

The more polluted the environment, the more important biodiversity is for food web stability

Leslie Garay-Narváez, Matías Arim, José D. Flores and Rodrigo Ramos-Jiliberto

L. Garay-Narváez and R. Ramos-Jiliberto (ramos.jiliberto@gmail.com), Centro Nacional del Medio Ambiente, Fundación de la Univ. de Chile, Av. Larrain 9975, CP 7880096, La Reina, Santiago de Chile, Chile. – M. Arim, Facultad de Ciencias and Centro Universitario Regional Este (CURE), Univ. de la República, Montevideo, Uruguay. – J. D. Flores, Dept of Mathematics, Univ. of South Dakota, 329 Dakota Hall, Vermillion, SD 57069, USA.

Human activities have led to massive influxes of pollutants, degrading the habitat of species and simplifying their biodiversity. However, the interaction between food web complexity, pollution and stability is still poorly understood. In this study we evaluate the effect exerted by accumulable pollutants on the relationship between complexity and stability of food webs. We built model food webs with different levels of richness and connectance, and used a bioenergetic model to project the dynamics of species biomasses. Further, we developed appropriate expressions for the dynamics of bioaccumulated and environmental pollutants. We additionally analyzed attributes of organisms' and communities as determinants of species persistence (stability). We found that the positive effect of complexity on stability was enhanced as pollutant stress increased. Additionally we showed that the number of basal species and the maximum trophic level shape the complexity–stability relationship in polluted systems, and that in-degree of consumers determines species extinction in polluted environments. Our study indicates that the form of biodiversity and the complexity of interaction networks are essential to understand and project the effects of pollution and other ecosystem threats.

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 threaten natural communities, driving the loss of species and their interactions (Primack 2008). Therefore, research on the effects that species richness and interactions (hereafter complexity) have 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 not well understood (Stouffer and Bascompte 2011, McCann 2012, Rooney and McCann 2012).

The study of the effects of complexity on the stability of ecological systems has become one of the cornerstones of ecological theory since the theoretical study of May (1972), which demonstrated that complexity by itself precludes stability (McCann 2000). Recent studies have been focused on revealing the form of the complexity–stability relationship by empirical means (reviewed by Ives and Carpenter 2007) and on searching for the attributes of species and communities that could produce greater stability of complex systems (Williams and Martinez 2000, Brose et al. 2006, Valdovinos et al. 2010). However, the scenarios in which the complexity–stability relationship has been mostly analyzed have rarely included explicitly specific

human-driven disturbances (Mulder et al. 2001, Dunne et al. 2002, Pfisterer and Schmid 2002, Ebenman et al. 2004, Eklöf and Ebenman 2006, Zhang and Zhang 2006, Romanuk et al. 2010). This is particularly true for pollutant driven disturbances, whose ecological consequences have been primarily studied considering systems of few species in which the role of complexity could not be determined (Rohr and Crumrine 2005, Liebig et al. 2008).

Some kinds of pollutants, particularly lipophilic pollutants such as polychlorinated dibenzodioxins and biphenyls, polybrominated biphenyls, aromatic hydrocarbons, organochlorine pesticides, and many metals are being released extensively to the environment either as industrial byproducts or as end products such as pesticides (Walker et al. 2001). Organisms incorporate these substances through both water and food (Kooi et al. 2008), and may accumulate them within their tissues. In addition, accumulable pollutants have the potential to be biomagnified, that is to say, increase their concentration within organisms as they are passed to higher levels in the food chains (Kelly et al. 2007). Therefore, accumulable pollutants are transmitted through trophic interactions, being spread in the community depending on its food web structure. Thus community complexity should 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 the ‘niche model’ (Williams and Martinez 2000), we built a set of 19600 model food webs of varying levels of species richness and network connectance. This algorithm generates model food webs whose structural properties are close to those observed in empirical trophic networks (Williams and 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 used 100 food webs.

