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LESLIE GARAY NARVÁEZ

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To my little princess…

BIOGRAPHY

Leslie Garay Narváez is a biologist of the Universidad Católica de Valparaíso. The year 2008 she began her PhD in science, mention in Ecology and Evolutionary Biology at the Universidad de Chile with the support of a CONICYT grant. As student of PhD Leslie had a staying in the laboratory of Dr. Matías Arim at the Universidad de la República in Uruguay with the suppot of a MECESUP grant. The research interests of Leslie are in the areas of Community Ecotoxicology, Food Web Modeling, Population and Community Ecology, Theoretical Ecology and Qualitative Modeling.

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Resumen

La investigación sobre el efecto que atributos estructurales de las redes tróficas ejercen sobre su dinámica es de importancia creciente en la actualidad ya que perturbaciones antropogénicas actúan simplificando los ecosistemas naturales a través de la pérdida tanto de especies como de sus interacciones. Sin embargo este tema se ha abordado considerando explícitamente sólo ambientes prístinos. Por ello en este estudio se investigó el efecto de los contaminantes sobre la relación complejidad-estabilidad, el efecto de razones de tamaño corporal depredador-presa sobre la relación complejidad-estabilidad en ambientes contaminados y el efecto de la modularidad sobre la persistencia de especies sujetas a estrés por contaminante. En cuanto a la relación complejidad-estabilidad, en este estudio se encontró que en ambientes contaminados, comparados con aquellos no contaminados, la magnitud del efecto positivo de la complejidad sobre la estabilidad fue incrementado. Adicionalmente se muestra que atributos estructurales de las redes tróficas que cambian sistemáticamente con la complejidad jugaron un rol importante dando forma a la relación complejidad-estabilidad sólo cuando el contaminante fue incorporado. Las especies con mayor tendencia a la extinción en sistemas contaminados fueron los consumidores generalistas. En la segunda sección se muestra que la razón de tamaño corporal depredador-presa genera una relación positiva complejidad-estabilidad, pero esta relación fue más fuerte a niveles altos de estrés por contaminante. Adicionalmente se encontró que bajas razones de tamaño corporal depredador-presa conducen a una persistencia más baja en las redes tróficas sujetas a contaminantes en comparación con las redes tróficas sin contaminante,

mientras que a altas razones de tamaño corporal depredador-presa se aseguró una persistencia de casi un cien por ciento de las especies tanto en redes con contaminantes como en redes sin contaminantes. Finalmente en la tercera sección se mostró que bajo un gradiente de estrés por contaminante el efecto de la modularidad sobre la persistencia (i.e. estabilidad) de las redes tróficas fue más pronunciado. El incremento en el estrés por contaminante también realzó una relación débil entre la riqueza de especies (i.e. complejidad) y la estabilidad de las redes a través del gradiente de modularidad, de tal manera que a bajo estrés por contaminante una alta riqueza de especies confirió mayor robustez a las redes tróficas frente a distintos niveles de modularidad. Al incorporar una perturbación de referencia que carecía de las características fundamentales de los contaminantes, los resultados fueron revertidos. A partir de esta investigación se obtiene que la mantención de la estructura de las redes tróficas sería clave para poder impedir la pérdida de especies e interacciones junto con sus consecuencias funcionales en ambientes perturbados por contaminación. Esto se debe a las características de los contaminantes acumulables, ya que su patrón de propagación, y por ello sus efectos finales sobre la dinámica de las comunidades depende fuertemente de la estructura subyacente de las redes tróficas.

Summary

The research about the effect that structural attributes of food webs exert on their dynamics is of increasing importance currently since human driven disturbances act simplifying natural ecosystems through the loss of both species and their interactions. Nevertheless this issue has been addressed considering explicitly only pristine environments. Thus in this study we investigated the effect of pollutants on the complexity-stability relationship, the effect of predator-prey body size ratio on the complexity-stability relationship in polluted environments and the effect of modularity on the persistence of species subjected to pollutant stress. Regarding the complexity-stability relationship, in this study it was found that in polluted systems as compared to non-polluted ones, the strength of the positive effect of complexity on stability was enhanced. Additionally we showed that food web attributes that change systematically with complexity play an important role in shaping the complexity-stability relationship only when a pollutant was incorporated. Species more prone to extinction in polluted systems were generalist consumers. In the second section we showed that predator-prey body size ratio generates a positive complexity-stability relationship, but this relationship was stronger under higher levels of pollutant stress. We additionally found that low predator-prey body size ratios drives to lower food web persistence as compared to food webs with no pollutant stress, while at higher predator-prey body size ratio the persistence of almost hundred per cent of species was ensured for both polluted and non-polluted food webs. Finally in the third section of this study we showed that under a gradient of pollutant stress the effect of modularity on food web persistence (i.e.

stability) was more pronounced. The increase in pollutant stress also enhanced a weak positive relationship between species richness (i.e. complexity) and stability of food webs across the gradient of modularity, in such a way that under pollutant stress higher species richness confers a higher robustness to food webs when facing different levels of modularity. Incorporating a reference perturbation that lacked the fundamental features of pollutants, the results were reversed. From this research it is obtained that maintaining the structure of food webs should be key in order to prevent species and interaction losses together with its functional consequences under environments disturbed by pollution. This is due to the characteristics of accumulable pollutants, since their pattern of propagation and therefore its final effects on community dynamics depends strongly on the underlying structure of food webs.

GENERAL INTRODUCTION

Theoretical background

The assumption that complexity promotes stability comes from the twentieth century when important ecologists like Odum (1953), MacArthur (1955) and Elton (1958) supported that more complex systems, with either a higher number of species or a higher number of interactions, should be more stable than more simple ones (Pimm, 1991). A main support for this view was that simple mathematical models were frequently unstable, with large oscillations in abundance and restricted conditions for species coexistence. However, no multispecies models were available at this time. A great debate was opened when Robert May in the early seventies of the past century found a negative association between complexity and stability (May 1972).

The findings of May (1972) gave rise to a long debate that transformed the study of the relationship between the complexity of ecological systems and their stability into one of the cornerstones of contemporary ecological theory. May's theoretical model incorporated the three main components of complexity considered so far: species richness, connectivity and interaction strength. By itself, each one of these components showed a potential to destabilize communities, contrasting with the wisdom of more diverse communities being more stable. Consequently the main contribution of May's model was to focus research on which attributes of biodiversity and in which conditions could promote or preclude stability. This implies a great impulse to the study of food webs with an attention to specific attributes that continue today (e.g. Valdovinos et al.

2010; Brose et al. 2006; Williams & Martinez 2000). In this line, some degree of consensus has been emerging about a main role of interaction strength (Csermely 2006), and its connection with the body size ratio between predators and prey (Emmerson & Raffaelli 2004; Brose *et al.* 2006). More recently the development of new methodological tools that confidently evaluate modularity in networks corroborated a main role of this attribute on network stability as were early suggested by May (Brose et al. 2006; Stouffer & Bascompte 2011).

Of special interest in this study are predator-prey body size ratios and modularity, which have been found to be important attributes of food webs, that influence the system dynamics in such a way that have been found to be highly stabilizing factors within complex ecological communities (Brose et al. 2006; Stouffer & Bascompte 2011).

The research about the effect that structural attributes of food webs exert on their dynamics is of increasing importance currently since human driven disturbances such as habitat destruction and fragmentation, climate change, overexploitation of natural resources, invasion of exotic species and pollution act simplifying natural ecosystems through the loss of both species and their interactions. Nevertheless this issue has been addressed considering explicitly only pristine environments (but see Mulder, Uliassi & Doak 2001; Pfisterer & Schmid 2002; Zhang & Zhang 2006; Romanuck et al. 2010). Our aim in this study was to extend complexity-stability theory to polluted environments since pollution is an important source of ecosystem disturbance (Primack, 2008) and it is actually one of the threats to biodiversity (MEA, 2005). Specifically, this thesis evaluates the different components of the complexity-stability relationships in scenarios of increasing levels of stress by pollutants. The attention is devoted to both, the effect of pollutant at the food web level and the interaction between contaminants and the complexity-stability relationship. To advance in these two points is essential to determine the applicability of results relating diversity with stability in pristine conditions to the more frequent polluted nature, and to be aware about the nature of feedbacks among the different components of global change. This thesis evaluate these previous results in the light of polluted environment were trophic interactions are routes for energy but also for pollutants.

Of particular interest in this study were lipophilic pollutants, which are being released extensively to the environment either as industrial byproducts or as end products such as pesticides (Walker et al. 2006). These compounds are taken by species through both water and food (Kooi et al. 2008), and therefore tend to accumulate in the tissue of organisms and be transmitted through food chains, having the potential to be biomagnified (i.e. increasing in concentration upper in the food web; e.g. Kelly et al. 2007). Therefore, the final effect of these pollutants on species dynamics should be determined not only by its concentration in the environment, but by the flux of material and energy through food webs, which depends on the strength of predator-prey interactions and the way they are organized in the network, the food web architecture.

Topology and dynamics of model food webs

This is a theoretical study where we used model food webs with the aim of study systematically the food web attributes of our interest. In order to generate these model food webs we used the algorithm widely known as "niche model" (Williams & Martinez

2000), . This algorithm generates model food webs whose structural properties are close to the ones observed in empirical trophic networks (Williams & Martinez 2008).

We modeled the biomass dynamics of populations within the food webs through the bioenergetic model of Yodzis and Innes (1992) generalized by Williams and Martinez (2004) for food webs of multiple species. This is a widely used and accepted model in the ecological literature. Additionally we modeled the total amount of pollutant accumulated within organisms (Kooi et al. 2008) and the pollutant in the environment. This is a simple way to incorporate the pollutant dynamics and its accumulation, in a framework similar to the used by ecological models.

Dissertation outline

Our aim in this study was to advance in extending the complexity-stability theory of food webs to the case of polluted environments. This study was organized in three sections, each of them comprise a paper that address one of the three specific objectives of the dissertation. These objectives were to analyze: i) the effect exerted by pollutant stress on the relationship between complexity and stability, ii) the effect of predator-prey body size ratio on the relationship between complexity and stability of polluted food webs, and iii) the effect of network modularity on the persistence of species subjected to increasing levels of pollutant stress.

Complexity as a main driver of species persistence in polluted environments.

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Running headline: Complexity-stability relationship in disturbed environments.

Summary

1. Human activities are impacting ecosystems, simplifying they biodiversity structure and degrading the environment by the massive deposition of pollutants. The effect of species richness, connectivity and more recently modularity had dominated the analyses of the effect of ecosystems degradation on food web stability. In spite of its pervasive impacts and being recognized as a main threat to biodiversity, the interaction between food web complexity, pollutant and stability has not been widely considered. Pollutant directly affects organism performance and could be accumulated and transported through the trophic interactions, exerting effects tightly dependent on the organization of the community components.

2. In this study we evaluated the effects of species richness and network connectance on the stability of model communities across a gradient of pollutant stress. The biomass dynamics in our model was governed by bioenergetic scaling, incorporating the dynamics of pollutant in the environment as well as within organisms. Food web metrics and organisms attributes were respectively related with the propensity of communities to loss species and to the chance of each organisms of become extinct.

3. We found a positive effect of complexity on stability in both polluted and non-polluted systems. Nevertheless, this positive effect was enhanced as pollutant stress increased, suggesting that complexity should be a more relevant determinant of stability in polluted systems. Additionally we showed that the number of basal species, number of top species and maximum trophic position, attributes that change systematically with complexity, play an important role in shaping the complexity-stability relationship in

presence of pollutant stress. Finally we found that generalists consumers were more prone to extinction in polluted systems.

4. In a world increasingly polluted, with a degraded biodiversity and simplified food webs, our study indicates that ecosystems stability results from the interaction among these three factors and that any analyses excluding one of them will provide a partial view of the problem. Further, biodiversity and the web interactions are probably essential to deal with pollution and other threats to ecosystems.

Key-words: complexity, stability, richness, connectance, pollution, biomagnification

Introduction

Human activities may produce serious disturbances to ecosystems on earth, including habitat destruction and fragmentation, climate change, overexploitation of natural resources, invasion of exotic species and pollution. These disturbances threat natural communities, driving the loss of species and their interactions (Primack 2008). Therefore, the research about the effects that the richness of both species and their interactions (hereafter complexity) has on the stability of ecological communities is of increasing interest (McCann 2007, Bascompte 2009). However, the functional consequences of these losses are still debated and poorly understood (Stouffer & Bascompte 2011, McCann 2012, Rooney & McCann 2012).

The study of the effects that complexity has on the stability of ecological systems became one of the cornerstones of ecological theory since May (1972), through a theoretical study, demonstrated that complexity by itself precludes stability. In recent times this line of research has been focused on revealing the shape of the complexity-stability relationship by empirical means (see Ives & Carpenter 2007 for a review), and on searching the attributes of species and communities that could determine complex systems being more stable (e.g. Valdovinos et al. 2010, Brose, Williams & Martinez, 2006; Williams & Martinez 2000). Nevertheless the scenarios in which the complexity-stability relationship has been analyzed have not included human driven disturbances in a realistic way (but see Mulder, Uliassi & Doak 2001, Pfisterer & Schmid 2002, Zhang & Zhang 2006, Romanuck et al. 2010). This is particularly true for pollutant driven disturbances, whose ecological consequences have been primarily studied considering systems composed by few species (e.g. Rohr & Crumrine 2005, Liebig et al. 2008), in which the role of complexity could not be disclosed.

