with which to explore important problems in community ecology (Cohen *et al.* 1990; Pimm 2002; Pascual & Dunne 2006). If we wish to understand the effects of threats facing the environment, such as habitat destruction or invasive species, it is essential that we improve our understanding of how food-web structure affects stability or species persistence (May 1973). Because of the complexity of empirical food webs, many dynamic studies of food-web behaviour—both empirical and theoretical—have concentrated on the smaller scale of trophic modules (Holt 1997; McCann *et al.* 1998; Emmerson & Yearsley 2004; Bascompte *et al.* 2005; Otto *et al.* 2007).

Four trophic modules have received particular attention in the literature (Fig. 1a): tri-trophic food chains (Hastings & Powell 1991; McCann & Yodzis 1994), omnivory (Kuijper *et al.* 2003; Tanabe & Namba 2005; Vandermeer 2006; Namba *et al.* 2008), exploitative competition (Holt *et al.*

1994; Huisman & Weissing 2001), and apparent competition (Holt *et al.* 1994; Grover & Holt 1998). Theoretically, scientists have examined these modules and uncovered the role of omnivory (McCann & Hastings 1997), the stabilizing effect of weak links (McCann *et al.* 1998), and the effect of predator–prey body-mass ratios (Otto *et al.* 2007). Empirically, it has been shown that the influence of the pattern and strength of interactions on coexistence of competitors is greater than that of spatial processes (Amarasekare 2000). Moreover, it has been observed that apparent competition may be important in structuring larger ecological communities (Bonsall & Hassell 1997; Morris *et al.* 2004).

Dynamic studies of trophic modules, however, leave open the question of which modules actually compose empirical food webs. To address this question, scientists have investigated the three-species trophic modules that make up complex food webs and can be viewed as their simple building blocks (Milo *et al.* 2002; Arim & Marquet 2004; Bascompte & Melián 2005; Camacho *et al.* 2007; Stouffer *et al.* 2007). Such studies provide an indication of

the modules that are structurally over/under-represented within empirical food webs; for example, tri-trophic food chains and omnivory modules appear more frequently than expected by chance and exploitative competition and apparent competition modules less frequently than expected by chance (Stouffer *et al.* 2007). Nonetheless, these studies have heretofore been unable to address if there is a dynamic justification for why a particular module appears with greater or less frequency (Prill *et al.* 2005).

Importantly, many conclusions about food-web dynamics have been reached through investigations conducted exclusively at the reduced scale of an isolated module. We wish, however, to get insight into community-scale problems such as the collapse of global fisheries or the consequences of global change. This implies that we must test the assumption that modules' behaviour in isolation indeed predicts the properties of a larger system in which the modules are embedded.

In this manuscript, we study the dynamic properties of the above four modules in isolation and of entire food webs in order to address a fundamental question in the link between modules and whole food web studies. Namely, is a community persistent solely because it is composed of persistent sub-elements, or is a community persistent because of how the individual, and potentially less persistent, sub-elements come together and interact? Here we investigate three fundamental questions regarding the relationship between food-web structure and dynamics. (i) How do isolated modules differ in their long-term persistence? (ii) How does the frequency of different modules in a food web influence that food web's persistence? (iii) How does a module's effect on whole food-web persistence relate to its observed frequency in empirical food webs?

METHODS

We combine knowledge of food-web structure with a dynamic model of energy flow between species that provides time series of species abundances. Beyond the dynamic model's formulation, a few additional inputs are necessary: the number of species, the network of interactions between these species, species' body sizes, and interaction strengths. We assign each of these factors so that the modules and food webs are as ecologically realistic as possible. Importantly, our methodology ensures that both the modules in isolation or embedded within food webs are equivalently parametrized by utilizing the same methodology for each.

