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Food web modularity and biodiversity promote species persistence in polluted environments

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Pollution represents a major threat to biodiversity. A wide class of pollutants tends to accumulate within organisms and propagate within communities via trophic interactions. Thus the final effects of accumulable pollutants may be determined by the structure of food webs and not only by the susceptibility of their constituent species. Species within real food webs are typically arranged into modules, which have been proposed to be determinants of network stability. In this study we evaluate the effect of network modularity and species richness on long-term species persistence in communities perturbed by pollutant stress. We built model food webs with different levels of modularity and used a bioenergetic model to project the dynamics of species. Further, we modeled the dynamics of bioaccumulated and environmental pollutants. We found that modularity promoted the stability of food webs subjected to pollutant stress. We also found that richer food webs were more robust at all modularity levels. Nevertheless, modularity did not promote stability of communities facing a perturbation that shared most features with the pollutant perturbation, but does not spread through trophic interactions. The positive effect of both modularity and species richness on species persistence was cancelled and even reversed when the structure of food web departed from a realistic body size distribution or a hierarchical feeding structure. Our results support the idea that modularity implies important dynamic consequences for communities facing pollution, highlighting a main role of network structure on ecosystem stability.

The distribution of trophic interactions determines the structure of food webs as well as their stability and the persistence of their constituent species (Thébault and Fontaine 2010, McCann 2012). Several structural attributes of food webs have been suggested as important determinants of their stability, such as the frequency of modules of omnivory (McCann and Hastings 1997) and their location within the network (Kondoh 2008), food chain length (Pimm and Lawton 1977, Sterner et al. 1997), nestedness (Thébault and Fontaine 2010), allometric degree distributions (Otto et al. 2007) and modularity (Pimm and Lawton 1980, Milo et al. 2002, Melián and Bascompte 2002, Krause et al. 2003, Ruiz-Moreno et al. 2006). Modularity refers to the tendency of a group of species to have more mutual interactions than with other species in the food web (Rezende et al. 2009). This food web property has long been proposed as a determinant of stability (May 1972), and only recently have suitable algorithms been developed to confirm the ubiquity of modules in real communities (Krause et al. 2003, Olesen et al. 2007, Allesina and Pascual 2009, Rezende et al. 2009, Guimerà et al. 2010, Ramos-Jiliberto et al. 2010). However, the dynamical consequences of modularity have been not clearly established, because conflicting results suggested that its role in network stability depends on the type of perturbation at hand as well as on the measure of stability used (e.g. species persistence versus community resilience, Thébault and Fontaine 2010). It has been suggested that modularity may confer stability to complex ecological networks against perturbations (May 1972, Ruiz-Moreno et al. 2006) by confining the effects of disturbances within modules (Stouffer and Bascompte 2011). Nevertheless, Stouffer and Bascompte (2011) evaluated the relationship between modularity and stability in food webs subjected to a special kind of perturbation: the primary extinction of a single species. In the wild, ecological systems are frequently facing disturbances of different natures and modes of action. Little is known about the relationship between structure and dynamics of food webs experiencing perturbations such as pollution, which currently represents one of the major threats to biodiversity (MEA 2005). Pollution affects several interacting species simultaneously. In addition, a wide group of pollutants, including many pesticides, industrial byproducts and heavy metals have the potential to accumulate within the tissues of organisms (Newman and Clements 2008). Organisms take these pollutants directly from the medium (typically water) as well as from their food (Kooi et al. 2008). As a consequence, pollutants can be transmitted and propagated through the web of trophic interactions. Most if not all ecosystems around the globe are in some degree affected by pollutants (Groom et al. 2006). The lack of a robust theoretical framework about the effect of pollutants on food web dynamics and stability represents a main limitation of ecological theory, which should be addressed urgently.

There are two parallel ways by which the structure of food web connections among species could determine the effect of pollution on community dynamics. First, pollutants are transmitted through trophic interactions, being accumulated by consumers which are directly injured. Secondly, well-known indirect effects take place after injured species change their abundance or phenotypic traits which could directly or indirectly affect the fitness of their connected, albeit unpolluted, coexisting populations. While the latter mechanism is common to all perturbed communities, the former may take place when the stressor itself is propagated through the trophic interactions, as is the case of pollution or parasite-mediated diseases (Lafferty et al. 2008). For this reason, exposure to a pollutant of only a small subset of the species in the community may lead to noticeable effects on community dynamics.

