

Food web complexity and higher-level ecosystem services

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Abstract

Studies mostly focused on communities of primary producers have shown that species richness provides and promotes fundamental ecosystem services. However, we know very little about the factors influencing ecosystem services provided by higher trophic levels in natural food webs. Here we present evidence that differences in food web structure and the richness of herbivores in 19 plant-herbivore-parasitoid food webs influence the service supplied by natural enemies, namely, the parasitism rates on hosts. Specifically, we find that parasitoids function better in simple food webs than in complex ones, a result relevant to biological control practice. More generally, we show that species richness *per se* only contributes partially to the understanding of higher-level ecosystem services in multitrophic communities, and that changes in food web complexity should also be taken into account when predicting the effects of human-driven disturbances in natural communities.

Keywords

Biodiversity, clustering, ecosystem function, food web structure, higher-level interactions, indirect effects, omnivory, parasitoids.

Ecology Letters (2003) 6: 587–593

INTRODUCTION

The looming global biodiversity crisis has spawned an intense and controversial debate focused on whether and how changes in biodiversity might influence ecosystem functioning. Most studies of diversity-ecosystem function relationships have been performed in single trophic levels, mostly plant communities, and have documented that taxonomic and functional-group diversity influences a range of ecosystem services such as primary production, nutrient fluxes and decomposition rates (Daly 1997; Chapin *et al.* 2000; Loreau *et al.* 2001; Kinzig *et al.* 2002; Loreau *et al.* 2002). However, both the determinants of ecosystem services in multitrophic communities and functions performed by higher trophic levels than primary producers have been rarely reported (Duffy 2002; Paine 2002; Setälä 2002; Wilby & Thomas 2002). Whereas the theory behind possible effects of plant richness on functions is well developed (e.g. Tilman *et al.* 1997; Loreau 1998; Yachi & Loreau 1999), the theoretical background on diversity-ecosystem function relationship is absent for multitrophic systems, with a very few exceptions (Loreau 1996; Zheng *et al.* 1997). Indeed, one challenge is establishing a link between food web theory and research on diversity-ecosystem function (Loreau *et al.* 2001; Raffaelli *et al.* 2002).

Although evidence clearly connects consumers and ecosystem functioning (e.g. top-down control), these connections are rarely reported explicitly. Only a few studies have shown how diversity of higher trophic levels affects functions performed at the base of food webs (see Duffy 2002 for a review). In some cases, the effects of consumers on lower trophic levels are mediated mostly through indirect interactions, involving multiple trophic levels (Wootton 1994). For instance, the transmission of predatory effects through trophic cascades has important consequences on primary production and nutrient cycling (Pace *et al.* 1999; Schmitz *et al.* 2000). Food web theory has shown that the pattern of trophic interactions has large effects on community dynamics (e.g. Pimm 1982; Polis & Strong 1996), specifically the configuration of weak and strong consumer-resource interactions (de Ruiter *et al.* 1995; Berlow *et al.* 1999; Neutel *et al.* 2002). Recent works have hypothesized that the degree of compartmentalization observed in many biological and technological networks might have important consequences for the stability and function of these networks (Watts & Strogatz 1998; Álbért & Barabási 2002; Montoya & Solé 2002), as was suggested in earlier studies (May 1972; Pimm & Lawton 1980). Nonetheless, there have been remarkably few investigations into the consequences for ecosystem functioning of topology or

distribution of interaction strengths in complex food webs (DeAngelis 1992; de Ruiter *et al.* 1995; Petchey *et al.* 1999).

We investigated the consequences of different aspects of food web complexity on a service typical of higher trophic levels in natural plant-herbivore-parasitoid food webs, the total mortality (i.e. parasitism) rate [Total parasitism rates (TPR)] inflicted on each herbivore. Parasitoids are extensively used for the biological control of insect pests, and parasitism rates represent a key measure of their ability to provide this service in both biological control (Hawkins *et al.* 1993; Wilby & Thomas 2002) and natural systems (Hawkins & Cornell 1994). Previous analysis of the dataset explored here showed no relationship between parasitism rates and richness of parasitoid species (Rodríguez & Hawkins 2000). Here we focus on whether and how this function is affected by (1) species richness of different trophic levels, (2) food web structure, in terms of number of links, number of links of omnivory and degree of compartmentalization, and (3) direct and indirect effects considering positive and negative interaction strengths along food chains.