Some kinds of organic pollutants, particularly lipophilic pollutants such as polychlorinated dibenzodioxins (PCDDS), polychlorinated biphenyls (PCB), polybrominated biphenyls (PBBS) and organochlorine pesticides, are being released extensively to the environment either as industrial byproducts or as end products such as pesticides (Walker et al. 2006). Organisms incorporate these substances through both water and food (Kooi et al. 2008), and are accumulated within the tissues. In addition, organic pollutants have the potential to be biomagnified, that is to say, increase their concentration within organisms as they locate upper in the food chains (e.g. Kelly et al. 2007). Therefore, an interesting property of accumulable pollutants is that they are transmitted through the web of trophic interactions, being spread in the community in dependence on the trophic structure of the network. Thus, community complexity could play a role in determining the effects of pollutants on species' growth rates, and hence in shaping community dynamics and stability (Sherwood et al. 2002).

In this study we evaluated the effect exerted by pollutant stress on the relationship between complexity and stability of food webs. Species richness and network connectance were used as measures of complexity, while stability was evaluated through species persistence. In addition, we analyzed properties of the species and communities that, varying systematically with complexity, could explain the obtained results.

Methods

Using the algorithm widely known as "niche model" (Williams & Martinez 2000), we built a set of 19,600 model food webs of varying levels of species richness and network connectance. This algorithm generates model food webs whose structural properties are close to the ones observed in empirical trophic networks (Williams & Martinez 2008). To evaluate the effect of complexity on food web stability over a gradient of pollutant stress, we generated food webs with the following levels of connectance: 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25; and richness: 20, 25, 30, 35, 40, 45 and 50. For each combination of connectance and richness we generated 100 food webs in form of adjacency matrices.

Empirical and model food webs show certain structural attributes that change systematically with connectance and richness (Riede et al. 2011). We evaluated the importance of these covariates as determinants of the complexity-stability relationship in polluted and unpolluted environments. Thus, we built food webs of four types, for each level of connectance and richness: i) with no topological constraints (hereafter non-constrained FWs), ii) with a fixed number (= 5) of producer species (hereafter P-FWs), iii) with a fixed maximum trophic position (= 4 ± 0.2) (hereafter TP-FWs), and iv) with a fixed number of top predators (= 3) (hereafter T-FWs).

To model the biomass dynamics of populations within the food web we implemented the bioenergetic model of Yodzis and Innes (1992) generalized by Williams and Martinez (2004) for food webs of multiple species. We additionally modeled the total amount of pollutant accumulated within organisms (Kooi et al. 2008) and the pollutant in the environment. Models of both biomass and pollutant dynamics have allometric parameters, whose values were obtained following Brose et al. (2006a) and Hendricks et al. (2001). Values of allometric parameters scale to the power of body mass. For detailed information about the model, parameter definitions and values see Supplementary Information.

Finally we coupled the dynamics of species and pollutant to the topological structure obtained from the niche model and run one simulation of 5000 time steps for each adjacency matrix. Initial values for biomasses were taken randomly from a uniform distribution between 0.05 and 1, while initial values for accumulated pollutant and for pollutant in the environment were set to zero. Species with densities bellow 10^{-30} were considered to be extinct and forced to zero.

Stability was measured at the end of each simulation as species persistence, defined as the fraction of the initial species that exhibited positive population densities at the end of a simulation. The effect of species richness and network connectance on community stability was obtained through a multiple regression analysis (see details in Supplementary Information). In addition, at the end of each simulation we recorded in each food web the following characteristics of extinct species: i) trophic position (following the algorithm of Levine, 1980), ii) in-degree (number of species that are prey of the focal species), and iii) out-degree (number of species that predate on the focal species). For these measures we calculated their mean value in extinct species in relation to the corresponding mean value in all species within the food web.

Results

In food webs with no topological constraints and not subjected to pollutant stress, species persistence increased with connectance and richness. Nevertheless the interaction effect between both factors was negative (Fig. S1C), which produced that at higher values of both connectance and richness, persistence was lower than expected by an additive effect (Fig. 1A). As the pollutant stress increased the main effects from regression analysis decreased (Fig. S1A and S1B). However the interaction term was negative under low pollutants stress and increased to positive values at higher stress levels (Fig. 1B, 1C and 1D; and Fig. S1C). This results in that the positive effect of both connectance and richness on persistence was enhanced for increasing levels of pollutant stress (Fig. 1B, 1C and 1D). Even though species persistence was higher for all levels of richness and connectance in non-polluted food webs as compared to the polluted ones, it is remarkable that in polluted food webs the values of persistence for the higher levels of both connectance and richness were over 0.9, close to the ones obtained for the same levels of complexity in non-polluted systems.

Figure 1 here

When evaluating the role of food web attributes as possible determinants of the observed results we found that when pollutant was not included the results were the same for the four tested types of food webs (Figs. 1A, 1E, 1I and S2A). In contrast, when pollutant stress was incorporated into model food webs, only topologies with fixed number of top predators (Fig. S2) behaved the same as the webs with unconstrained topologies (Fig. 1A, 1B, 1C and 1D). This shows that changes in both the number of producer species and in the maximum trophic position associated to changes in complexity played no role in shaping the complexity-stability relationship in non-polluted systems. Nevertheless, these attributes control the shape of the complexity-stability relationship in polluted systems. The number of producer species increases with richness and decreases with connectance in non-constrained food webs (Fig. S5A). We found that fixing the number of producer species suppressed the positive effect of connectance on species persistence (Fig. 1F, 1G and 1H; and Fig. S1D) but enhanced the positive effect of richness (Fig. 1F, 1G and 1H; and Fig. S1E). This indicates that the increase in the number of producer species has a negative effect on species persistence. When prevented the decrease (with increasing connectance) or increase (with increasing richness) of the number of producer species, species persistence was shown to be suppressed and enhanced, respectively. On the other hand, fixing the maximum trophic position, which in non-constrained food webs increased with connectance and richness (Fig. S5C), enhanced the strength of the relationship between connectance/richness and persistence (Fig. 1J, 1K and 1L; and Fig. S1G and S1H). Accordingly, the negative effect of the interaction connectance-richness on persistence was reinforced (Fig. 1J, 1K and 1L; and Fig. S1I) and, unlike the non-constrained topology, it was negative through all levels of pollutant stress (Fig. 1J, 1K and 1L; and Fig. S1C). Finally this led to that increasing the maximum trophic position had a positive effect on species persistence since preventing its increase (with connectance and richness) supressed the persistence of species, specially at high complexity levels.

In non-constrained food webs, without pollutant stress, the species that went extinct during the simulations exhibited a high mean trophic position relative to all species in the food webs. However, the relative mean trophic position of extinct species decreased with species richness and network connectance (Fig. 2A). When the pollutant was incorporated to the systems, the trophic position of extinct species fell bellows the mean trophic position of the food web for most levels of richness and connectance (Fig. 2B). This indicates extinct species in polluted environments were intermediate within food chains. The mean number of prey or in-degree in extinct species was lower than the average when the pollutant was not incorporated (Fig. 2C). This value increased whit pollutant approaching the mean value of the food web (Fig. 2D), showing a decrease with food web complexity similar to the observed in trophic position. Finally, the relative mean number of predators or out-degree of extinct species increased with richness and connectance (Fig. 2E), exhibiting a slight decrease when pollutant stress was incorporated (Figs. 2F). The effect of connectance on these three metrics was suppressed when food webs were constrained (Fig. S3 and S4). This suggests that changes in food web attributes driven by changes in connectance (i.e. decreased number of producers and increased maximum trophic position) are involved in the relationship between connectance and the attributes of extinct species. Finally the effect of richness on the attributes of extinct species was not qualitatively altered in constrained food webs. Results for non-polluted and high stress by pollution systems are presented because the different level of pollutant stress did not affect results.

Figure 2 here

Discussion

In this work it has been shown that systems under the effect of stress by pollutant show the positive effect of complexity on stability reported for simulations without stressors (e.g. Brose et al. 2006a). However, in polluted systems complexity appear as a more relevant determinant of stability. In these food webs the addition (or deletion) of species or links produce lager changes in species persistence, indicating a main role of biodiversity complexity on ecosystems potential to deal with polluted environments. In fact, only at large levels of connectance and richness polluted and unpolluted communities show similar patterns of persistence (see Fig. 1).

Results herein reported are in line with previous theoretical work (e.g. Brose et al. 2006b) indicating a positive complexity-stability relationship in size-structured food webs. In our models predators were two orders of magnitude higher than their prey species, a ratio close to the pattern found in nature (Brose et al. 2006a) and generating stable food webs (Brose et al. 2006b). Empirical patterns are consistent with these theoretical results reporting a positive complexity-stability relationship when stability is measured at the community level (reviewed in Ives & Carpenter, 2007; Campbell, Murphy & Romanuk 2010).

In a time when the determinant of positive complexity-stability relationship is starting to be understood, the role played by other factors or processes have been practically neglected (Rooney & McCann 2012). Nevertheless, Romanuk et al. (2010) found that the positive relationship of stability (measured as variability community abundance) with diversity was unaffected by different levels of decrease in water volume of aquatic rock pools. Microcosms experiments suggested that for a set of environmental conditions food webs converge to similar levels of connectance (Fox & McGrady-Steed 2002). On the other hand, some of the first attempts to collect food webs from different places were oriented to evaluate the effect of environmental variability on complexity (Briand 1983). Connectance (Briand 1983) and food chain length (Jennings & Warr 2003) were negatively related with disturbance. Interaction strength and specifically the stability role of weak links on the whole food web are related with its potential to dumping changes in abundance or environmental conditions (McCann et al. 1998, Berlow 1999, McCann 2000, Berlow et al. 2004). These previous results indicate that the complexity-stability relationship is probably dependent on the biotic and abiotic environment were food web are located. Here, we found that stress by pollutant directly interact with the complexity-stability relationship, positioning its analysis in an explicit gradient of environmental conditions. Further, pollutant gradients involve a main component of global change interrelated with the loss of species and food web simplification, which are typically considered as measures of complexity (i.e. May 1972, Brose et al. 2006b).

This study also advanced in the structure of "complexity"—richness and connectance—identifying food web attributes—number of basal species, number of top species and maximum trophic position —that change systematically with complexity and play an important role in shaping the complexity-stability relationship. Further, the roles of these additional attributes are of particular importance when pollutant is incorporated. For example, in polluted systems the increase in the number of producers (correlated to species richness) had a negative effect on persistence. Community carrying capacity was set at a fixed level. Therefore, increasing the number of producers within food webs reduced the biomass of each producer species. With a Type III functional response, lower biomass densities of preys lead to a reduced total consumption of predators over all their prey species. The combined effect of a low flux of biomass up to the food web and the effect of the pollutant stress could account for the lower persistence observed in food webs with a fixed number of producers. On the other hand, the positive effect on persistence of increasing the maximum trophic position could be explained as follows: the maximum trophic position tends to increase with richness and connectance, so added species or links tend to be stacked up within the network as complexity increases. On other side when fixing the maximum trophic position below its potential value, the increase either in richness or connectance lead to added species or links being more aggregated toward the base of the food webs. Therefore in networks with non-fixed maximum trophic position, as compared to those in which this structural attribute was fixed, the staking up of species or links lead to a lower probability of having species with high in-degree, which are the ones more prone to extinction in polluted environments. Therefore are food webs with higher species persistence. In this sense, our theoretical model makes a set of relevant predictions that could be evaluated in future experiments or field patterns.

At the species level our analysis advanced on the determinants of species vulnerability to environmental pollutants. A pattern that could be expected was the positive effect of in-degree on species extinction on polluted environments because the stressor is incorporated and biomagnified by several routes. In-degree should be as important as biomagnification because it leads to the extinction of intermediate species instead of top predators, which were identified as more vulnerable in previous empirical work (e.g. Rasmussen et al. 2009, Bisi et al 2012). These results provide new evidence about the potential susceptibility of species having multiple preys. In this scenario, as the pollutant is transported through the food web, multiple available prey no longer ensures the survivorship of their predator. On the contrary, many prey provide more entries of the pollutant to the predator's biomass, and therefore a lower growth rate.

This work constitutes a step forward in using ecological network theory for nature conservancy research and understanding of ecosystems structure and function (Brose 2010). On management grounds changes in biodiversity and food web structure are suggested to be more intricately related with environmental pollutant than previously though. Not only because biodiversity loss, food web simplification and pollutants are part of a common process of environmental degradation, but also because they mutually interact in a degree not previously recognized in determining ecosystems stability. On theoretical grounds, gradients in complexity essentially considered species richness and connectance neglecting co-variation in other food web attributes directly related with species and community stability, number of producers, number of top species and maximum trophic position. The scenarios herein evaluated provides new vision to the complexity-stability relationship, reveling structural attributes of communities that permit them to overcome or perish under human driven disturbances such as pollution with accumulable pollutants.

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Figure Captions

Figure 1: Complexity-Stability relationship in systems with increasing levels of polllutant stress. In A,B,C and D are plots for food webs with no topological restrictions (non-constrained FWs), in E, F, G and H are food webs with 5 basal species (P-FWs), and finally in I, J, K and L are food webs with maximum trophic position were fixed at 5 and 4±0.2 (TP-FWs). Data for plots were generated from coefficients of linear regression analysis of connectance and richness as independent variables and persistence as the dependent variable. With γ_j =400 for low pollutant stress, γ_j =100 for medium pollutant stress, γ_j =10 for high pollutant stress.