Modularity has the potential to limit the propagation of both pollutants and their indirect effects through the food web. This effect should be more pronounced in smaller communities, since community size per se slows the propagation of effects to the entire system. This is expected because as community size increases, the number of steps for an effect to be propagated between two distant species also increases. In addition, species richness is directly connected with the structure of the whole food web (Dunne et al. 2002, McCann 2012), potentially interacting with the role of modularity on the stability of communities. Therefore, in this study we evaluate the effects of modularity and species richness on the persistence of species in model food webs subjected to stress exerted by an accumulable pollutant.

Methods

Food webs were generated by means of the generalized niche model (GNM; Stouffer et al. 2006). This algorithm has connectance, species richness and diet contiguity as input parameters. We built a set of 1500 model food webs with connectance 0.25, three levels of species richness and five levels of network modularity. We defined connectance as directed connectance (i.e. the quotient between the number of actual feeding links and the richness squared). The modularity level of food webs was measured with the algorithm of Leicht and Newman (2008). The different levels of modularity were obtained by varying the parameter representing diet contiguity in the generalized niche model (Guimerà et al. 2010). The parameter of diet contiguity represents how close are predator's prey species within the niche axis. A diet contiguity of zero, its minimal value, is equivalent to the generalized cascade model (Stouffer et al. 2005) where species are organized hierarchically on the niche axis without a determined proximity. The maximum value of diet contiguity is one, and is equivalent to the niche model from Williams and Martinez (2000). In the niche model the prey species of a given predator are the one next to each other on the niche axis. This result in interval sets of preys within the niche axis, which generates modularity (Guimerà et al. 2010). Thereby an increase in the value of diet contiguity results in an increase in the level of modularity. Therefore from the model food webs generated with values of diet contiguities between 0.2 and 1 we selected food webs with modularity values of 0.14, 0.16, 0.18, 0.2 and 0.22, with a deviation of ± 0.01. For each combination of richness and modularity we generated 100 different food webs.

To model the biomass dynamics of populations within the food webs we used as a base the bioenergetic model of Yodzis and Innes (1992) generalized by Williams and Martinez (2004) for many species food webs. We additionally developed equations for modeling the dynamics of the total amount of pollutant accumulated within organisms (Kooi et al. 2008) and of the pollutant in the environment. Models of both biomass and pollutant dynamics have allometric parameters, whose values were obtained following Brose et al. (2006) and Hendricks et al. (2001). Values of allometric parameters scale to a power of body mass. This model has already been used successfully in the context of food webs subjected to pollution by showing that increasing levels of biodiversity should increase species persistence as pollutant stress increases (Garay-Narváez et al. 2013). The bioenergetic model is particularly convenient for our purposes since, state variables are in terms of biomass and not of individuals, which is convenient to model the pollutant concentration. For detailed information about the model and its parameters see Supplementary Material Appendix A1.

Finally, we coupled the dynamics of species and pollutant to the topological structure obtained from the generalized niche model and ran two simulations of 5000 time steps for each of the 1500 model food webs. Initial values for biomasses were taken randomly from a uniform distribution between 0.05–1, initial values for bioaccumulated pollutant and for the environmental pollutant concentration were set to zero. Species with densities below 10^{-30} were considered as extinct and forced to zero. In order to distinguish the effects of pollution from the effects of other kinds of perturbations that are not propagated though trophic interactions, we compared our results with those obtained from 1500 model food webs to which we applied a generic pulsed perturbation. This perturbation adds an additional density dependent mortality rate to the species biomass dynamics. The generic perturbation enters the community in the same way than the pollutant but, unlike pollutants, did not propagate through the trophic interactions (see Supplementary material Appendix A1 for further details).

To isolate the effect of the modularity from the effect diet contiguity (Guimerà et al. 2010), we repeated our analyses on food webs with different modularity values but with a single value of diet contiguity. Additionally, we assessed if the effect of modularity remained the same when we moved away from a realistic food web structure. For addressing this point, we performed the same analyses using food webs with randomized body size distributions and with random topology and random body size distributions. In summary, the analyses were performed on four types of model food webs, which had 1) hierarchical feeding (using the generalized niche model), modularity associated to diet contiguity and realistic body size distribution. This is our main objects of study since resemble natural food webs; 2) hierarchical feeding with controlled diet contiguity = 0.2 and realistic body size distribution; 3) hierarchical feeding with controlled diet contiguity = 0.2 and random body size distribution; 4) random topology (Erdös–Renyi model) and random body size distribution. See Supplementary material Appendix A2 for more details and results.