Empirical and model food webs show certain structural attributes that change systematically with connectance and richness (Riede et al. 2010). We evaluated the importance of these covariates as determinants of the complexity–stability relationship in polluted and unpolluted environments. Thus for each level of connectance and richness 100 food webs were selected for each of the following four types of networks: 1) with no topological constraints (hereafter non-constrained FWs), 2) with five producer species (hereafter P-FWs), 3) with maximum trophic level within 4 ± 0.2 (hereafter TL-FWs), and 4) with three top predators (hereafter T-FWs). The number of producers used to select P-FWs and the value of the maximum trophic level used to select TL-FWs were taken from average values of this attributes obtained in non-constrained food webs at intermediate levels of both connectance and richness (Supplementary material Appendix 1 Fig. A5). The number of top predators used to select T-Fws was chosen arbitrarily.

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), in which the temporal change of biomass density of species i , B_i , is represented by:

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

where $r_i = 0$ and $x_i = 0$ for consumer and producer species respectively. The first two terms depict logistic growth rate for producers and exponential decrease for consumers in the absence of interactions. The last two terms correspond respectively to increase and decrease in biomass due to predation. Function F is the functional response of consumers. Function κ_i (Supplementary material Appendix 1 Eq. A10) represents the harmful effect of the pollutant on

the growth rate of species i and allowed us to evaluate four different scenarios for pollutant stress: without stress, low stress, medium stress and high stress. We used a generic gradient of pollutant stress and avoid referring to specific values associated with a particular pollutant.

We additionally modeled the dynamics of the amount of pollutant accumulated within the population A_i (Kooi et al. 2008) and the pollutant in the environment C as:

$$\frac{dA_i}{dt} = \omega_i C B_i + B_i \kappa_i \sum_{j=prey} x_j y_{ij} G_{ij} - x_i A_i - \sum_{j=cons} \frac{B_j x_j y_{ji} G_{ji}}{\epsilon_{ji} f_{ji}} - \rho_i A_i \quad (2)$$

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: 1) metabolic losses of accumulated pollutant, 2) predation, and 3) excretion and egestion of accumulated pollutant, respectively. Function G is the functional response in terms of accumulated pollutant. The dynamics of the pollutant in the environment C was modeled as:

$$\frac{dC}{dt} = \Pi(t) + \sum_i \rho_i A_i - \sum_i \omega_i C B_i - \Psi C \quad (3)$$

where the first and last terms represent the input of pollutant to the environment (Supplementary material Appendix 1 Eq. A9) and the decay rate of the pollutant. Models of both biomass and pollutant dynamics have allometric parameters, whose values were obtained from Brose et al. (2006) and Hendriks et al. (2001). Values of allometric parameters scale to the power of body mass (Supplementary material Appendix 1 Eq. A2–A4). For detailed information about the model, parameter definitions and values see Supplementary material Appendix 1.

Finally, we coupled the dynamics of species and pollutant to the topological structure obtained from the niche model and ran one simulation of 5000 time steps for each food web (Supplementary material Appendix 2 Fig. A1). Initial values for biomasses were chosen 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 below 10^{-30} were considered to be extinct and forced to zero. There is no permanent pollutant stress exerted on the community. A pulse of pollutant perturbed the species during the phase of transient dynamics, since the pollutant was degraded at the end of each simulation. This pulse of pollutant acts via reducing the species’ growth rate.

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 the Supplementary material). Additionally, at the end of each simulation we recorded in each food web the following characteristics of extinct species: 1) trophic level (following the algorithm of Levine 1980), 2) in-degree (number of species that are prey of the focal species), and 3) out-degree

(number of species that predate on the focal species). For these measures we calculated their mean values in extinct species for a given level of connectance and richness over all simulations divided by the corresponding mean value for all species for the respective level of connectance and richness over all simulations. All codes were implemented and executed in MATLAB (R2011b, Mathworks Inc.).

Results

In the absence of pollutants, and without topological constraints, species persistence increased with connectance and richness. Nevertheless, the interaction effect between these factors was negative (Fig. 1C), with the result that at higher values of both connectance and richness persistence was lower than expected with an additive effect (Fig. 2A). As the pollutant stress increased the main effects from the regression analysis decreased in magnitude (Fig. 1A–B). However, the interaction term changed from negative to positive, indicating a transition from antagonistic to synergistic relationships between connectance and species richness (Fig. 1C, Fig. 2A–D). This resulted in the

overall positive effect of both connectance and richness on persistence being enhanced by increasing levels of pollutant stress (Fig. 2A–D). Even though species persistence was greater for all levels of richness and connectance in non-polluted food webs 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 above 0.9, close to the values obtained for the same levels of complexity in non-polluted systems.