Figure 2: Attributes of extinct species versus richness in non-constrained food webs. Each point corresponds to the mean of the value of an attribute for extinct species in relation to the mean of the value of the attribute for all species in the food web. In A and B mean trophic position of extinct species relative to the mean trophic position of the food web (RMTP) for food webs without pollutant and with high pollutant stress, in C and D mean in-degree of extinct species relative to the mean in-degree of the food web (RMID) for food webs without pollutant and with high pollutant stress, and finally in E and F mean out-degree of extinct species relative to the mean out-degree of the food web (RMOD) for food webs without pollutant and with high pollutant stress. Different points represent levels of connectance (see legend within each plot). With γj =400 for low pollutant stress, γj =100 for medium pollutant stress, γj =10 for high pollutant stress. Circles, squares, diamonds, downward-triangles, leftward-triangles, rightward-triangles and upward-triangles correspond to 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25 level of

connectance respectively. Results not shown for low and medium levels of pollutant stress because there are no qualitative changes when compared with systems with high level of pollutant stress.

Figure 1

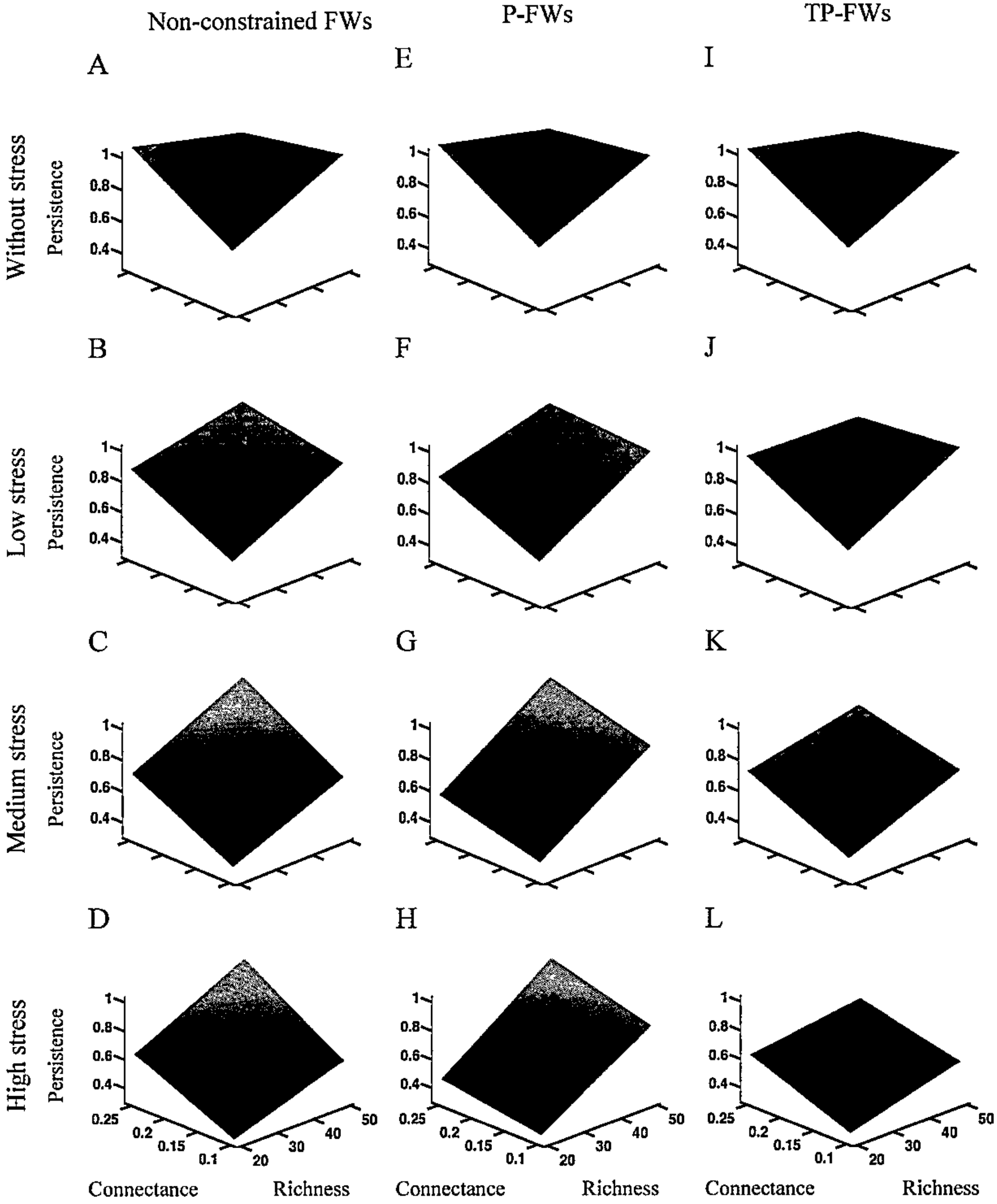
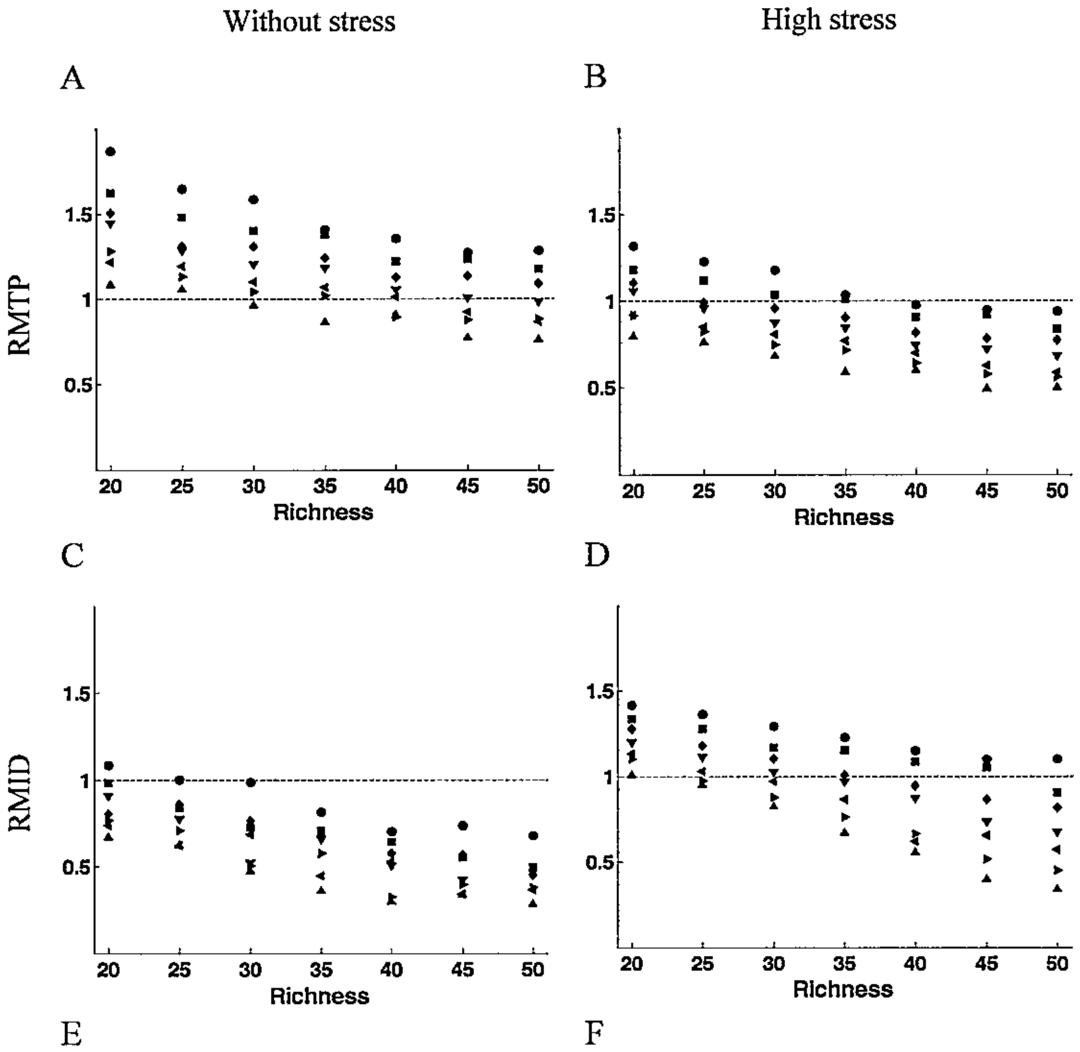
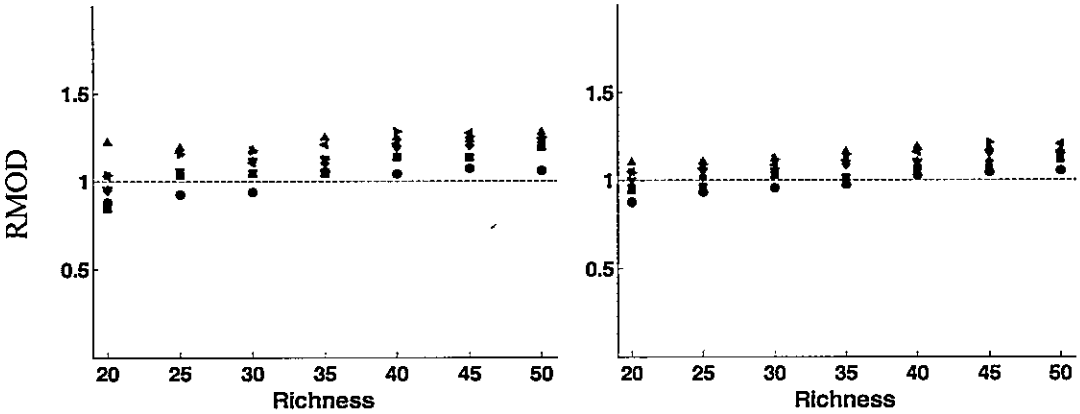

Non-constrained FWs
P-FWs
TP-FWs
A
E
I
Without stress
B
F
J
Low stress
C
G
K
Medium stress
D
H
L
High stress
Persistence
1
0.8
0.6
0.4
0.25
0.2
0.15
0.1
20
30
40
50
Connectance
Richness

Figure 2


Without stress
High stress
A
B
RMTP
1.5
1
0.5
20
25
30
35
40
45
50
Richness
C
D
RMID
E
F


RMOD
1.5
1
0.5
20
25
30
35
40
45
50
Richness
1.5
1
0.5
20
25
30
35
40
45
50
Richness

SA1. Supporting materials and methods.

The dynamic model

We used the bioenergetic model of Yodzis and Innes (1992) generalized to food webs of many species by Williams and Martinez (2004), where the temporal change of biomass of the species is represented by:

$$\frac{dB_i}{dt} = B_i r_i \kappa_i \left(1 - \frac{B_i}{K_i}\right) - x_i B_i + B_i \kappa_i \sum_{j=prey} x_i y_{ij} F_{ij} - \sum_{j=cons} \frac{B_j x_j y_{ji} F_{ji}}{\varepsilon_{ji} f_{ji}} \tag{S1}$$

Parameter r_i is the maximum mass-specific production rate, K_i is the system's carrying capacity, defined as K_{TOT}/number of producers in the food web, x_{i} is the mass-specific metabolic rate of species i, y_{ij} is the maximum consumption rate of species i when consuming species j, ε_{ij} is the conversion efficiency of consumed resources to biomass of consumer i, f_{ji} represents ingestion efficiency. K_{TOT} and f_{ji} were set to 5 and 1 respectively; ε_{ij} was set to 0.45 for herbivores and 0.85 for carnivores (Yodzis & Innes 1992). Function κ_i represents the harmful effect of the pollutant on growth rate of species i (see below), and F_{ij} is the functional response of predator i consuming prey species j. Parameters r_i, x_{i} and y_{ij} are allometric parameters computed following Brose et al. (2006), as:

$$r_i = 1 \tag{S2}$$

$$x_i = \frac{a_x}{a_r}\left(\frac{Mc}{Mp}\right)^{-0.25} \tag{S3}$$

$$y_{ij} = \frac{a_y}{a_x} \tag{S4}$$

where a_x, a_r and y_{ij} were fixed for invertebrate species at 0.314, 1 and 8 respectively. Predator-prey body size ratio was fixed at 2 and body size increased as a power of the trophic level (Brose et al. 2006).

The functional response of predator *j* consuming prey species *i* was represented by:

$$F_{ij} = \frac{B_i^h}{B_0^h + \sum\limits_{k=recursos} \alpha_{jk} B_k^h} \tag{S5}$$

were B_0 is half saturation constant fixed at 0.5 (Martinez et al. 2006; Brose et al. 2006), α_{ij}, is the preference of predator *i* for prey species *j*, that were equal for all prey of a given predator species *i* so if n_i is the number of prey of species *i*, $\alpha_{ij} = 1/n_i$ for each species *j* in the diet of species *i*. The *h* exponent was set to 2.