Bioenergetic model

We simulate the dynamics of species biomass over time and flow of energy through the food web with a multispecies consumer-resource model (Yodzis & Innes 1992). The

model is parametrized as in previous studies of both module (Bascompte *et al.* 2005; Otto *et al.* 2007) and food-web (Brose *et al.* 2006b; Williams 2008) dynamics. The change in biomass density B of species i is described by

$$\frac{dB_i}{dt} = r_i G_i B_i - x_i B_i + x_i B_i \sum_{j=\text{prey}} y_j F_{ij} - \sum_{k=\text{pred}} \frac{x_k y_k B_k F_{ki}}{e_{ki}}, \quad (1)$$

where r_i is the mass-specific maximum growth rate, G_i is normalized growth rate of the primary producer, F_{ij} is a type II functional response, x_i is the mass-specific metabolic rate, y_j is a species' maximum consumption rate relative to its metabolic rate, and e_{ij} is the fraction of the biomass of species j lost due to consumption by species i that is actually metabolized. Note that $x_i = 0$ for producer species and $G_i = 0$ for consumer species.

For the producer growth rates, we use a neutrally-stable Lotka–Volterra competition model defined as

$$G_i = 1 - \sum_{j=\text{prod}} \frac{B_j}{K}, \quad (2)$$

where K is the carrying capacity and the sum is over all producer species. Additional simulations (not reported here) demonstrate that the results presented here are qualitatively identical for different growth rate models, including those in which basal species do not interact or in which they interact competitively.

A type II functional response is defined as

$$F_{ij} = \frac{w_{ij} B_j}{B_0 + \sum_{k=\text{prey}} w_{ik} B_k}, \quad (3)$$

where w_{ij} is the relative inverse attack rate in a type II functional response, which can also be considered as the interaction strength of i consuming j , and B_0 is the half-saturation density. We use a type II functional response, which assumes that all species have the same handling time, because it has previously been shown that more complicated functional responses only introduce minor differences in this type of model system (Williams 2008).

The time scale of the system is defined by normalizing the mass-specific growth rate of basal species to unity. We similarly normalize x_i and y_j by the metabolic rates giving

$$r_i = 1 \quad (4)$$

$$x_i = \frac{a_x}{a_r} \left(\frac{M_i}{M_b} \right)^{-1/4} \quad (5)$$

$$y_j = \frac{a_y}{a_x}, \quad (6)$$

where a_r , a_x , and a_y are allometric constants and M_b is the body size of basal species (Brose *et al.* 2006b). The allometric scaling of each of these rates allows us to simplify

the system and avoid an overabundance of parameters (Brose *et al.* 2006b; Williams 2008). We use the following set of parameters: $e_{ij} = 0.85$; $K = 1$; $M_b = 1$; $a_r = 1$; $a_x = 0.2227$ and $a_y = 1.7816$ (all consumers are simulated as invertebrates).

All simulations start with random initial biomass densities B_i selected from a uniform distribution in the range [0.05, 1]. In the numerical integration, we use Hindmarsh's ODE solver LSODE (Radhakrishnan & Hindmarsh 1993). Species are considered extinct if their biomass $B \leq 10^{-30}$. Module simulations were run to 4000 module timesteps. Because of potentially longer transient behaviour, the whole food-web simulations were run to 10 000 model timesteps, but the reported patterns hold from 1000 timesteps onward. Note that running the model for a greater number of timesteps will lead to slightly lower persistence values because of additional extinctions which arise due to population fluctuations in the system, as noted in previous studies (Brose *et al.* 2006b; Williams 2008).

Model-generated food webs

We consider model-generated food webs with size $S = 50$ and average directed connectance $C \in \{0.10, 0.12, 0.14, 0.16, 0.18, 0.20\}$. Directed connectance is defined as $C = L/S^2$, where L is the number of interactions in the web. These directed connectances are consistent with values typically observed empirically (Pascual & Dunne 2006). To generate the food webs, we utilize the niche model (Williams & Martinez 2000) because it is a leading static food-web model that explains a large number of empirical food-web properties (Stouffer *et al.* 2005, 2006; Williams & Martinez 2008). Importantly, this includes module over/underrepresentation (Stouffer *et al.* 2007). Additional simulations (not reported here) suggest that the results presented here are qualitatively identical with larger food webs ($S = 100$).