Food web stability was measured at the end of each simulation as species persistence, defined as the number of surviving species over the initial number of species in the food web. All codes were implemented and executed in MATLAB (R2011b).

Results

Figure 1 shows the relationship between modularity level, species richness and species persistence in three perturbation

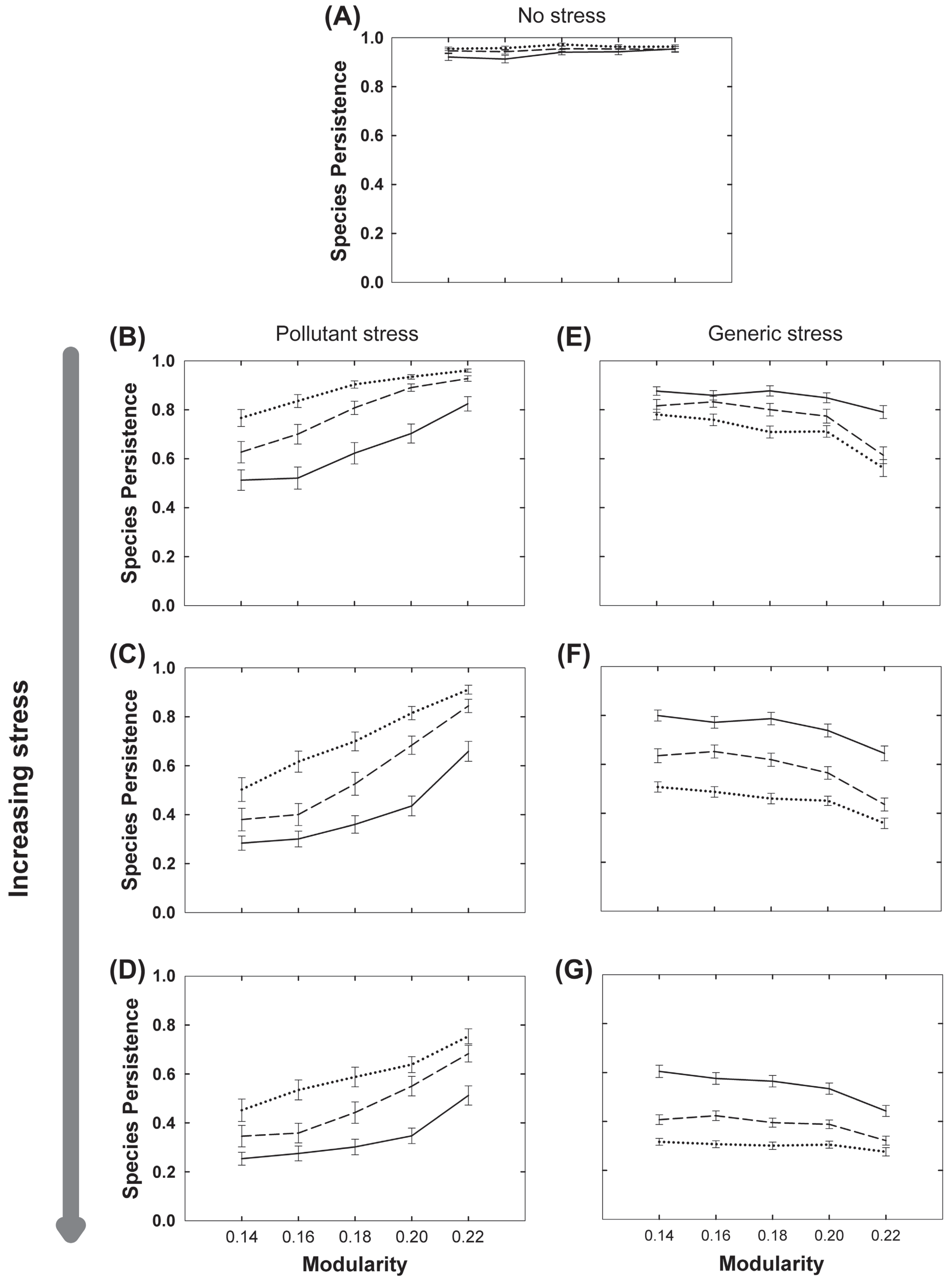

Figure 1. Modularity–persistence relationship in systems with increasing levels of pollutant stress. (A) is a plot for unperturbed food webs. (B), (C) and (D) are plots for food webs with low, medium and high levels of pollutant stress, respectively. (E), (F) and (G) are plots for food webs with low, medium and high levels of a generic stress respectively. Continuous, dashed and dotted lines correspond to food webs of 20, 30 and 40 species respectively. Error bars represent 95 per cent confidence intervals arround the mean value of species persistence. $\gamma_j = 100$ for low pollutant stress, $\gamma_j = 50$ for medium pollutant stress, $\gamma_j = 10$ for high pollutant stress.

scenarios: 1) without stress (Fig. 1A), 2) with increasing levels of stress by an accumulable pollutant (Fig. 1B–D) and ii) with increasing levels of a generic, non-accumulable perturbation (Fig. 1E–G).

In undisturbed systems (Fig. 1A) nearly 100% of the initial species persisted in the food webs after running the dynamic model, almost independently of the level of modularity and species richness. For all the levels of species richness low levels of modularity resulted in the decrease of species persistence from its maximum value.

The effects of modularity and species richness on species persistence were positive for all levels of pollutant stress (Fig. 1B–D). Species persistence of the poorest food webs increased with modularity both in polluted (Fig. 1B–D) and non-polluted systems (Fig. 1A). On the other hand, the richest food webs maintained an almost maximum persistence through the entire gradient of modularity for a low level of pollutant stress (Fig. 1B). This suggests that under low levels of pollutant stress species richness makes food webs more robust to changes in modularity. In all the studied food webs a low modularity level led to decreased species persistence, which produced a positive relation between modularity and species persistence (Fig. 1B–D).

Conversely, with the generic perturbation the effects of both modularity and species richness on species persistence became increasingly negative as the level of the generic perturbation increased (Fig. 1E–G). This contrasts with the positive relation between species richness/modularity and persistence found in food webs subjected to pollutant stress.