The total amount of pollutant accumulated within organisms of species *i*, B_i, is modeled through:

$$\frac{dB_i}{dt} = \omega_i C B_i + B_i \kappa_i \sum_{j=prey} x_i y_{ij} G_{ij} - x_i B_i - \sum_{j=cons} \frac{B_j x_j y_{ji} G_{ji}}{\varepsilon_{ji} f_{ji}} - \rho_i A_i \tag{S6}$$

where the first two terms correspond to the inputs of pollutant to species *i* from the environment and food respectively. The last three terms describe the losses of pollutant from species *i* due to: i) metabolic losses of biomass, ii) predation, and iii) excretion and egestion, respectively. Parameters ω_i and ρ_i are allometrically scaled following Hendricks et al. (2001).

The dynamics of the pollutant in the environment *C* was modeled as:

$$\frac{dC}{dt} = \Pi(t) + \sum_i \rho_i A_i - \sum_i \omega_i x_i C - \psi C \tag{S7}$$

where the function ∏(t) describes the input of the pollutant to the environment, ρ_i is the depuration rate of the pollutant (through excretion and egestion) of species i, A_i is the total amount of pollutant stored into individuals of species i; ω_i is the organisms' uptake rate of pollutant from the environment (i.e. by non-dietary routes) by species i and ψ is the decay rate of the pollutant in the environment due to biological and physicochemical processes, which was fixed at 10^{-4}.

A pulsed incorporation of pollutant to the environment was described by a peak function

$$\Pi(t) = \frac{P}{\sqrt{\pi\sigma}} \exp\left(-\frac{(t-M)^2}{\sigma}\right) \tag{S8}$$

where $P = 2x10^{10}$ is the total amount of pollutant to be released in a single pulse, M is the maximum (i.e. peak) pollutant concentration fixed at 500, and $\sigma=10^5$ is a shape parameter.

In our model we assume that the pollutant accumulated within the body of organisms (on a per unit biomass basis), reduce the growth rate of their population through an increase in the energy demand for detoxification and tissue repair. This energy reallocation results in a reduced biomass growth. Therefore, the deleterious effect of the pollutant was incorporated into the first and third term of equation 1 by means of the function

$$\kappa_j = 1 - \frac{A_j}{A_j + \gamma_j B_j + 1} \tag{S8}$$

which decreases from unity towards zero as accumulated pollutant A_j increases. Parameter γ_j sets the abruptness of the dose-effect curve and therefore represents the sensitivity of the species to pollutant accumulation. Highly sensitive species have small values of γ_j while tolerant species have large values. In this study γ_j was set to 10, 100 and 400 for high, medium and low pollutant stress.

Data analysis

For each type of topological structure we evaluated the effect of complexity on stability through a multiple regression analysis by taking species persistence as the dependent variable and both richness and connectance as the independent variables. We used the average persistence calculated over the 100 matrix replicates for each combination of connectance and richness to estimate the regression coefficients.

In addition, for the topology without constraints we characterized in each simulation the species that went extinct by calculating the mean value of each trait of interest among the extinct species, relative to the mean value of the trait among the entire set of species in the web. The measured traits were: trophic position, in-degree, out-degree and body size. All codes were implemented and executed in MATLAB.

Figure S1. Shape of complexity-stability relationship for increasing levels of pollutant stress. Linear regression coefficients obtained through the regessions of complexity versus stability for food webs of Non-constrined FWs (without topological constraints), P-FWs (with 5 basal species) and TP-FWs (with maximum trophic position of 4 ± 0.2). N=no pollutant stress, L= low pollutant stress (γ_j =400), M= medium pollutant stress (γ_j =100), H= high pollutant stress (γ_j =10).

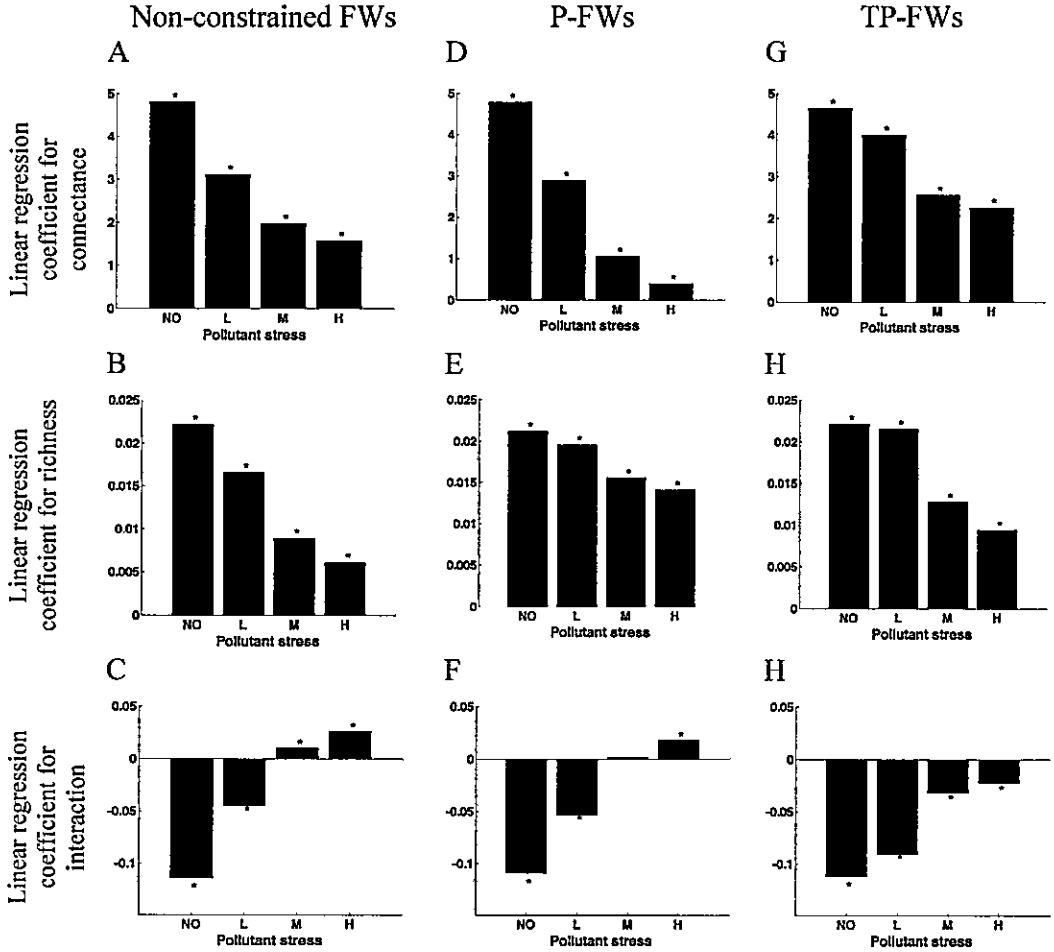


Figure S2. Complexity-Stability relationship in systems with increasing levels of polllutant stress. Relation between peristence with connectance and richness computed from a mutiple regression. T-FWs corresponds to the number of top species fixed at 3. Levels of pollutant stress were set as γ_j =400 for low, γ_j =100 for medium, and γ_j =10 for high pollutant stress.

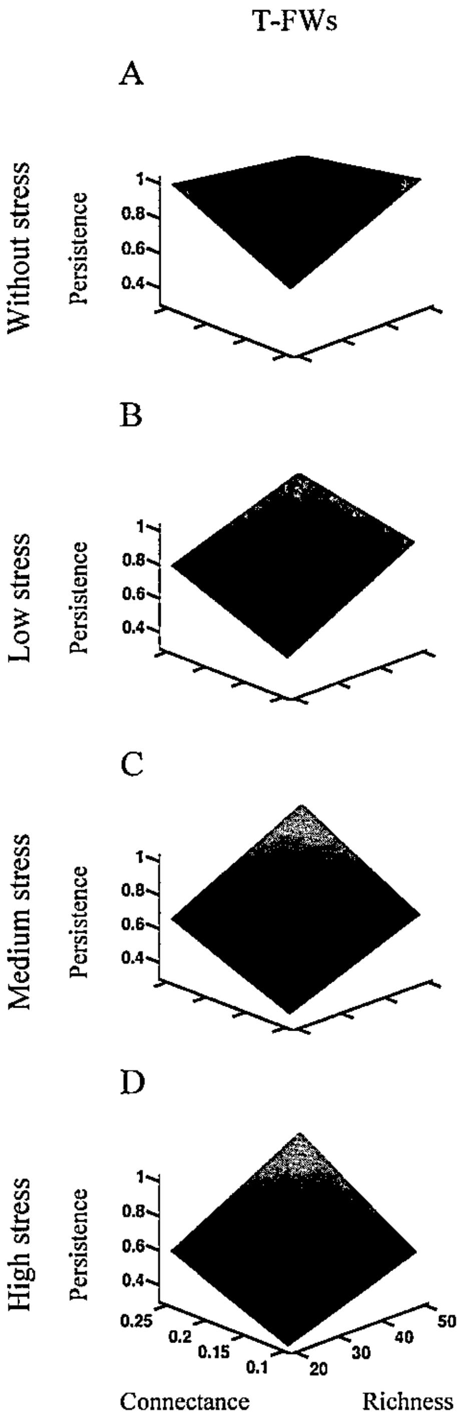

T-FWs
A
Without stress
Persistence
1
0.8
0.6
0.4
B
Low stress
Persistence
1
0.8
0.6
0.4
C
Medium stress
Persistence
1
0.8
0.6
0.4
D
High stress
Persistence
1
0.8
0.6
0.4
0.25
0.2
0.15
0.1
20
30
40
50
Connectance
Richness

Figure S3: Attributes of extinct species versus richness in food webs with fixed number of producer species. Each point shows the mean value of an attribute measure of extinct species in relation to the mean value of the attribute over all species in the food web. Plots A and B show the mean trophic position of extinct species relative to the mean trophic position of all species in the food web (RMTP). Plot A in food webs without pollutant, and plot B with high pollutant stress. Plots C and D show the mean in-degree of extinct species relative to the mean in-degree of all species in the food web (RMID). Plot C in food webs without pollutant, and plot D with high pollutant stress. Finally plots E and F show the mean out-degree of extinct species relative to the mean out-degree of all species in the food web (RMOD). Plot E in food webs without pollutant, and plot F with high pollutant stress. Different symbols represent levels of connectance. Circles, squares, diamonds, downward-triangles, leftward-triangles, rightward-triangles and upward-triangles indicate connectance levels of 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25 respectively. With $\gamma_j = 10$ for high pollutant stress. Results not shown for low and medium levels of pollutant stress because there are no qualitative changes when compared with systems with high level of pollutant stress.