Evaluating the role of additional food web attributes, we found that when the pollutant was not included the results were the same for the four tested types of food webs (Fig. 2A, E, I, Supplementary material Appendix 2 Fig. A2A). In contrast, in polluted food webs only topologies with a fixed number of top predators (i.e. T-FWs; Supplementary material Appendix 2 Fig. A2) behaved the same as the webs with unconstrained topologies (Fig. 2A–D); therefore we will discuss this scenario no further. The number of producer species and the maximum trophic level associated with changes in complexity became determinants of the complexity–stability relationship in polluted systems. The number of producer species increased with richness and decreased with connectance in

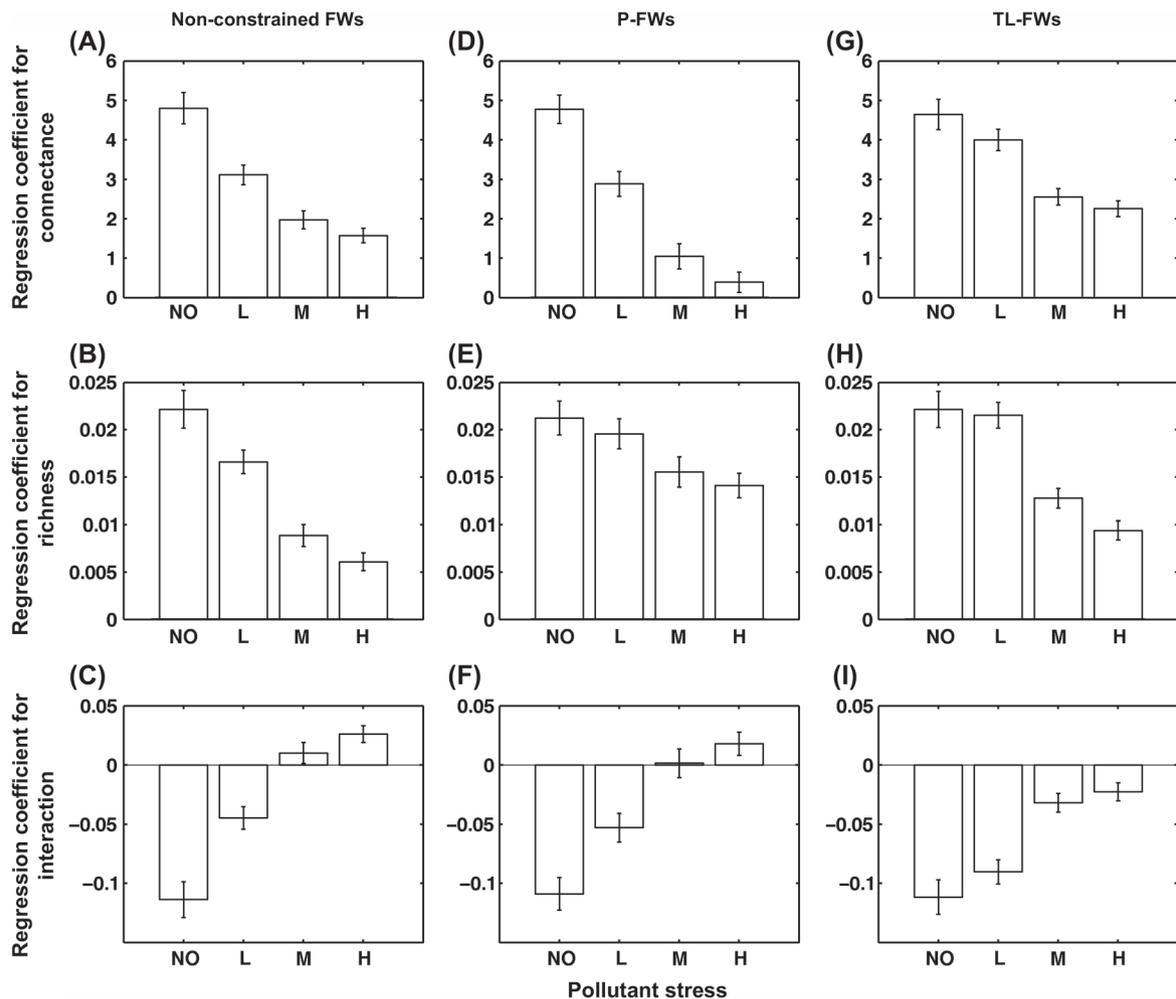


Figure 1. Shape of the complexity–stability relationship for increasing levels of pollutant stress. Linear regression coefficients obtained through the regressions of complexity versus stability for food webs: Non-constrained FWs (without topological constraints; A–C), P-FWs (with five basal species; D–F) and TL-FWs (with maximum trophic level of 4 ± 0.2 ; G–I). 95% confidence intervals are shown. N = no pollutant stress, L = low pollutant stress ($\gamma_i = 400$), M = medium pollutant stress ($\gamma_i = 100$), H = high pollutant stress ($\gamma_i = 10$).