To make our modules and food webs as empirically realistic as possible, we assign interaction strengths and species' body sizes (see below) to emulate the empirically observed distributions. We assign interaction strengths w_{ij} from a log-normal distribution (Wootton 1997; Bascompte *et al.* 2005) with log-mean $\mu = -3.0$ and log-standard deviation $\sigma = 1.5$. For each combination of S and C , we generate 250 different network structures and for each we run 125 different dynamic simulations which maintain the network structure but have randomly-assigned species' body masses and interaction strengths, for a total of 187 500 simulations.

Body-mass assignment algorithm

Rather than use fixed predator–prey body-mass ratios as in similar previous studies (e.g., Brose *et al.* 2006b; Otto *et al.* 2007; Williams 2008), we utilized a 'nested sampling

algorithm' (Sivia & Skilling 2006; Skilling 2006) to stochastically assign species' masses. The algorithm simultaneously draws species' masses such that the distribution of all predator–prey body-mass ratios in a food web emulates the empirically-observed distribution. The nested sampling algorithm is a Markov Chain Monte Carlo procedure used to generate random samples from an analytically intractable probability distribution, as in the case for the masses of many highly-interconnected species. For the predator–prey body-mass ratios, we use a best estimate log-normal distribution with log-mean $\mu = 6.1$ and log-standard deviation $\sigma = 5.75$, as observed empirically (Brose *et al.* 2006a; Otto *et al.* 2007). All basal species are set to have the same body size $M_b = 1$.

Counting the frequency of trophic modules in an entire food web

The number of modules within each food web are directly enumerated (Milo *et al.* 2002; Camacho *et al.* 2007; Stouffer *et al.* 2007). Each connected triplet of species within the network corresponds to one of 13 unique three-species modules (Milo *et al.* 2002; Camacho *et al.* 2007; Stouffer *et al.* 2007). The number of appearances N_i of module i is therefore the number of connected triplets whose pattern of interactions is the same as the module of interest. Importantly, the four modules we consider—tri-trophic food chains, omnivory, exploitative competition, and apparent competition—on average represent 95% of the three-species modules observed empirically (Camacho *et al.* 2007). Note that we can divide the number of appearances N_i of any module i into its basal and non-basal components N_i^b and N_i^{nb} (where $N_i^b + N_i^{nb} = N_i$), respectively, to assess if this distinction impacts the resulting influence on the persistence of whole food webs. For all whole food-web calculations, we consider the initial frequency of each module to determine how the initial structure and modules contribute to the web's persistence.

Measuring correlation between module frequency and whole food-web persistence

To measure the relationship between module frequency and whole food-web persistence, we perform a multivariate linear regression controlling for the frequency of all modules present in the food web and the interactions between them. While an average of 95% of the modules found in empirical and model food webs are the four that we focus our analysis upon, we include the sum total of frequencies of all other modules in our analysis to also control for this potentially confounding factor. There are thus five explanatory variables in our analysis, the number N_i of each of the tri-trophic chain, simple omnivory, apparent competition, and

exploitative competition modules as well as the number N_{other} of the nine other unique three-species modules.

The multivariate model takes the form

$$P_W = \mathcal{B} + \sum_{i=1}^4 c_i N_i + c_{\text{other}} N_{\text{other}}, \quad (7)$$

where P_W is the fractional persistence of the food web in the dynamic simulation, \mathcal{B} is a constant, the slopes c_i measure the influence of the different modules, the sum over i includes the four modules detailed in the manuscript, and c_{other} measures the influence of the other three-species modules. To visualize the magnitude and direction of the effect of an individual module j on overall persistence P_W , one can plot the partial residuals of the model given by eqn 7 against the number of modules N_j .

Module's propensity for multiple extinctions

Given the three species which make up a module—be they in isolation or embedded within a larger food web—we can directly calculate the number which have persisted throughout a dynamic simulation (out of the possibilities of 1, 2, or 3 species going extinct). A module's propensity to exhibit multiple extinctions, therefore, is equal to the fraction of modules in which either 2 or 3 species go extinct during the simulations. A propensity for such extinctions is important in food webs because of the potentially large perturbation they represent.