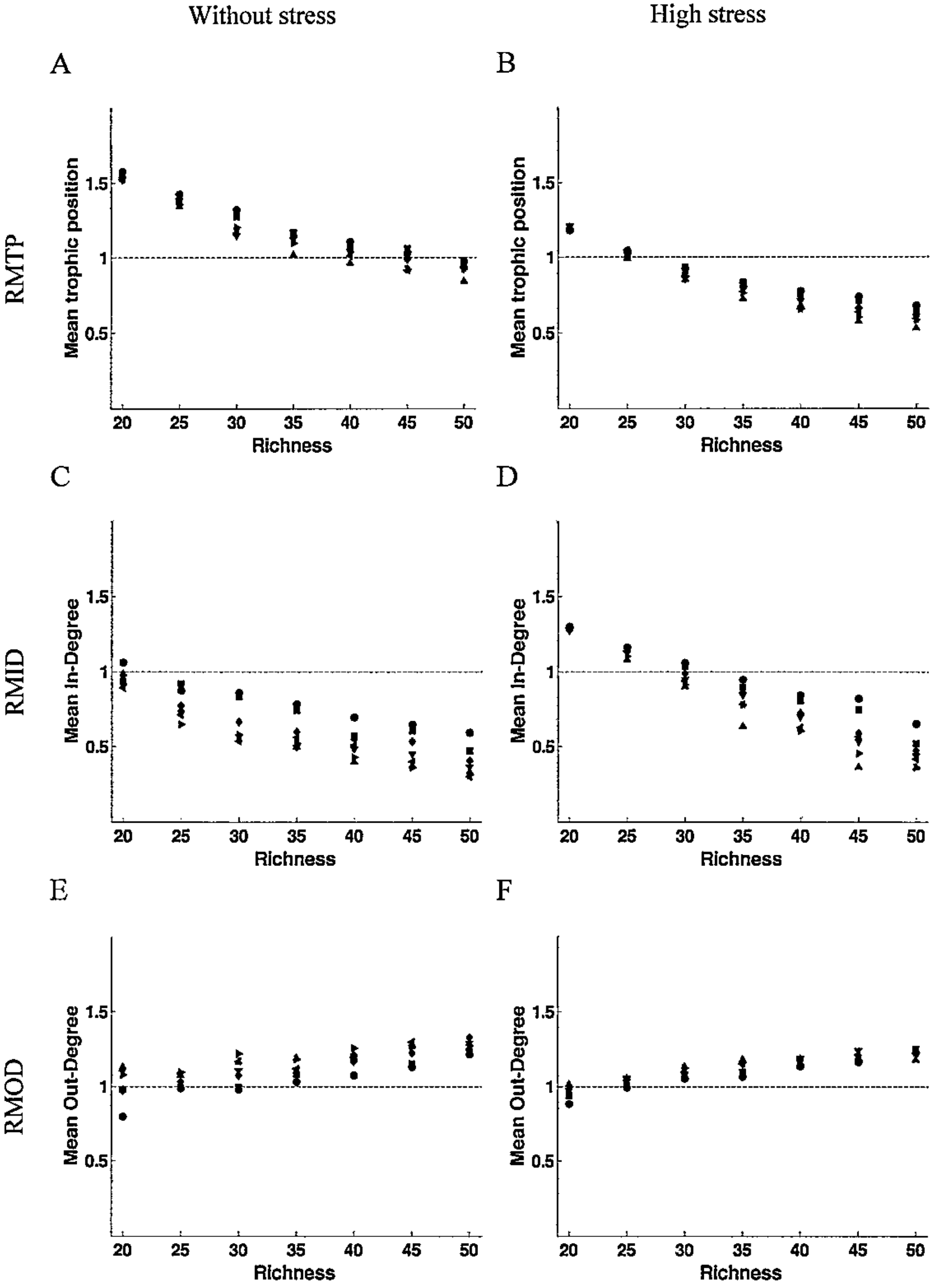
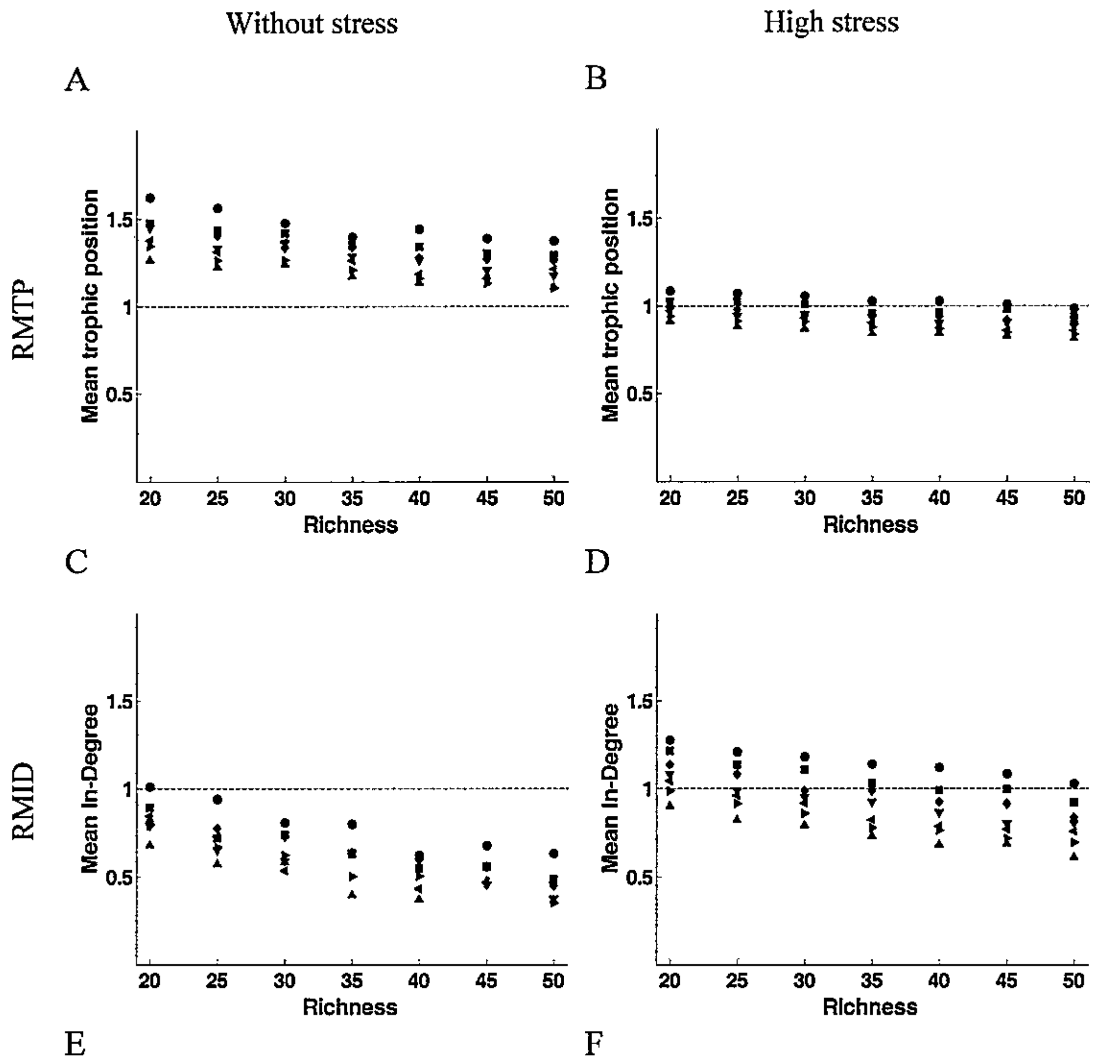
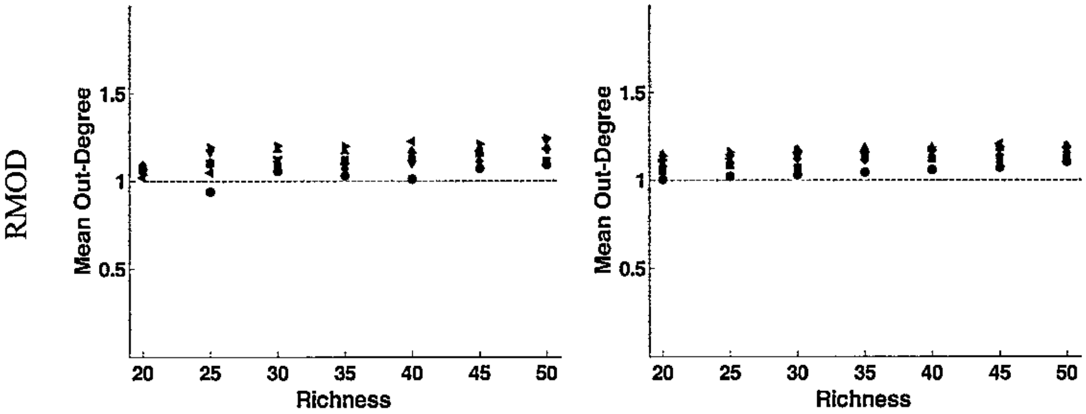

Without stress
High stress
A
B
C
D
E
F
RMTP
RMID
RMOD
Mean trophic position
Mean In-Degree
Mean Out-Degree
1.5
1
0.5
20
25
30
35
40
45
50
Richness

Figure S4: Attributes of extinct species versus richness in food webs with fixed maximum trophic position. Description of figure is the same as for figure S3.




RMOD
Mean Out-Degree
1.5
1
0.5
20
25
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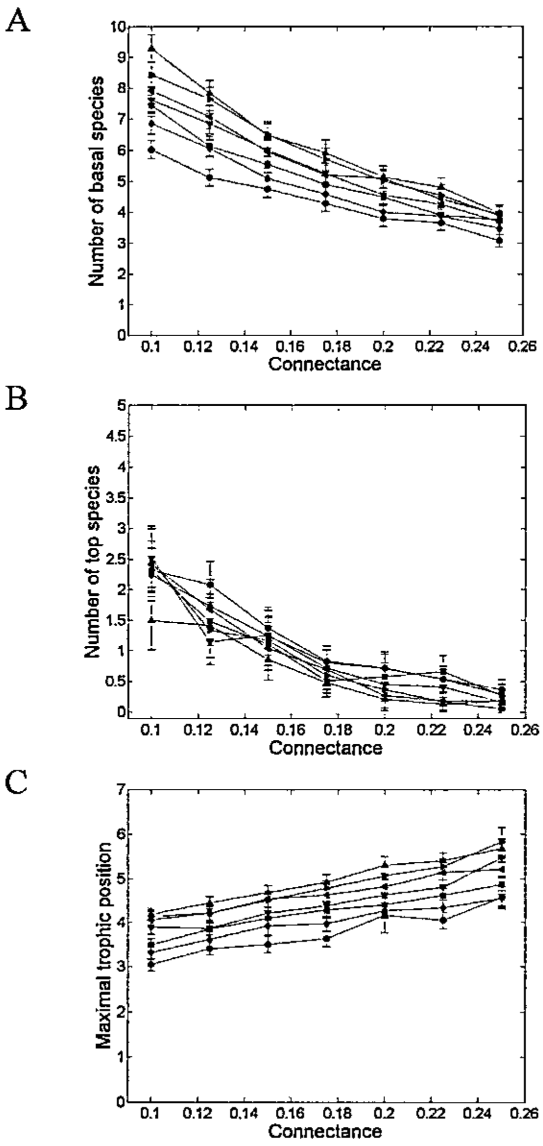
35
40
45
50
Richness
Mean Out-Degree
1.5
1
0.5
20
25
30
35
40
45
50
Richness

Figure S5. Effect of complexity on network attributes of non-constrained food webs. Changes in the number of basal species (A), number of top species (B) and maximum trophic position (C) with connectance (x-axis) and richness (different curves). Plots were generated from the model with no topological constraints. Circles, diamonds, squares, downward-triangles, leftward-triangles, rightward-triangles and upward-triangles correspond to 20, 25, 30, 35, 40, 45 and 50 species richness respectively.



SA2. Supporting references

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Yodzis, P. & Innes, S. (1992). Body size and consumer-resource dynamics. American Naturalist, **139**, 1151-1175.

Predator-prey body size ratio has a stronger stabilizing effect in polluted environments

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Abstract

Interaction strength is considered to be one of the structural determinants of the effect of food webs stability. Interaction strengths within food webs are associated to the ratio of body size between predators and their prey. Currently, when human driven disturbances are affecting ecosystems, it should be expected that the structure of and interaction strengths in food webs interact with such perturbations determining the stability of ecosystems. One of the most hazardous perturbations affecting ecosystems today is pollution. Lipophilic pollutants particularly, widely released to the environment, tend to accumulate in the tissues of organisms and be transmitted through the food chains. The final effect of these pollutants on species dynamics should be determined by the flux of biomass within food webs, which depends on the organization of interactions within the network and their strengths. In this study we evaluate the effects of predator-prey body size ratio, species richness and network connectance on the persistence of species in model food webs stressed by an accumulable pollutant. For our analyses we generated model food webs with different levels of complexity and run dynamic simulations using different levels of predator-prey body size ratio. We used the bioenergetic model for the dynamics of species biomasses. For the dynamics of bioaccumulated and environmental pollutant we developed appropriate expressions. As response variable we measured species persistence at the end of each simulation. In line with previous research, without pollution increasing body size ratio reverses, from negative to positive, the relationship between food web complexity and stability. We found three major novel outcomes as pollutant stress was increased: i) the body size ratio at which the sign of the complexity-stability relationship was reversed diminishes down to near unity ii) species persistence decreased with pollutant stress, but this effect was most strong at low body size ratios, iii) the positive relationship between species richness and persistence became stronger, iv) the strongest relationship between species richness and persistence was obtained at the body size ratio that best represent empirical observations. Pollutant driven perturbations has the potential to affect the complexity-stability relationship in food webs, making biodiversity a critical determinant of ecosystems stability.

Key-words: interaction strength, stability, complexity, pollution, predator-prey body size ratio.

Introduction

Since the foundational research of Robert May (1972) it has been recognized that interaction strength is one of the structural determinants of the effect of complexity on food webs stability. It has been shown that weak interaction strengths confer stability both in relatively simple food webs modules (McCann 1998) and in more complex networks (Kokkoris et al. 1999, Csermely 2006). Moreover, the distribution of interaction strengths within empirical food webs has been shown to be strongly skewed towards weak interaction strengths (Wootton 1997, Wootton 2005).

The distribution pattern of predator and prey body sizes dictates how interaction strengths are arranged within food webs (Jonsson and Ebenman 1998, Emmerson and Raffaelly 2004). Particularly it has been found that the increase in predator-prey body size ratio leads to an increase of per-capita interaction strength and to a decrease of per unit biomass interaction strength (Emmerson and Raffaelly 2004, Brose et al. 2006a). This effect of interaction strength determined by body size ratios could determine the stability of the whole food web (Brose et al. 2006b). In this sense, increasing ratios confers ecosystem stability and reverse the complexity-stability relationship from negative to positive (Brose et al. 2006b). This could be explained by the weaker interaction strengths among species on a per unit biomass basis that are generated at higher predator-prey body size ratios (Brose et al. 2006b).

Communities' size structure and interaction strength are expected to interact with human driven disturbances determining the stability of ecosystems (e.g. Kokkoris et al 1999). However, at the food web level no theoretical evidence has been presented for this kind of interactions. Pollution represents one of the most frequent example of such perturbations (Garay et al. 2012). A wide class of chemical pollutants is composed by lipophilic substances, which tend to accumulate in the tissues of organisms and be transmitted through the food chains (Kooi et al. 2008, Kelly et al. 2007). Therefore, the final effect of these pollutants on species dynamics should be determined by the flux of material and energy through food webs, which depends on the strength of predator-prey interactions and the way they are organized in the network. Thus, in this study we analyze the interplay between body size ratios and network topology as modulators of stability in communities subjected to pollutant stress. In particular, we evaluate the effects of predator-prey body size ratio, species richness and network connectance on the persistence of species in model food webs stressed by an accumulable pollutant.