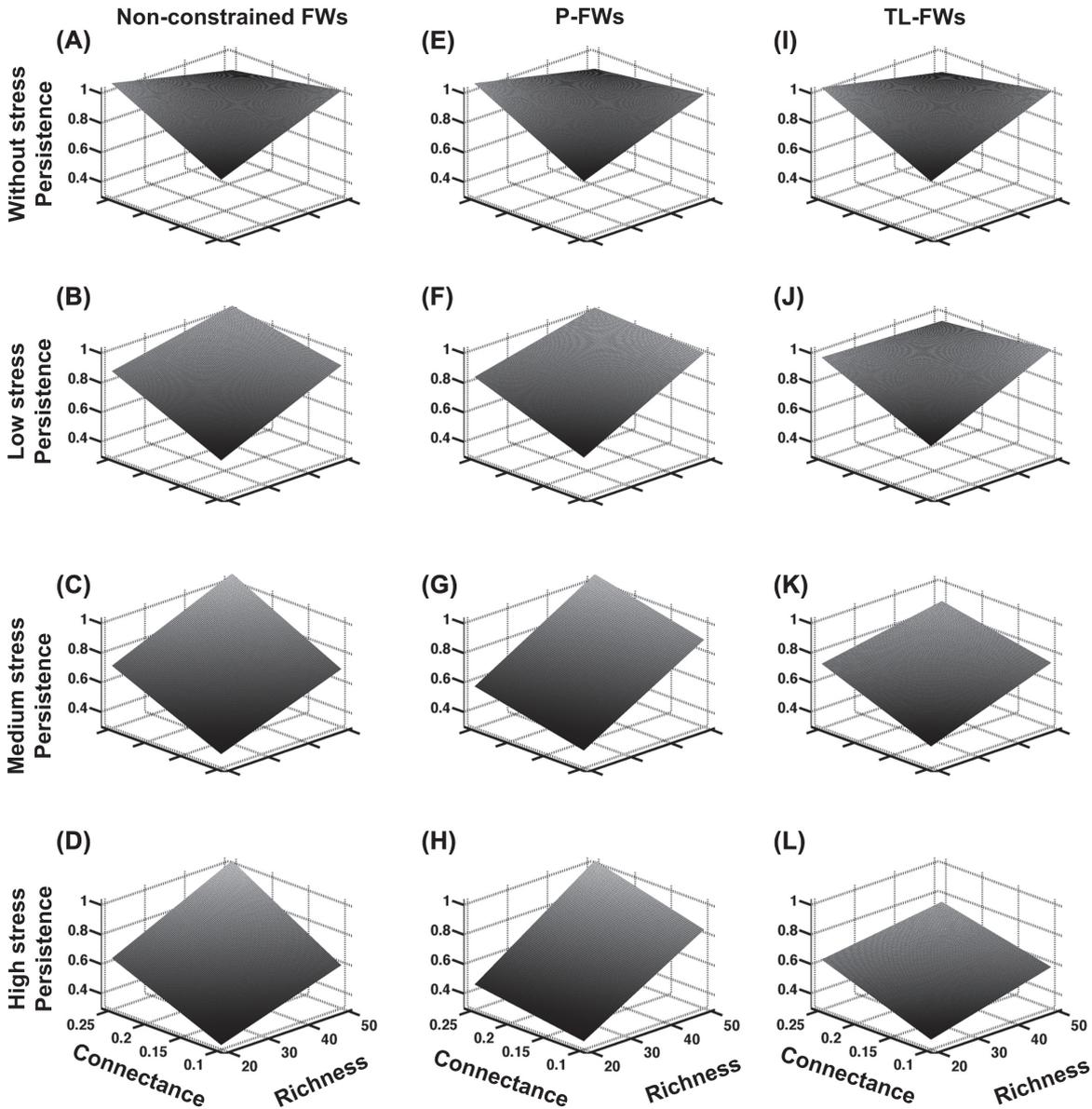


Figure 2. Complexity–stability relationship in systems with increasing levels of pollutant stress. (A–D) show results obtained from food webs: non-constrained FWs (without topological constraints), (E–H) P-FWs (with five basal species), and (I–L) TL-FWs (with maximum trophic level of 4 ± 0.2). Data for plots were generated from coefficients of linear regression analyses in which connectance and richness were independent variables and persistence was the dependent variable. Parameter γ_i was set to 400, 100 and 10 for low, medium and high pollutant stress, respectively.

non-constrained food webs (Supplementary material Appendix 2 Fig. A3A). We found that for topologies with a fixed number of producer species (i.e. P-FWs) the positive effect of connectance on species persistence was suppressed (Fig. 1D, Fig. 2F–H) while the positive effect of richness was enhanced (Fig. 1E, Fig. 2F–H). This indicates that selecting topologies with a fixed number of producers, thus preventing the decrease of the number of producer species, associated with increased connectance or decreased richness, led to lower species persistence. By contrast, in topologies with a fixed maximum trophic level (i.e. TL-FWs), which in non-constrained food webs increased with connectance and richness (Supplementary material Appendix 2 Fig. A3C), the strength of the relationship

between connectance/richness and persistence was enhanced, as is shown by the main effects from the regression analysis (Fig. 1G–H). The negative interaction between connectance and richness on persistence was reinforced, and unlike the non-constrained topology, it was negative through all levels of pollutant stress (Fig. 1I). Accordingly, increases in the maximum trophic level with connectance and richness had a positive effect on species persistence, since preventing its increase (with connectance and richness) by selecting topologies with a fixed maximum trophic level suppressed the persistence of species, specially at high complexity levels (Fig. 2J–L).

In non-constrained and non-polluted food webs, species that went extinct during the simulations exhibited a high