RESULTS

For modules in isolation, we measure community persistence P_M as the fraction of simulations in which all three species in the module persist over a given number of timesteps (Kondoh 2003). Modules exhibit a consistent decrease of persistence versus time, and differences between the modules' persistence can be observed within a few hundred model timesteps (Fig. 1b). The isolated modules are distinguished by both the rate of decrease of persistence and their asymptotically-approached persistence value. Because we are interested in long-term persistence, we focus upon asymptotic persistence which decreases from tri-trophic food chain to omnivory to apparent competition and lastly to exploitative competition (Fig. 1c).

Moving to whole food-webs, we measure persistence P_W as the fraction of species that persist after a specified number of timesteps (Brose *et al.* 2006b; Williams 2008). We compare the relationship between the persistence of a food web with the frequency of the modules of which the web is composed. We observe significant correlations between the persistence of whole food webs and the frequency of individual modules (Fig. 2). For the four modules studied in

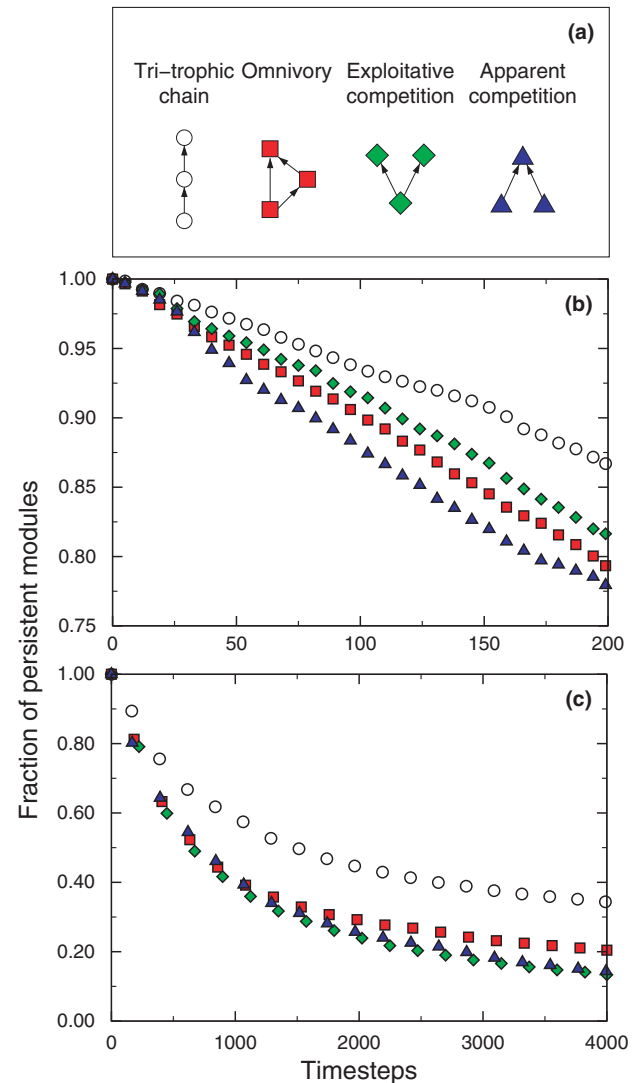


Figure 1 Persistence of trophic modules in isolation. (a) Modules analyzed: the tri-trophic food chain, omnivory, exploitative competition, and apparent competition. (b,c) The fraction of persistent modules as a function of the number of timesteps. Each module exhibits a consistent decrease of persistence across time. The differences between the modules can be observed within a few hundred timesteps, with modules distinguished by their rate of decrease (b). We also note that, at a larger number of timesteps, the modules appear to asymptotically approach unique values of long-term persistence (c). Notably, the tri-trophic food chain is the most persistent module at both short and long time-scales. Symbols and colours are the same in all panels.

isolation, we find positive partial correlations for the tri-trophic food chain and omnivory and negative partial correlations for exploitative competition and apparent competition ($P < 10^{-16}$ for all correlations).