Methods

To model the biomass dynamics of populations within the food webs we implemented the bioenergetic model of Yodzis and Innes (1992) generalized by Williams and Martinez (2004) for food webs of multiple species. We additionally modeled the total amount of pollutant accumulated within organisms (Kooi et al. 2008) and the pollutant in the environment. Models of both biomass and pollutant dynamics have allometric parameters, whose values were obtained following Brose et al. (2006b) and Hendricks et al. (2001). Values of allometric parameters scale to the power of body mass. Following Brose et al. (2006b) in this work we assumed that body mass of consumer species depends on predator-prey body size (mass) ratio Z and trophic position T in the following way:

$$M_C = Z^T \tag{1}$$

Trophic position was calculated following Levine (1980). We tested five levels of predator-prey body size ratios on logaritmic base 10 scale: Z= 0, 1, 2, 3 and 4 to assign the body size of consumer species within the food webs. Producers' body sizes were set to unity. For detailed information about the model, parameter definitions and values see Supplementary Information.

Using the algorithm widely known as "niche model" (Williams and Martinez 2000), we built a set of 900 model food webs of varying levels of species richness and network connectance. This algorithm generates model food webs whose structural properties are close to the ones observed in empirical trophic networks (Williams and Martinez 2008). Levels of species richness were set at 20, 30 and 40, while levels of connectance were 0.1, 0.15 and 0.2. For each combination of richness and connectance we generated 100 food webs.

Finally we coupled the dynamics of species and pollutant to the topological structure obtained from the niche model and run ten simulations of 5000 time steps for each adjacency matrix. Initial values of biomasses were taken randomly from a uniform distribution between 0.05 and 1. Initial values of the accumulated pollutant within populations and of the pollutant in the environment were set to zero. Species with densities bellow 10^{-30} were considered to be extinct and forced to zero. Stability was measured at the end of each simulation as species persistence, defined as the fraction of the initial species that exhibited positive population densities at the end of a simulation.

Results

We found that with no pollutant stress and at low predator-prey body size ratio (Fig. 1A) species persistence was between 40% and 70 %, observed with the higher and the lower species richness respectively. This indicates a negative relationship between persistence and species richness. At predator-prey body size ratio of 2 and higher the food web persistence for all levels of species richness was near ninety percent, and shows a positive relation at predator prey body size ratio of 4. These results mimic those previously reported with similar approaches (Brose et al. 2006b).

Figure 1 here

When incorporating a low level of pollutant stress (Fig. 1B) the negative relationship between species richness and food web persistence was reversed at a predator-prey body size ratio of about 2. As pollutant stress was increased three changes in results were observed: i) the body size ratio at which the complexity-stability relationship is reversed diminishes down to near 1, ii) at low body size ratios species persistence decreased, and iii) the positive relationship between species richness and persistence became stronger. Connectance had no qualitative effect of the results. Therefore figures only show food webs with a connectance of 0.15.

Discussion

Our results are in line with those of Brose et al. (2006b) who found that higher predator-prey body size ratios should turn a negative relationship between complexity and stability into a null or positive relation. Further, we found that environmental conditions and specifically pollutant has the potential to affect the complexity-stability relationship in a way where biodiversity became a more important determinant of ecosystems stability. These involve changes in the size ratio threshold for a positive effect of richness on persistence and a stepper effect of richness in the face of environmental pollutants. Note that the value of size ratio where the effect of richness was stepper (around 2) matches the range of body size ratios found from empirical data (Brose et al. 2006a, Brose et al. 2006b). Thus pollutants exert a higher impact on complexity-stability relationship at predator-prey ratios observed in nature.

Effects to highlight are by the one hand that increasing levels of pollution produced a steepness of the persistence-size ratio relationship. In unpolluted systems, communities of 40 and 20 species showed 60% and 30% of difference in persistence when compared size ratios of 0 and 4. However, these differences rose to 90% and 70% in highly polluted systems. On the other hand the stronger effect of species richness at high level of pollutant stress indicated that more simple communities are especially vulnerable to pollution. This effect could be due to that at high species richness there are more possible targets to which the pollutant can be propagated and accumulated, its effect being diluted within richer food webs. Nevertheless, higher body size ratios represent an insurance against this kind of environmental disruption. This result reinforce the view of body size structure of communities as a main component of biodiversity organization (Ritchie 2010, Arim et al. 2011, Yvon-Durocher et al. 2011b, Borthagaray et al. 2012, McCann 2012). Further, the eventual reinforcement of different components of global change is now a matter of concern (Scheffer et al. 2009). Changes in the size structure of communities are expected from changes in temperature (Yvon-Durocher et al. 2011a), ecosystems size (Marquet and Taper 1998, Burness et al. 2001), fragmentation (Borthagaray et al. 2012), and species invasion (Woodward and Hildrew 2001, Roy et al. 2002). Our results indicate that these changes further have the potential to determine the effect of pollutants ecosystems stability, which implies a prediction of reinforcement among components of global change.

In this study we showed that weak interaction strengths stabilize food webs in a way other than dampening predator-prey dynamics (McCann 2000). In food webs, weaker interaction strength per unit biomass led to a decrease in the flux and propagation of pollutant within the network, thus preventing bioaccumulation and harmful effects of pollution. Within natural food webs the distribution of interaction strength is more complex, with a high frequency of lower interaction strengths (Raffaelly 1996, Wootton 1997). In line with the findings of Berlow (1999), McCann (2000) and Brose et al. (2006b) our results suggest that conserving the weak interaction strengths within food webs should protect species from extinction when facing perturbation by pollution.

Acknowledgements

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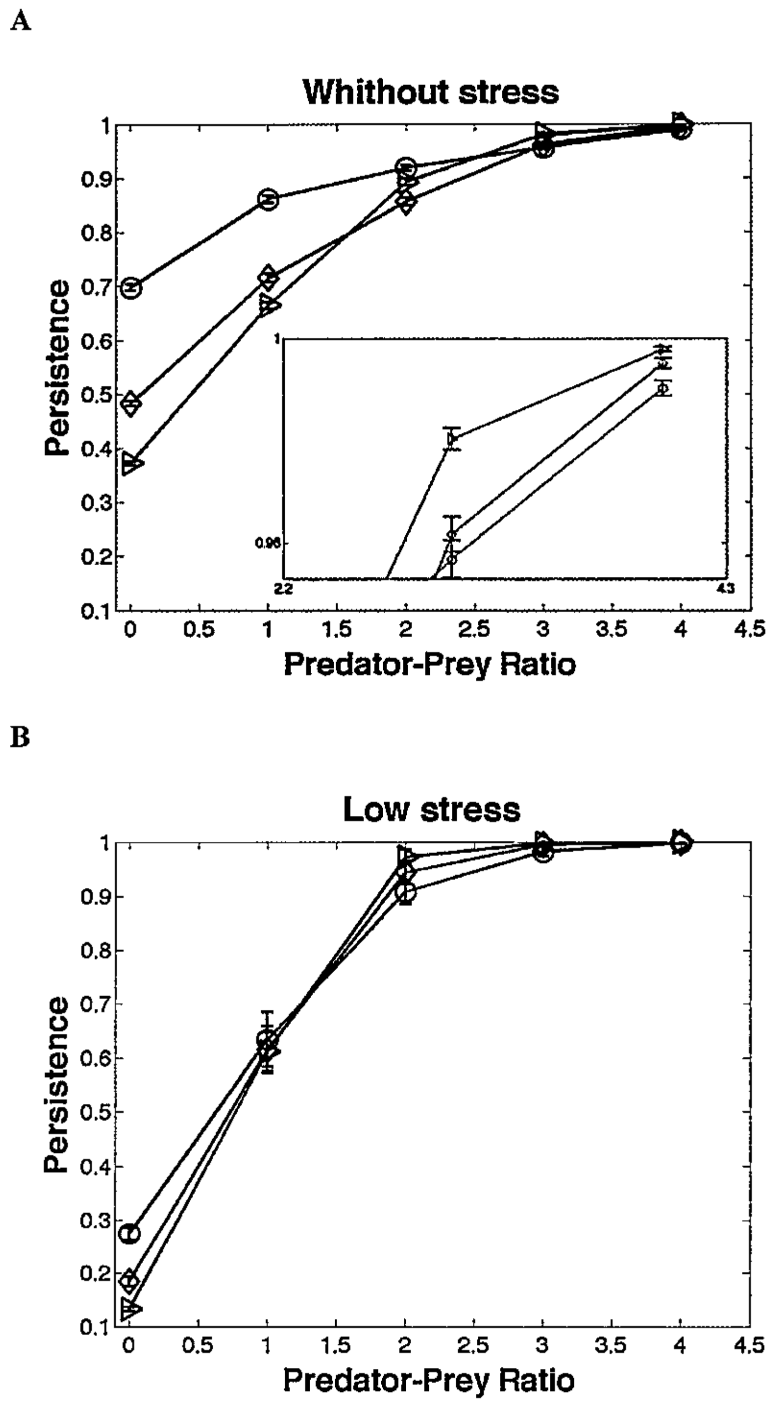
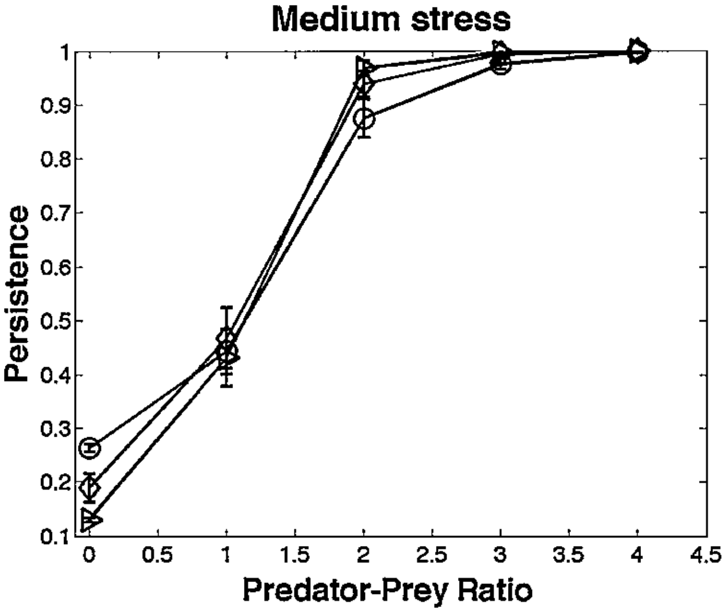
Figure Captions

Figure 1: Effect of predator-prey body size ratio on food web persistence. Plot A shows results for systems without pollutant stress. Plots B-D show results for systems with low (γ_j =1000), medium (γ_j =800) and high (γ_j =100) levels of pollutant stress respectively. Circles, diamond and triangules correspond to levels 20, 30 and 40 of species richness. Plot in A correspond to 10 simulations by 100 adjacency matrices while plots in B-E correspond to 2 simulations by 25 adjacency matrices.

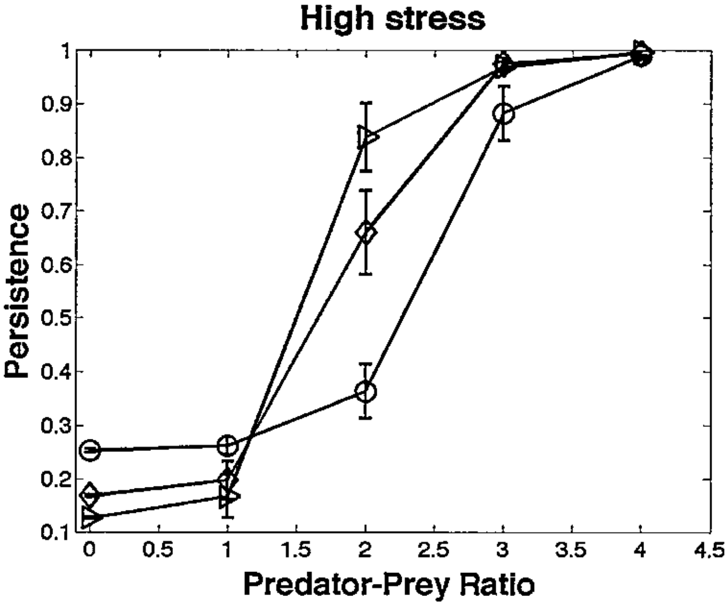
Figure 1


A
Whithout stress
Persistence
Predator-Prey Ratio
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
1
0.96
22
43
B
Low stress
Persistence
Predator-Prey Ratio
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5

C


Medium stress
Persistence
Predator-Prey Ratio
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5

D


High stress
Persistence
Predator-Prey Ratio
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5

Appendix 1

The dynamic model

We used the bioenergetic model of Yodzis and Innes (1992) generalized to food webs of many species by Williams and Martinez (2004), where the temporal change of biomass of the species is represented by:

$$\frac{dB_i}{dt} = B_i r_i \kappa_i \left(1 - \frac{B_i}{K_i}\right) - x_i B_i + B_i \kappa_i \sum_{j\text{-}prey} x_i y_{ij} F_{ij} - \sum_{j\text{-}cons} \frac{B_j x_j y_{ji} F_{ji}}{\varepsilon_{ji} f_{ji}} \tag{S1}$$

Parameter r_i is the maximum mass-specific production rate, K_i is the system's carrying capacity, defined as K_{TOT}/number of producers in the food web, x_i is the mass-specific metabolic rate of species i, y_{ij} is the maximum consumption rate of species i when consuming species j, ε_{ij} is the conversion efficiency of consumed resources to biomass of consumer i, f_{ji} represents ingestion efficiency. K_{TOT} and f_{ji} were set to 5 and 1 respectively; ε_{ij} was set to 0.45 for herbivores and 0.85 for carnivores (Yodzis & Innes 1992). Function κ_i represents the harmful effect of the pollutant on growth rate of species i (see below), and F_{ij} is the functional response of predator i consuming prey species j. Parameters r_i, x_i and y_{ij} are allometric parameters computed following Brose et al. (2006), as:

$$r_i = 1 \tag{S2}$$

$$x_i = \frac{a_x}{a_r}\left(\frac{Mc}{Mp}\right)^{-0.25} \tag{S3}$$

$$y_{ij} = \frac{a_y}{a_x} \tag{S4}$$

where a_x, a_r and y_{ij} were fixed for invertebrate species at 0.314, 1 and 8 respectively. Predator-prey body size ratio increased as a power of the trophic level (Brose et al. 2006) and was set to 0, 1, 2, 3 or 4 to evaluate the effect of predator-prey body size ratio on the complexity-stability relationship.