Regarding realistic structural attributes (Supplementary material Appendix A2 Fig. A1–A3) we found that the effect of both modularity and species richness on species persistence did not change qualitatively when fixing diet contiguity. This was observed under both kinds of perturbations (Supplementary material Appendix A2 Fig. A1). Nevertheless results were reversed in food webs subjected to pollutant stress when, in addition to fixing diet contiguity, we randomize body sizes within the food web (Supplementary material Appendix A2 Fig. A2). Under this scenario the relationship between modularity and species persistence became negative, and the effect of species richness on food web stability became null. Additionally, when both topology and body size structure were randomized we found no effect of modularity on species persistence independent of the kind of perturbation, while the effect of species richness became null in food webs subjected to pollutant stress and was unaffected in food webs under the reference perturbation (Supplementary material Appendix A2 Fig. A3).

Discussion

The results presented here are congruent with the view of modularity as a main determinant of ecosystem stability (May 1972, Stouffer and Bascompte 2011). In general, modularity is expected to inhibit the propagation of perturbations to the whole food web (May 1972). Previous studies showed that modularity buffers the propagation of extinctions, providing robustness to local perturbations (Stouffer and Bascompte 2011). In this study we showed that modularity effectively promoted the stability of trophic networks subjected to pollutant stress, a perturbation that is transported through the trophic interactions. The opposite results were obtained when food webs were faced with the generic perturbation. This suggests that the propagation of the pollutant through food consumption should be a key property affected by modularity, leading to the enhancement of species persistence. Further, we also found that biodiversity probably has a main role in the stability of food webs exposed to pollutants since richer food webs were more robust at all modularity levels. Additionally, the effect of biodiversity in terms of species richness could interact with food web topology at low pollutant stress, since poorer communities were more affected by modularity when subjected to pollution while richer communities were more stable at lower modularity. Such hypothetical synergistic effects of disturbances require further attention in future theoretical and empirical studies. Our findings of a positive effect of modularity and species richness on species persistence were qualitatively unaffected for a fixed level of diet contiguity (= 0.2), and were cancelled and even reversed when the structure of food web departed from a realistic body size distribution or a hierarchical feeding structure. These suggest that preserving realistic structural attributes such as the body size distribution within the food web and the hierarchical topological structure plays a major role in maintaining the positive effect of modularity and richness on species persistence.