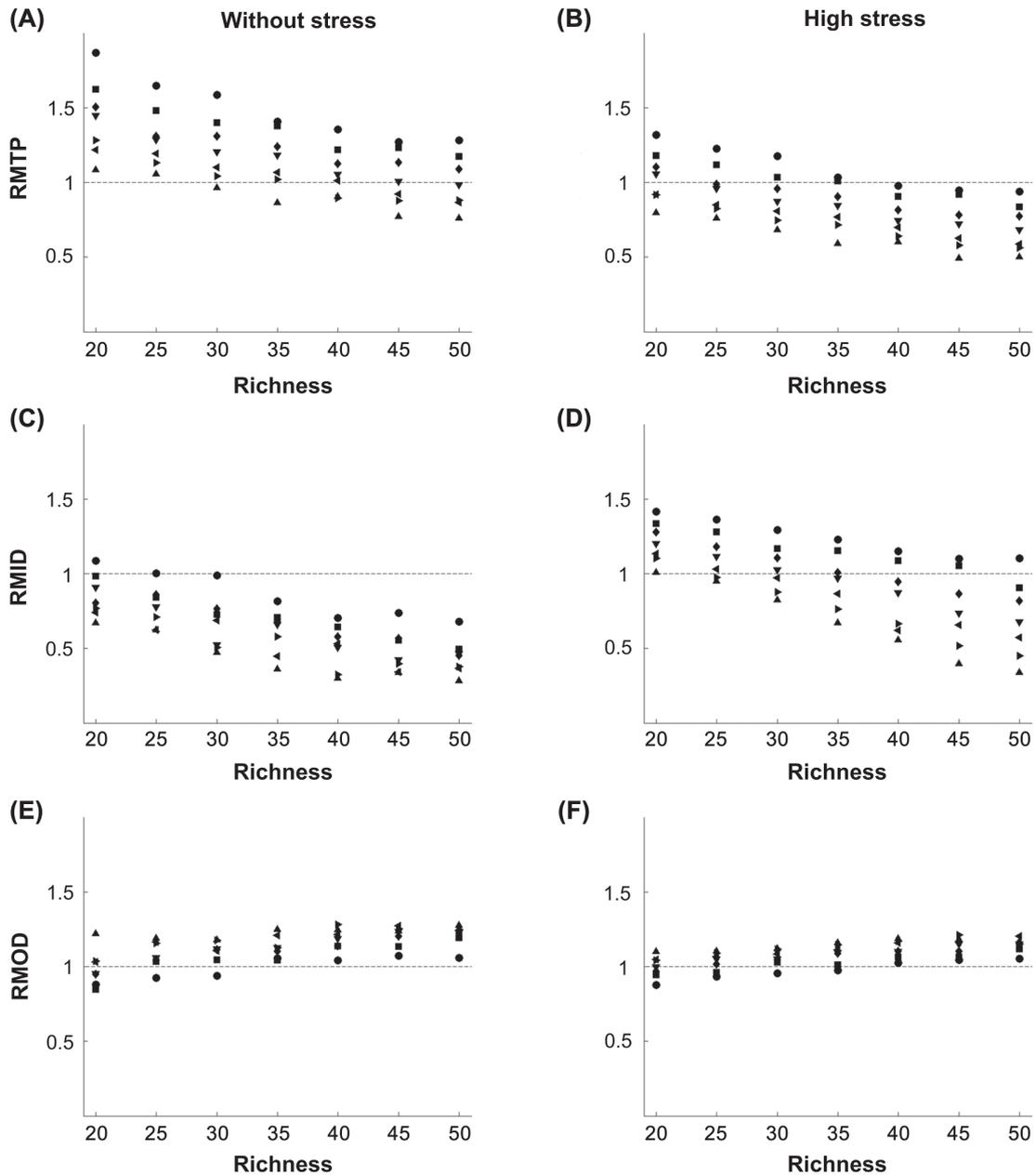


Figure 3. Attributes of extinct species versus species richness in non-constrained food webs. Left and right columns show results for food webs without and with high pollutant stress, respectively. (A–B): mean trophic level of extinct species relative to the mean trophic level of food webs (RMTP). (C–D) mean in-degree of extinct species relative to the mean in-degree of food webs (RMID). (E–F) mean out-degree of extinct species relative to the mean out-degree of food webs (RMOD). Circles, squares, diamonds, downward-triangles, leftward-triangles, rightward-triangles and upward-triangles represent 0.1, 0.125, 0.15, 0.175, 0.2, 0.225 and 0.25 of web connectance respectively. Results for low and medium stress levels showed minimal differences with those of high stress.

mean trophic level relative to all species in the food webs. However, the relative mean trophic level of extinct species decreased with species richness and network connectance (Fig. 3A). When the pollutant was incorporated into the systems, the trophic level of extinct species fell below the mean trophic level of the food web for most levels of richness and connectance (Fig. 3B). This indicates that extinct species in polluted environments had an intermediate trophic level within food chains. The mean number of prey of extinct species was lower than the average when the pollutant was not incorporated (Fig. 3C). This value

increased with stress, approaching the mean value of the food web (Fig. 3D), and showed a decrease with complexity. Finally, the relative mean number of predators of extinct species increased with richness and connectance (Fig. 3E), exhibiting a slight decrease when pollutant stress was incorporated (Fig. 3F). The effect of connectance on these three metrics was suppressed when food webs were constrained (Supplementary material Appendix 2 Fig. A4, A5). This suggests that changes in food web attributes driven by changes in connectance (i.e. decreased number of producers and increased maximum trophic level) 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.

Discussion

In this study we showed that food webs disturbed by pollution maintain the positive relationship between complexity and stability reported for undisturbed (Brose et al. 2006) and disturbed communities (Dunne et al. 2002, Ebenman et al. 2004, Eklöf and Ebenman 2006). However, in polluted systems complexity appears to be a more relevant determinant of stability. In these food webs the addition (or deletion) of species or links produced greater changes in species persistence, indicating a main role of biodiversity complexity in the potential of ecosystems to deal with polluted environments. In fact, polluted and unpolluted communities showed similar patterns of persistence only at high levels of connectance and richness (Fig. 1).