We note that the modules in isolation are always 'grounded'—in that they are associated with basal producer

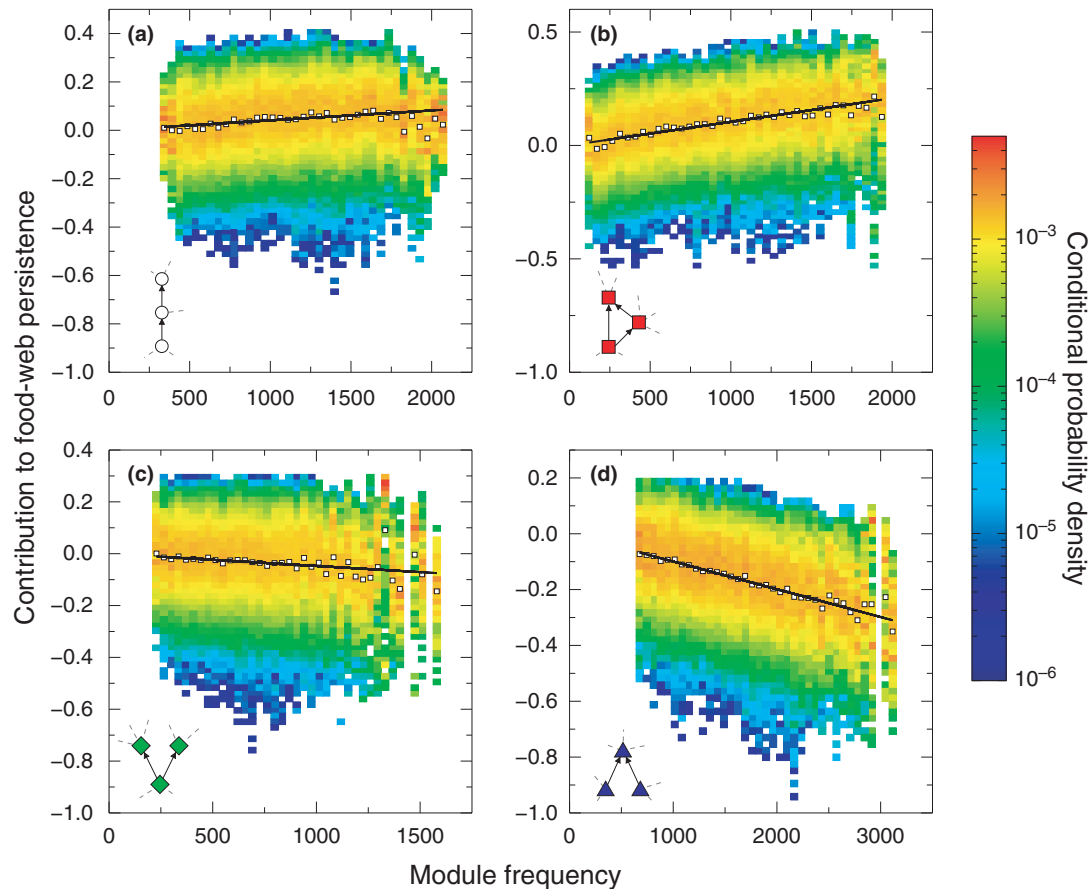


Figure 2 Relationship between module frequency and whole food-web persistence. (a) The tri-trophic food chain, (b) omnivory, (c) exploitative competition, and (d) apparent competition. On the x -axes we show the frequency of a module and on the y -axes the module's contribution to whole food-web persistence when statistically controlling for the effects of all others. A module's contribution to whole food-web persistence is equal to the partial residuals of the model given by eqn 7 and thus the fraction of overall persistence accounted for by that particular module. We show the conditional probability density of the module's contribution (scaled according to the colour bar at right), whereas the white squares are the average at a given level of module frequency. The black line represents the best-fit linear relationship. The frequencies of all modules are significantly correlated to whole food-web persistence ($P < 10^{-16}$).

species—whereas modules within the food web are ‘free-floating’—in that they need not include any basal species. The relationships we observe could, in theory, be a result of this distinction. To see if this is in fact the case, we repeated our analysis but considered the frequency of grounded and free-floating modules independently. While there are minor quantitative differences, the overall pattern holds; increased food-web persistence is most strongly correlated with greater frequency of omnivory modules followed by the tri-trophic food chain, exploitative competition, and apparent competition.