The functional response of predator j consuming prey species i was represented by:

$$F_{ij} = \frac{B_i^h}{B_0^h + \sum_{k=recursos} \alpha_{jk} B_k^h} \tag{S5}$$

were B_0 is half saturation constant fixed at 0.5 (Martinez et al. 2006; Brose et al. 2006), α_{ij}, is the preference of predator i for prey species j, that were equal for all prey of a given predator species i so if n_i is the number of prey of species i, $\alpha_{ij} = 1/n_i$ for each species j in the diet of species i. The h exponent was set to 2.

The total amount of pollutant accumulated within organisms of species i, B_i, is modeled through:

$$\frac{dB_i}{dt} = \omega_i C B_i + B_i \kappa_i \sum_{j=prey} x_i y_{ij} G_{ij} - x_i B_i - \sum_{j=cons} \frac{B_j x_j y_{ji} G_{ji}}{\varepsilon_{ji} f_{ji}} - \rho_i A_i \tag{S6}$$

where the first two terms correspond to the inputs of pollutant to species i from the environment and food respectively. The last three terms describe the losses of pollutant from species i due to: i) metabolic losses of biomass, ii) predation, and iii) excretion and egestion, respectively. Parameters ω_i and ρ_i are allometrically scaled following Hendricks et al. (2001).

The dynamics of the pollutant in the environment C was modeled as:

$$\frac{dC}{dt} = \Pi(t) + \sum_i \rho_i A_i - \sum_i \omega_i x_i C - \psi C \qquad \text{(S7)}$$

where the function $\prod(t)$ describes the input of the pollutant to the environment, ρ_i is the depuration rate of the pollutant (through excretion and egestion) of species i, A_i is the total amount of pollutant stored into individuals of species i; ω_i is the organisms' uptake rate of pollutant from the environment (i.e. by non-dietary routes) by species i and ψ is the decay rate of the pollutant in the environment due to biological and physicochemical processes, which was fixed at 10^{-4}.

A pulsed incorporation of pollutant to the environment was described by a peak function

$$\Pi(t) = \frac{P}{\sqrt{\pi\sigma}} \exp\left(-\frac{(t-M)^2}{\sigma}\right) \qquad \text{(S8)}$$

where $P = 2\text{x}10^{10}$ is the total amount of pollutant to be released in a single pulse, M is the maximum (i.e. peak) pollutant concentration fixed at 500, and $\sigma=10^5$ is a shape parameter.

In our model we assume that the pollutant accumulated within the body of organisms (on a per unit biomass basis), reduce the growth rate of their population through an increase in the energy demand for detoxification and tissue repair. This energy reallocation results in a reduced biomass growth. Therefore, the deleterious effect of the pollutant was incorporated into the first and third term of equation 1 by means of the function

$$\kappa_j = 1 - \frac{A_j}{A_j + \gamma_j B_j + 1} \qquad \text{(S8)}$$

which decreases from unity towards zero as accumulated pollutant A_j increases. Parameter γ_j sets the abruptness of the dose-effect curve and therefore represents the sensitivity of the species to pollutant accumulation. Highly sensitive species have small values of γ_j while tolerant species have large values. In this study γ_j was set to 100, 800 and 1500 for high, medium and low pollutant stress.

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Modularity stabilizes food webs subjected to pollutant stress.

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Abstract

Pollution represents one of the mayor threats to biodiversity. A wide class of pollutants is prone to accumulate within the tissues of the organisms, being consequently transmitted and propagated through food webs via consumer-resource interactions. Thus, the final effects of accumulable pollutants could be determined by the structure of food webs and not only by the susceptibility of the constituent species. One important structural attribute of food webs is modularity. Modularity has been proposed as a determinant of network stability and species persistence. In this study we evaluate the effect of network modularity and species richness on long-term species persistence in communities subjected to pollutant stress. For our analyses we used model food webs with different levels of modularity that were generated with the generalized niche model. For the dynamics of species biomasses we used de bioenergetic model, and for the dynamics of bioaccumulated and environmental pollutant we developed appropriate expressions. As response variable we measured species persistence at the end of each simulation. We found that modularity promoted the stability of food webs subjected to pollutant stress, and this effect was more pronounced at higher exposure to pollutants. In addition we found that food webs with higher species richness were more robust to decreased modularity. Incorporating a reference perturbation that lacked the fundamental features of pollutants, the results were reversed. This work advance in the consolidation of modularity, very ubiquitous in natural systems, as an important structural attribute of food webs, related to ecosystems stability and more so when facing pollution events. Our results reveal some structural properties of the communities leading to the loss of biodiversity, to be considered at the present time when human driven disturbances are affecting the structural complexity of ecological networks and reducing the variety of species and interactions observed in nature.

Key-words: modularity, stability, richness, pollution.

Introduction

It has become clear that food web interactions are not randomly arranged within ecological networks (e.g. Montoya et al. 2006) and that the structure of interactions within ecological systems determine network stability and species persistence (Thébault and Fontaine 2010, Rooney and McCann 2011). Some of the structural attributes of food webs that have been suggested as important determinants of stability are: the frequency of modules of omnivory (Fagan 1997, McCann and Hastings 1997, Emmerson and Yearsley 2004), nestedness (Thébault and Fontaine 2011), allometric degree distribution (Otto et al. 2007) and modularity (Pimm and Lawton 1980, Milo et al. 2002, Krause et al. 2003, Melián and Bascompte 2002, Ruiz-Moreno et al. 2006). Modularity, the degree of species organization into densely connected modules or compartments, has been found to be ubiquitous in real communities (Krause et al. 2003, Alesina and Pascual 2009, Rezende et al. 2009, Guimerà et al. 2010, Olesen et al 2007, Ramos-Jiliberto et al. 2010). Regarding its dynamical consequences, it has been suggested that modularity confers stability to complex ecological networks against perturbations (May 1972, Ruiz-Moreno et al. 2006) by confining the effects of disturbances within modules, thus impeding their spreading to the entire web (Stouffer and Bascompte 2011). Stouffer and Bascompte (2011) were the first in showing that modularity, through confining perturbations within a module, conferred stability to food webs that were subjected to a local perturbation, the deletion of a single species at a time. Nevertheless ecological systems are frequently facing perturbations that affect many species simultaneously and whose sphere of action is determined by the structure and dynamics of food webs. Little is known about the relationship between structure and dynamics of food webs experiencing such perturbations, such as pollution.

Pollution is currently one of the major threats to biodiversity (MEA 2005). Of particular interest are accumulable pollutants such as organic lipophilic pollutants, which are taken by organisms through both water and food (Kooi et al. 2008). These pollutants can be accumulated within the tissues of organisms (Newman and Clements 2008), having the potential to increase in concentration upper in the food webs, phenomenon known as biomagnification (e.g. Kelly et al. 2007). Since one of the sources of pollutant inflow into organisms is their food, pollutants are transmitted and propagated through the web of trophic interactions. For this reason, exposure to a pollutant of indeed a small subset of the species in the community may lead to its transport to and accumulation in many species, which could drive noticeable effects on community dynamics (e.g. Garay et al. 2012). Therefore, the final effects of accumulable pollutants in complex communities should not only depend on the susceptibility to the pollutant of each species, but on the structure of the web of trophic interactions. In this vein, we would expect that the effects of pollution on community dynamics should be suppressed in modular communities, through inhibiting the propagation of the stressor through the entire system. 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

In this study we used model food webs. The structure of interactions of the model food webs was obtained from the generalized niche model (Stouffer et al. 2006), which uses connectance, species richness and diet contiguity as input parameters. From the generalized niche model we built a set of 1,500 model food webs with a connectance of 0.25 and with three levels of species richness and five levels of network modularity. For each combination of richness and modularity we generated 100 food webs in form of adjacency matrices.

The levels of modularity were obtained through varying the parameter representing diet contiguity in the generalized niche model (Guimerà et al. 2010). For every value of diet contiguity the model yields a range of values of modularity. From 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.

To model the biomass dynamics of populations within the food webs we used a base the bioenergetic model of Yodzis and Innes (1992) generalized by Williams and Martinez (2004) for food webs of multiple species. We additionally modeled the total amount of pollutant accumulated within organisms (Kooi et al. 2008) and 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 the power of body mass. For detailed information about the model and parameters definitions and values see Appendix 1.

Finally we coupled the dynamics of species and pollutant to the topological structure obtained from the generalized niche model and run 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 accumulated pollutant within populations and for the pollutant concentration in the environment were set to zero. Species with densities bellow 10^{-30} were considered as extinct and forced to zero. In order to distinguish the effect of any global perturbation from the effect of pollution perturbation within the food webs we compare our results with the 1500 model food webs containing a reference model in which we apply a reduction in growth rate to all interacting species within the network.

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.

Results

In Figure 1 it is shown the relationship found between species persistence and both modularity level and species richness in three scenarios: i) without stress (Fig.1A), ii) with increasing levels of stress by an accumulable pollutant (Fig.1B-1D) and ii) with increasing levels of a reference, non-accumulable perturbation (Fig.1E-G).

Figure 1 here

In undisturbed systems (Fig. 1A) almost 100% of initial species persisted in the food webs after running the dynamic model, almost independently of the level of modularity and species richness. Only for the lowest level of species richness and at low levels of modularity the persistence shows a slight decrease from its maximum.

The effects of modularity and species richness on persistence become gradually positive as pollutant stress was increased (Fig. 1B-D). In food webs with the lowest species richness the persistence increases with modularity both in polluted (Fig. 1B-D) and non-polluted systems (Fig. 1A). On the other hand, food webs with the highest species richness maintained a maximum persistence through all the gradient of modularity for low to moderate levels of pollutant stress. Only under high stress a low modularity level decreased species persistence in food webs with the highest initial species richness, which led to a positive relation between modularity and persistence (Fig. 1D). This suggests that species richness makes food webs more robust to changes in modularity at least under moderate levels of pollutant stress.

On the other hand when we included the reference perturbation the effect of modularity and the effect of species richness on persistence become gradually negative as the level of the reference perturbation increases (Fig. 1 E-G). This contrasts with the positive relation between species richness/modularity and persistence found in food webs subjected to pollutant stress. Under this scenario the lower species richness makes food webs more robust to changes in modularity.

Discussion

In this study we showed that modularity effectively promoted the stability of trophic networks subjected to pollutant stress, a global perturbation that is transported through the trophic interactions. The opposite results obtained when including a reference perturbation that, as pollutant stress, affects multiple species within the network but, unlike pollutants, does not propagate through trophic interactions, suggest that the propagation of pollutant through food consumption should be a key property affected by modularity that lead to the enhancement of species persistence. In polluted systems species richness became an important determinant of food web stability since richer food webs were more robust to changes in modularity when food webs were subjected to pollutant stress. Conversely, systems with lower species richness proved to be the more sensitive to pollutant stress. These results suggest that the loss of species potentially driven by several sources of habitat degradation makes communities markedly fragile to pollution. Such hypothetical synergistic effects of disturbances require further research.

Stouffer and Bascompte (2011) considering a local perturbation (i.e. single species removal) showed that modularity had a positive effect on species persistence of model food webs. Nevertheless in this study we showed that modularity also conferred stability to food webs facing a global perturbation, particularly a perturbation transported through trophic interactions.

Recently Thébault and Fontaine (2010), after simulating the dynamics of model food webs but without including any environmental disturbance, found that modularity had a negative effect on food web persistence. In this study we obtained opposite results, where modularity and species richness had a null or positive effect on species persistence in the absence of perturbations. This discrepancy between our results and those of Thébault and Fontaine (2010) 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 ones; and the chosen levels of modularity (between 0.14 and 0.22) matches the range of modularity observed in empirical food webs (Guimerà et al. 2010). On the other hand, Thébault and Fontaine (2010) used communities of only two trophic levels and a wide range of modularity values (between 0.3 and 0.8).