A closer examination of our results suggests a double structural pattern of food webs with increasing modularity (results not shown): 1) a higher level of network connectivity, measured as average betweenness centrality of species, which means that an average species of more modular food webs has a more important role in communicating other species, and 2) a lower steepness of the cumulative out-degree distribution (fitted to an exponential distribution), which means that there was an increased proportion of species with an elevated number of predators at higher modularity levels. In food webs subjected to the reference perturbation, as connectivity increases with modularity, the propagation of the lethal effects through the network also increases. Therefore one might expect a higher adverse effect on the network and a lower species persistence as modularity increases. With pollutants nevertheless, it is the bioconcentration of pollutants which exerts effects on species, and therefore the increase in connectivity with modularity do not necesarily propagates effects, but the pollutant itself. On the other hand, and due to the decrease in the steepness of the out-degree distribution, modularity would result in a higher pollutant transport to higher trophic levels (i.e. biomagnification), lower retention at low and intermediate trophic levels, and thus higher overall species persistence. Consequently, it is expected that adverse effects of pollutants affect a higher number of species at lower levels of modularity. This opens a line of research towards finding and understanding the functional significance of structural patterns that change in conjunction with modularity, and that apparently are unique to the nonrandom structure of food webs.

It should be considered that a recent theoretical analysis found a negligible or slightly negative effect of modularity on the persistence of model food webs (Thébault and Fontaine 2010). In this study we obtained different results, in which modularity and species richness had a null or positive effect on species persistence in the absence of perturbations. This discrepancy should be attributed to the large differences in the structure of the model communities, and/or in the experimental levels of modularity. Our model food webs had multiple trophic levels, like real webs, and the chosen levels of modularity (between 0.14 and 0.22) matched the range of modularity observed in empirical food webs (Guimerà et al. 2010). On the other hand, Thébault and Fontaine (2010) used communities of two trophic levels, which constrain the propagation of effects, and a different range of modularity values (between 0.3 and 0.8). These methodological differences could account for the alternative view of the role of modularity suggested by these two theoretical analyses.

Modularity may have a more pronounced effect on network stability when faced with pollutant stress. It has been shown that modularity of food webs should arise through spatial habitat structuring (Holt 2002, Krause et al. 2003), body size structure (Petchey et al. 2008), phylogenetic patterns within communities (Cattin et al. 2004), or through any combination of these factors (Rezende et al. 2009). The present study suggests that the loss of modularity had a stronger negative effect on food web persistence as pollutant stress increased and community size decreased. These results are especially important at the present time, when human-driven disturbances such as fragmentation, extinctions, and invasion of exotic species are reducing the modularity of natural communities (Rooney and McCann 2012). Specifically, our study calls attention to the synergetic role of food web structure – modularity in this case – and species biodiversity on the stability of polluted food webs. Considering, that pollution (MEA 2005, Groom et al. 2006), species loss (May et al. 1995) and simplification of food web structure (McCann 2007, Bascompte 2009) are pervasive and ongoing processes of global change, the understanding of their interactions must be a main focus of research. As was found in the present analysis, the scarcity of studies in this area limits our understanding of the determinants of ecosystem stability and their relationship with global change.

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References

Allesina, S. and Pascual, M. 2009. Food web models: a plea for groups. – Ecol. Lett. 12: 652–662.

Bascompte, J. 2009. Disentangling the web of life. – Science 325: 416–419.

Brose, U. et al. 2006. Allometric scaling enhances stability in complex food webs. – Ecol. Lett. 9: 1228–1236.

Cattin, M.-F. et al. 2004. Phylogenetic constraints and adaptation explain food-web structure. – Nature 427: 835–839.

Dunne, J. A. et al. 2002. Food-web structure and network theory: the role of connectance and size. –Proc. Natl Acad. Sci. USA 99: 12917–12922.

Garay-Narváez, L. et al. 2013. The more polluted the environment, the more important biodiversity is for food web stability. – Oikos 122: 1247–1253.

Groom, M. J. et al. 2006. Principles of conservation biology. – Sinauer.

Guimerà, R. et al. 2010. Origin of compartmentalization in food webs. – Ecology 91: 2941–2951.