To better understand the mechanisms behind the differences we observe between persistence of modules in isolation and that of modules embedded within food webs, we analyze each module's propensity of multiple extinctions. Isolated tri-trophic food chain, omnivory, exploitative competition, and

apparent competition modules exhibit propensities of 0.63, 0.75, 0.73, and 0.99, respectively. Note that while the omnivory module is more persistent than the exploitative competition module, for example, it exhibits a greater chance of multiple extinctions. In contrast, embedded tri-trophic food chain, omnivory, exploitative competition, and apparent competition modules exhibit propensities of 0.41, 0.37, 0.48, and 0.40, respectively. It appears that relative vulnerability to multiple extinction events likely influences how the different modules contribute to whole food-web persistence.

As a step beyond our dynamic simulations, we examine how our results compare to the three-species modules that actually make up empirical food webs (Stouffer *et al.* 2007; Fig. 3). It has been observed that the tri-trophic food chain and omnivory are typically over-represented in empirical food webs (Bascombe & Melián 2005; Stouffer *et al.* 2007)

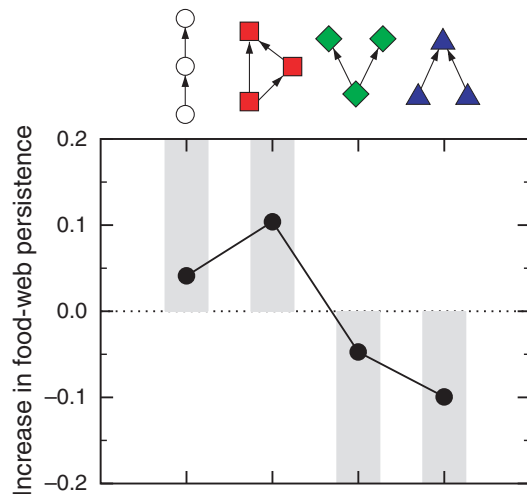


Figure 3 Relationship between modules' influence on food-web persistence and empirical module over/under-representation. The black circles show the expected increase in whole food-web persistence for a food web with 1000 additional modules of that particular type (*Methods*). This is equivalent to the slopes observed in Fig. 2. The gray bars represent the direction of structural over/under-representation observed in a majority of empirical food webs (Stouffer *et al.* 2007). There is clear visual agreement between the two.

while exploitative competition and apparent competition are typically under-represented (Stouffer *et al.* 2007). Upon comparing to our results, we observe a clear match with whether the frequency of a module is positively or negatively correlated with whole food-web persistence.

DISCUSSION

In our investigation of the relationship between food-web structure and food-web persistence, we observe clear relationships for both isolated modules and whole food webs. First, different module structures in isolation asymptotically approached unique values of long-term persistence (Fig. 1). Second, the frequency of different module structures in food webs are significantly associated with the persistence of entire food webs (Fig. 2).

Intriguingly, the modules which are most persistent in isolation are not necessarily those whose frequencies are most strongly associated with increases in whole food-web persistence. Based upon our analysis of isolated modules, one could reasonably expect to observe more tri-trophic food chains than the other three modules and more omnivory than apparent competition and exploitative competition. In contrast, we observe that having more omnivory modules has a greater positive effect on food-web persistence than having more tri-trophic food chains. It

seems apparent that the relationship between food-web structure and food-web persistence provides an excellent example where the whole is greater than the sum of its parts (May 1986; Johnson 2001).

The observed differences between the tri-trophic food chain and omnivory modules are noteworthy as they could explain some of the historical difficulty in reaching a definitive conclusion as to the effect of omnivory in food webs (McCann *et al.* 1998; Arim & Marquet 2004; Bascompte & Melián 2005; Vandermeer 2006; Stouffer *et al.* 2007). We confirm here that greater presence of omnivory is associated with greater food-web persistence (McCann *et al.* 1998). Additionally, note that the exploitative competition module is unstable in isolation due to competitive exclusion. Nevertheless, and surprisingly, this module is not the most negatively correlated with whole food-web persistence when embedded within the food web. Our results confirm that caution must be taken when assuming that one can directly scale up from the module, microcosm, or mesocosm scale to that of entire food webs (García-Domingo & Saldaña 2008; Kondoh 2008; Bascompte & Stouffer 2009).