In this study we showed that modularity, a key structural attribute of food webs, had a more pronounced effect on network stability when facing pollutant stress. It has been shown that modularity of food webs should arise through spatial habitat structure (e.g. Holt, 2002, Krause et al. 2003), body size structure (e.g. Petchey et al. 2008), phylogenetic patterns within communities (Cattin et al. 2004), or through any combination of them (Rezende et al. 2009). This research showed that the loss of modularity had a stronger negative effect on food web persistence as pollutant stress increased. These results turns specially important at the present time when human driven disturbances such as fragmentation and invasion of exotic species are reducing the modularity of natural communities though the loss of structural complexity of the habitat and the addition of generalist species (Rooney and McCann, 2012).

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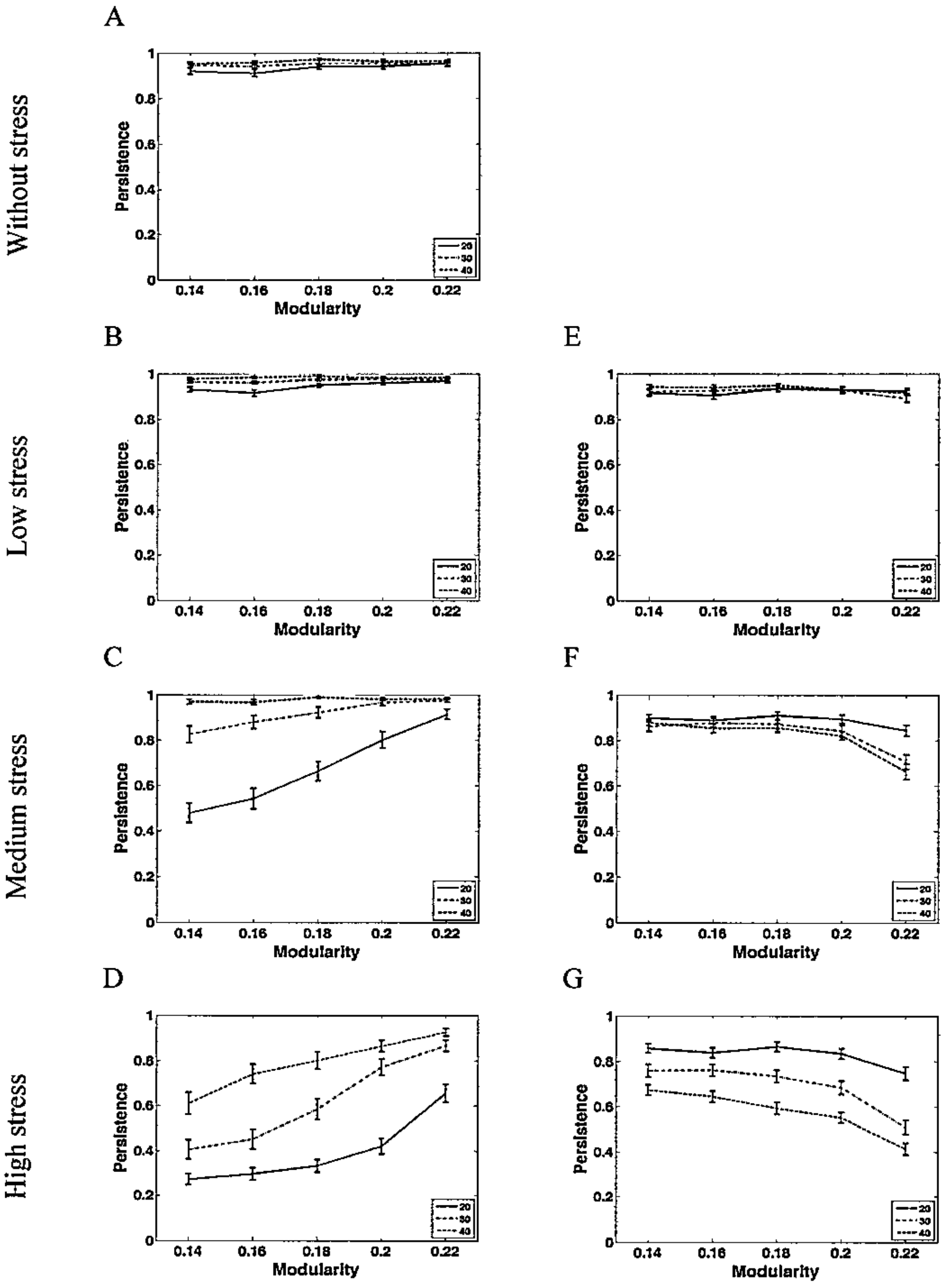
Figure Captions

Figure 1: Modularity-Persistence relationship in systems with increasing levels of polllutant stress. In A is plot for unperturbed food webs. In B,C and D are plots for food webs with low, medium and high levels of pollutant stress respectively. In E, F and G are plots for food webs with low, medium and high levels of a reference perturbation respectively. Curves within plots correspond to different levels of diversity (see the leyends for each curve at the bottom of each plot). With g_j =1000 for low pollutant stress, g_j =500 for medium pollutant stress, g_j =100 for high pollutant stress.

Figure 1


A
B
C
D
E
F
G
Without stress
Low stress
Medium stress
High stress
Persistence
Modularity
0
0.2
0.4
0.6
0.8
1
0.14
0.16
0.18
0.2
0.22
20
30
40

Appendix 1

The dynamic model

We used the bioenergetic model of Yodzis and Innes (1992) generalized to food webs of many species by Williams and Martinez (2004), where the temporal change of biomass of the species is represented by:

$$\frac{dB_i}{dt} = B_i r_i \kappa_i \left(1 - \frac{B_i}{K_i}\right) - x_i B_i + B_i \kappa_i \sum_{j=prey} x_i y_{ij} F_{ij} - \sum_{j=cons} \frac{B_j x_j y_{ji} F_{ji}}{\varepsilon_{ji} f_{ji}} \qquad \text{(S1)}$$

Parameter r_i is the maximum mass-specific production rate, K_i is the system's carrying capacity, defined as K_{TOT}/number of producers in the food web, x_i is the mass-specific metabolic rate of species *i*, y_{ij} is the maximum consumption rate of species *i* when consuming species *j*, ε_{ij} is the conversion efficiency of consumed resources to biomass of consumer *i*, f_{ji} represents ingestion efficiency. K_{TOT} and f_{ji} were set to 5 and 1 respectively; ε_{ij} was set to 0.45 for herbivores and 0.85 for carnivores (Yodzis and Innes 1992). Function κ_i represents the harmful effect of the pollutant on growth rate of species *i* (see below), and F_{ij} is the functional response of predator *i* consuming prey species *j*. Parameters r_i, x_i and y_{ij} are allometric parameters computed following Brose et al. (2006), as:

$$r_i = 1 \qquad \text{(S2)}$$

$$x_i = \frac{a_x}{a_r}\left(\frac{Mc}{Mp}\right)^{-0.25} \qquad \text{(S3)}$$

$$y_{ij} = \frac{a_y}{a_x} \qquad \text{(S4)}$$

where a_x, a_r and y_{ij} were fixed for invertebrate species at 0.314, 1 and 8 respectively. Predator-prey body size ratio was fixed at 2 and body size increased as a power of the trophic level (Brose et al. 2006).

The functional response of predator j consuming prey species i was represented by:

$$F_{ij} = \frac{B_i^h}{B_0^h + \sum_{k=recursos} \alpha_{jk} B_k^h} \qquad \text{(S5)}$$

were B_0 is half saturation constant fixed at 0.5 (Martinez et al. 2006; Brose et al. 2006), α_{ij}, is the preference of predator i for prey species j, that were equal for all prey of a given predator species i so if n_i is the number of prey of species i, $\alpha_{ij} = 1/n_i$ for each species j in the diet of species i. The h exponent was set to 2.

The total amount of pollutant accumulated within organisms of species i, B_i, is modeled through:

$$\frac{dB_i}{dt} = \omega_i C B_i + B_i \kappa_i \sum_{j=prey} x_i y_{ij} G_{ij} - x_i B_i - \sum_{j=cons} \frac{B_j x_j y_{ji} G_{ji}}{\varepsilon_{ji} f_{ji}} - \rho_i A_i \qquad \text{(S6)}$$

where the first two terms correspond to the inputs of pollutant to species i from the environment and food respectively. The last three terms describe the losses of pollutant from species i due to: i) metabolic losses of biomass, ii) predation, and iii) excretion and egestion, respectively. Parameters ω_i and ρ_i are allometrically scaled following Hendricks et al. (2001).

The dynamics of the pollutant in the environment C was modeled as:

$$\frac{dC}{dt} = \Pi(t) + \sum_i \rho_i A_i - \sum_i \omega_i x_i C - \psi C \qquad \text{(S7)}$$

where the function ∏(t) describes the input of the pollutant to the environment, ρ_i is the depuration rate of the pollutant (through excretion and egestion) of species i, A_i is the total amount of pollutant stored into individuals of species i; ω_i is the organisms' uptake rate of pollutant from the environment (i.e. by non-dietary routes) by species i and ψ is the decay rate of the pollutant in the environment due to biological and physicochemical processes, which was fixed at 10^{-4}.

A pulsed incorporation of pollutant to the environment was described by a peak function

$$\Pi(t) = \frac{P}{\sqrt{\pi\sigma}} \exp\left(-\frac{(t-M)^2}{\sigma}\right) \tag{S8}$$

where $P = 2\text{x}10^{10}$ is the total amount of pollutant to be released in a single pulse, M is the maximum (i.e. peak) pollutant concentration fixed at 500, and $\sigma=10^5$ is a shape parameter.

In our model we assume that the pollutant accumulated within the body of organisms (on a per unit biomass basis), reduce the growth rate of their population through an increase in the energy demand for detoxification and tissue repair. This energy reallocation results in a reduced biomass growth. Therefore, the deleterious effect of the pollutant was incorporated into the first and third term of equation 1 by means of the function

$$\kappa_j = 1 - \frac{A_j}{A_j + \gamma_j B_j + 1} \tag{S8}$$

which decreases from unity towards zero as accumulated pollutant A_j increases. Parameter γ_j sets the abruptness of the dose-effect curve and therefore represents the sensitivity of the species to pollutant accumulation. Highly sensitive species have small values of γ_j while tolerant species have large values. In this study γ_j was set to 100, 500 and 1000 for high, medium and low pollutant stress.

In the case of the reference perturbation we set the pollutant to zero and introduced in the biomass dynamics an additional mortality rate proportional to species biomass. The decrease in mortality rate had three levels, low, medium and high, obtained randomly from uniform distributions with standard deviation of 0.0025 and with means 0.003, 0.01 and 0.02 respectively.

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GENERAL DISCUSSION

Summary of results

In this study we investigated the effect of pollutants on the complexity-stability relationship, the effect of predator-prey body size ratio on the complexity-stability relationship in polluted environments and the effect of modularity on the persistence of species subjected to pollutant stress.

Regarding the complexity-stability relationship addressed in the first section, in this study it was found that in polluted systems as compared to non-polluted ones, the strength of the positive effect of complexity on stability was enhanced Additionally we showed that food web attributes that change systematically with complexity play an important role in shaping the complexity-stability relationship only when a pollutant was incorporated. Species more prone to extinction in polluted systems were generalist consumers. This suggest that structural attributes of food webs of lower level than complexity should be drivers that permit ecological systems to withstand human driven disturbances such as pollution.

In the second section we showed that predator-prey body size ratio generates a positive complexity-stability relationship, but this relationship was stronger under higher levels of pollutant stress. We additionally found that low predator-prey body size ratios drives to lower food web persistence as compared to food webs with no pollutant stress while at higher predator-prey body size ratio the persistence of almost hundred per cent of species was ensured for both polluted and non-polluted food webs. Higher predator-prey body size ratios drive lower per unit biomass interaction strength, which may inhibits the flux of pollutants through the food web, providing some kind of protection to pollutant exposure.

Finally in the third section of this study we showed that under a gradient of pollutant stress modularity effectively promoted the food web persistence (i.e. stability). The increase in pollutant stress also enhanced a weak positive relationship between species richness (i.e. complexity) and stability of food webs across the gradient of modularity, in such a way that under pollutant stress higher species richness confers a higher robustness to food webs when facing different levels of modularity. Additionally we evaluated a reference perturbation, which was included as an additional mortality rate within the growth rates of all component species. We obtained opposite results for the reference perturbation. Modularity had a negative effect on stability, and the weak positive relationship between species richness and food web persistence was reversed into a negative one.

Final remarks

This study present novel advances in the fields of ecotoxicology and community ecology. On the one hand we evaluated the effect of pollutants considering the complex structure of natural systems. On the other hand we extended the theory around the complexity-stability debate by including an environmental perturbation that nowadays is one of the major threats to biodiversity, pollution (MEA 2005, Primack 2008).

From this research it is obtained that maintaining the structure of food webs should be key in order to prevent species and interaction losses together with its functional consequences (McCann 2007) under environments disturbed by pollution. This is due to the characteristics of accumulable pollutants, since their pattern of propagation and therefore its final effects on community dynamics depends strongly on the underlying structure of food webs. Global change is threating biodiversity, ecosystem function and the sustainability of human society. This thesis analyzed the interrelationship among environmental stressors—in this case trophically transmitted pollutants—species richness and food web structure as determinants of ecosystems stability. The kind of interrelationship herein reported indicates that the different components of global change are interrelated in a way that seriously limit the extrapolation of theoretical or empirical results on the base of some of them.

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