METHODS

We analysed food webs focused on grass-feeding *Tetramesa* (Hymenoptera: Eurytomidae) originally reported by Dawah *et al.* (1995), based on the dissection of ca. 165 000 grass stems, in which ca. 65 000 feeding relationships were observed. For this analysis, we selected the subset of the

original data analysed by Rodríguez & Hawkins (2000), comprising 13 herbivore species sampled in 14 sites throughout Great Britain at least 70 km apart in the period 1981–1983, 1985 and 1989. This results in 19 high quality food webs comprising plants (first trophic level), herbivores (second trophic level), primary parasitoids (third trophic level) and hyperparasitoids (fourth and fifth trophic levels) (Dawah *et al.* 1995; Rodríguez & Hawkins 2000) (Fig. 1). Among hyperparasitoids, we further differentiated specialist and generalist species; i.e. those feeding on one or several herbivorous species, respectively.

Total parasitism rates on each herbivore species in each web were calculated as the mean over the 5 years considered. They account for the total, combined effects of all the parasitoids attacking a particular herbivore species, showing the percentage of herbivore population that is parasitized by its set of natural enemies (see Dawah *et al.* 1995 for methodological details).

Three types of variables related to food web complexity were explored to examine the relationships between total parasitism rates and (1) biodiversity (i.e. total, parasitoid, and herbivore species richness), (2) food web topology (i.e. total number of links, number of links of hyperparasitism and degree of clustering), and (3) the balance of direct and indirect interactions within food chains, considering the positive or negative effect of parasitoids on controlling herbivores [i.e. net interaction effects (NIEs), see Fig. 2 for calculations]. Topological measures only took into account

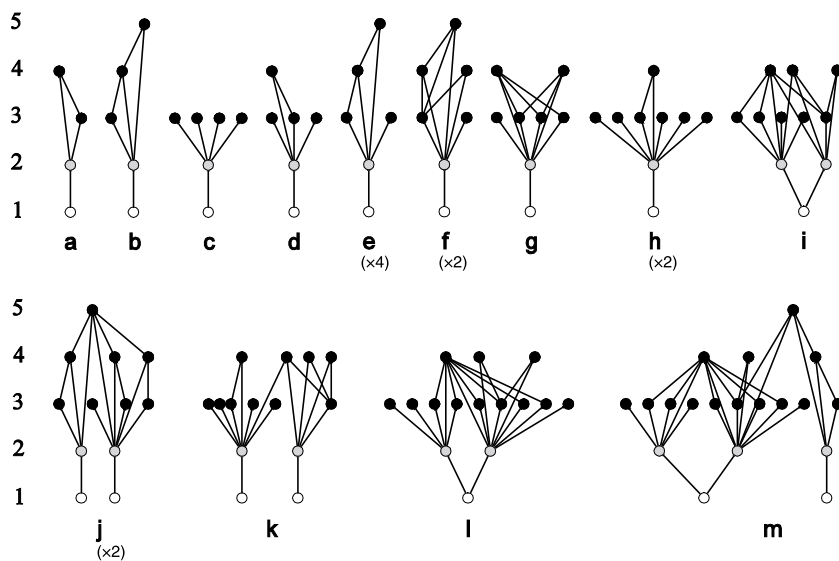


Figure 1 Food webs analysed. Numbers on the left indicate trophic level, and white, grey and black circles represent grass, herbivore and parasitoid species, respectively. In the latter, primary (third trophic level), secondary (fourth trophic level) and tertiary parasitoids are differentiated. Food webs f, h and j have identical structures in two different sites, and food web e is represented at four sites. The highly compartmentalized nature of these food webs allows us to differentiate subwebs over each herbivore within the local food web. The third trophic level is extremely herbivore-specific (primary parasitoids always belong just to one subweb), whereas the fourth trophic level exhibits two different feeding behaviours: generalist (i.e. they are present in more than one subweb) and specialist (only feed on one subweb).