It is possible that the higher persistence of the isolated tri-trophic food chain and omnivory modules is due to the fact that species on average occupy higher trophic levels and the extinction dynamics are thus slower. In the whole food web simulations, we likewise observe that webs with higher average trophic level also exhibit greater persistence. This implies that, if the objective was to maximize long-term persistence, a community would be better off having longer food chains as opposed to few, denser trophic levels. Depending on where they enter the community, this carries important implications for the potential effects of species invasions.

We recognize that there was no guarantee of uncovering significant patterns if they would only have been observed for more complicated modules composed of greater than three species (for reference, there are 199 and 9364 unique modules for four and five species, respectively). However, the fact that we have identified significant relationships between three-species modules and whole food-web persistence necessarily implies the existence of significant patterns at greater, more meso-scale, levels of combinations of modules.

Previous studies of food-web structure concluded that there is a conserved profile of module over/under-representation across a diverse set of empirical food webs (Camacho *et al.* 2007; Stouffer *et al.* 2007). Given our study, the deviations observed across communities may have important ecological implications. For example, some empirical food webs exhibited fewer than expected instances of omnivory and greater than expected exploitative competition and apparent competition (Stouffer *et al.*

2007). We would hypothesize that these empirical food webs consequently have reduced long-term persistence. It would be intriguing to examine if this decrease in long-term persistence is associated with an increase in short-term robustness and relates to some common feature among these food webs.

On the basis of empirical food-web structure, the interactions in which species partake appear to be those which maximize the persistence of the entire community as opposed to those which might ensure greater individual species persistence (Fig. 3). Generalizing, our findings imply that there may be significant dynamic justifications for empirically-observed food-web structure. It will be very interesting to expand upon our results to better address the question of causality in the relationships identified. Specifically, as an empirical community changes over time, are interactions and therefore modules reorganized such that those modules that remain enhance food-web persistence and stability? Conversely, if interactions in an empirical food web were dynamically rearranged in order to maximize whole food-web persistence, how would the resulting web compare to the original, empirically-observed, structures?

We show here the importance of local patterns of interactions on the persistence and maintenance of biodiversity in entire food webs. Studies such as this are critical, as we currently face grave threats to biodiversity and all associated ecosystem services (Dobson *et al.* 2006). From our results, it is possible to determine how specific species extinctions would affect persistence of empirical systems based solely upon those modules in which a species participates. If species are heterogeneously distributed across modules, some species will be found more frequently within modules that tend to make the web more persistent. Loss of these species would change both the food-web structure, and as we show here, its ability to persist. Performing such an assessment empirically could serve as a novel means to identify an ecosystem's keystone species (Paine 1969), or even keystone combinations of species' interactions, and also how best to consolidate efforts for species management and biodiversity maintenance.

ACKNOWLEDGEMENTS

We thank L.-F. Bersier, P.M. Buston, J. Dunne, M.A. Fortuna, L.J. Gilarranz, R. Guimerà, R.D. Holt, P. Jordano, M. Kondoh, A. Krishna, J. Lavabre, R.D. Malmgren, K.S. McCann, O. Petchey, F. Reed-Tsochas, and S. Saavedra for providing comments and suggestions on the manuscript. DBS acknowledges the support of a CSIC-JAE Postdoctoral Fellowship. JB acknowledges the European Heads of Research Councils, the European Science Foundation, and the EC Sixth Framework Programme through a EURYI (European Young Investigator) Award. We are thankful to

the Centro de Supercomputación de Galicia (CESGA) for computing facilities. All figures were generated with PyGrace (<http://pygrace.sourceforge.net>).

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Editor, Marcel Holyoak

Manuscript received 8 July 2009

First decision made 1 August 2009

Second decision made 5 October 2009

Manuscript accepted 13 October 2009