Hendriks, A. J. et al. 2001. The power of size. 1. Rate constants and equilibrium ratios for accumulation of organic substances related to octanol–water partition ratio and species weight. – Environ. Toxicol. Chem. 20: 1399–1420.

Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. – Ecol. Res. 17: 261–273.

Kooi, B. W. et al. 2008. Sublethal toxic effects in a simple aquatic food chain. – Ecol. Modell. 212: 304–318.

Kondoh, M. 2008. Building trophic modules into a persistent food web. – Proc. Natl Acad. Sci. USA 105: 16631–16635.

Krause, A. E. et al. 2003. Compartments revealed in food-web structure. – Nature 426: 282–285.

Lafferty, K. D. et al. 2008. Parasites in food webs: the ultimate missing links. – Ecol. Lett. 11: 533–546.

Leicht, E. A. and Newman, M. E. J. 2008. Community structure in directed networks. – Phys. Rev. Lett. 100: 118703.

May, R. M. 1972. Will a large complex system be stable? – Nature 238: 413–414.

May, R. M. et al. 1995. Extinction rates. – In: Lawton, J. H. and May, R. M. (eds). – Oxford Univ. Press.

McCann, K. S. 2007. Protecting biostructure. – Nature 446: 29–30.

McCann, K. S. 2012. Food webs. Monogr. Popul. Biol. – Princeton Univ. Press.

McCann, K. S. and Hastings, A. 1997. Re-evaluating the omnivory-stability relationship in food webs. – Proc. R. Soc. B 264: 1249–1254.

MEA, Millennium Ecosystem Assessment 2005. Ecosystems and human well-being: biodiversity synthesis. – World Resources Institute, Washington.

Melián, C. J. and Bascompte, J. 2002. Complex networks: two ways to be robust? – Ecol. Lett. 5: 705–708.

Milo, R. et al. 2002. Network motifs: simple building blocks of complex networks. – Science 298: 824–827.

Newman, M. C. and Clements, W. H. 2008. Ecotoxicology: a comprehensive treatment. – Taylor and Francis.

Olesen, J. M. et al. 2007. The modularity of pollination networks. – Proc. Natl Acad. Sci. USA 104: 19891–19896.

Otto, S. B. et al. 2007. Allometric degree distributions facilitate food-web stability. – Nature 450: 1226–1230.

Petchey, O. L. et al. 2008. Size, foraging and food web structure. – Proc. Natl Acad. Sci. USA 105: 4191–4196.

Pimm, S. L. and Lawton, J. H. 1977. On the number of trophic levels. – Nature 268: 329–331.

Pimm, S. L. and Lawton, J. H. 1980. Are food webs divided into compartments? – J. Anim. Ecol. 49: 879–898.

Ramos-Jiliberto, R. et al. 2010. Topological change of Andean plant–pollinator networks along an altitudinal gradient. – Ecol. Complex. 7: 86–90.

Rezende, E. L. et al. 2009. Compartments in a marine food web associated with phylogeny, body mass and habitat structure. – Ecol. Lett. 12: 779–788.

Rooney, N. and McCann, K. S. 2011. Integrating diversity, food web structure and stability. – Trends Ecol. Evol. 27: 40–46.

Ruiz-Moreno, D. et al. 2006. Exploring network space with genetic algorithms: modularity, resilience and reactivity. – In: Pascual, M. and Dunne, J. A. (eds), Ecological networks. Linking structure to dynamics in food webs. Oxford Univ. Press, pp. 187–208.

Sterner, R. W. et al. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. – Ecology 78: 2258–2262.

Stouffer, D. B. and Bascompte, J. 2011. Compartmentalization increases food-web persistence. – Proc. Natl Acad. Sci. USA. 108: 3648–3652.

Stouffer, D. B. et al. 2005. Quantitative patterns in the structure of model and empirical food webs. – Ecology 86: 1301–1311.

Stouffer, D. B. et al. 2006. A robust measure of food web intervality. – Proc. Natl Acad. Sci. USA 103: 19015–19020.

Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – Science 329: 853–856.

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

Williams, R. J. and Martinez, N. D. 2004. Stabilization of chaotic and non-permanent food web dynamics. – Eur. Phys. J. B 38: 297–303.

Yodzis, P. and Innes, S. 1992. Body size and consumer-resource dynamics. – Am. Nat. 139: 1151–1175.

Supplementary Material (Appendix oik-00764 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A2.