At a time when the determinants of a positive complexity–stability relationship is starting to be understood, the roles played by other factors or processes have been practically neglected (Rooney and McCann 2012). Nevertheless, Romanuk et al. (2010) found that in rock pool communities the positive relationship between stability (measured as variability of community abundance) and diversity was unaffected by different levels of decrease in water volume. Microcosm experiments suggested that for a set of environmental conditions food webs converge to similar levels of connectance (Fox and McGrady-Steed 2002). Some of the first attempts to collect food web information from different places, were oriented to evaluate the effect of environmental variability on complexity (Briand 1983); connectance (Briand 1983) and food chain length (Jennings and Warr 2003), were negatively related to disturbance. Interaction strength and specifically the stability role of weak links on the whole food web are related to its potential for damping 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 where the food web is located. Here we found that pollutant stress interacts 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 (May 1972, Brose et al. 2006).

This study also advanced in the understanding of the structure of ‘complexity’ (richness and connectance), identifying food web attributes – number of basal species, number of top species and maximum trophic level – 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 a pollutant is incorporated. In polluted systems an increase in the number of producers

(correlated with species richness) had a negative effect on persistence. Community carrying capacity was set at a fixed level; therefore, increasing the number of producer species reduced the biomass of each of them. With a type III functional response, lower prey biomass led to reduced total consumption by predators. The combined effect of a low biomass flux up the food web and the effect of the pollutant stress could account for the lower persistence observed in systems with a fixed number of producers. The positive effect on persistence of the increase in the maximum trophic level could be explained as follows: the maximum trophic level tends to increase with richness and connectance, so added species or links tend to be stacked up within the network as complexity increases. However, when the maximum trophic level was fixed below its potential value, the increase either in richness or connectance led to added species or links being more aggregated toward the base of the food webs. In networks with free maximum trophic level, the stacking up of species or links led to lower in-degree values of species, which was shown to prevent species extinctions in polluted environments. In this sense, our theoretical model makes a set of predictions that could be evaluated in future experiments or field studies. Recent theoretical studies report that species at higher trophic levels have a greater risk of extinction in the absence of perturbations (Binzer et al. 2011). These results are in line with our findings within non-polluted systems, in which the average trophic level of extinct species was above the average for all species through the food webs. An additional study of Riede et al. (2011) showed that under species deletion, species at higher trophic levels were more prone to extinction, since these species were less robust to secondary extinctions. We found that when the perturbation is an accumulative pollutant, intermediate species were important targets of the deleterious effect of the pollutant.

At the species level our analyses advanced in the understanding of the determinants of species vulnerability to environmental pollutants in a framework of complex communities. An outcome that could be anticipated was the effect of in-degree on species extinction in polluted environments, which should be due to that the negative effect of pollutant stress is compensated only with very high number of prey species, so that without pollutant top species were extinct because of low energy flow. When pollutant was incorporated top species were also extinct, but additionally species in lower trophic levels with intermediate values of in-degree were also extinct. The importance of in-degree for the maintenance of biodiversity in polluted ecosystems could indeed be comparable to that of biomagnification, because the former leads to the extinction of intermediate species instead of top predators, which were identified as more vulnerable in previous empirical work (Rasmussen et al. 1990, Bisi 2012).

This study attempts to produce a step forward in using ecological network theory for nature conservancy research and the understanding of ecosystem structure and function (Brose 2010). In terms of management, changes in biodiversity and food web structure are suggested to be more intricately related with environmental pollution than previously thought, not only because biodiversity loss, but

also because they interact to a degree not previously recognized in determining ecosystem stability. An important finding when considering that food web simplification and pollutants are part of a common process of environmental degradation. On theoretical grounds, gradients in complexity only considered species richness and connectance, neglecting co-variation in other food web attributes directly related to species and community stability, number of producers, number of top species and maximum trophic level. The scenarios herein evaluated provide a new view to the complexity–stability debate, revealing structural attributes of communities that permit their species to overcome or perish under human-driven disturbances such as pollution.

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Supplementary material (Appendix oik-00218 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.