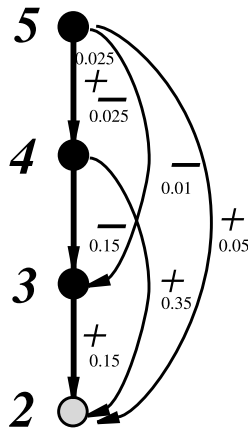


Figure 2 Calculation of net interaction effects. Every arrow points from enemy to victim, and only direct interactions are shown (shade and trophic-level codes are as in Fig. 1). The signs denote the effect (direct or indirect) of the interaction on the mortality of species 2 (herbivore). It is positive if mortality would increase and negative if it would decrease (see text for more details). The interaction between species 5 and 4 (a_{45}) has both a positive and a negative indirect effect on the total parasitism of species 2. It is positive if it is mediated by species 3 (a_{45}^I , species 5 reduces the population of 4, so that the population of 3 would increase, hence parasitism on 2 would increase), and negative otherwise (a_{45}^D , species 4 does not parasitize 3, so that the population reduction of 4 due to parasitism of 5 would decrease parasitism on 2). The net interaction effect (NIE) is the sum of all interaction strengths (a_{ij}) with their correspondent signs: $NIE = a_{23} + a_{24} - a_{34} + a_{25} + a_{35} + a_{45}^I + a_{45}^D$, where $a_{45} = a_{45}^I + a_{45}^D$. In the numerical example included here (corresponding to food web b in Fig. 1), $NIE = 0.15 + 0.35 - 0.15 + 0.05 - 0.01 + 0.025 - 0.025 = 0.39$.

the presence/absence of links, while NIEs also considered the sign and strength of links, measured by pairwise parasitism rates.

With regard to the degree of clustering, if node 1 is linked to node 2 and node 2 is linked to node 3 in a given food web, the clustering coefficient C (Watts & Strogatz 1998) measures the probability that node 1 will also be linked to node 3. The clustering coefficient is usually higher in real networks than in their random counterparts (C_{random}) (Watts & Strogatz 1998; Albert & Barabási 2002). A random net has the same number of species (S) as the real one, and the probability of connecting two species is the connectivity of the real web (number of actual links divided by the number of all possible links, S^2). We have used the standardized measure $C^s = (C - C_{\text{random}})/C$ for comparing the clustering across food webs of different size.

The calculation of NIEs considered both the sign and the strength of all pairwise interactions affecting each herbivore. In Fig. 2 this calculation is illustrated and a numerical example is given. Interaction strength between species A (enemy) and B (victim) is the percentage of individuals of

species B parasitized by species A (data on interaction strengths were originally reported in Dawah *et al.* 1995). The interaction is considered positive if it increases the parasitism suffered by the herbivore and negative otherwise. In Fig. 2, e.g. species 4 (hyperparasitoid) would increase total parasitism rate on species 2 (herbivore), hence the positive sign. By contrast, the arrow from four (hyperparasitoid) to three (primary parasitoid) has a negative sign because it reduces the population of species 3, and it would reduce the total parasitism of species 2. Thus, species 4 has a positive direct effect on the parasitism suffered by species 2, and a negative indirect effect mediated through intermediate species 3. The addition of all pairwise interactions results in the NIE.

We first explored simple associations of individual variables with TPR. We further investigated which variables underlie the variability in parasitism rates among webs. We used forward stepwise multiple regression analysis where the independent variables are individually added to the model at each step of the regression until the “best” regression model is obtained. The variable entered at each step is the one that produces the largest increase in R^2 , i.e. the one with the largest partial correlation with the independent variable. This procedure tests the significance of all the variables in the model, and those that are not significant are excluded before the next forward selection step (only intercepts and variables with significant ($P < 0.05$) contributions to the regression model were retained). Forward stepwise regression has two drawbacks that are easy to avoid. First, there is no guarantee that another set of independent variables would not explain together more of the variation of the dependent variable (Sokal & Rohlf 1995). We compared the model obtained by forward stepwise procedure with that obtained by backward elimination procedure and with the full model (i.e. before any elimination of variables). If the outcomes of forward and backward procedures are similar and the variance explained by the “best” model is close to that explain by the full model, then the set of predictor variables will be robust (e.g. Draper & Smith 1981). Second, we tested for multicollinearity between the predictor variables. In doing so, we (1) explored correlations among predictor variables, (2) calculated tolerances for each variable, and (3) tested the robustness of the model to different minimum tolerances of individual variables to be introduced as predictors.

RESULTS

Bivariate associations between individual independent variables and TPR indicate that higher complexity, both in terms of richness (total and herbivore) and food web topology (total and hyperparasitism links, and degree of clustering) is negatively associated with parasitism rates (Fig. 3). Further, the associations seem contrary to the expected influence of increasing complexity (e.g. richness) at

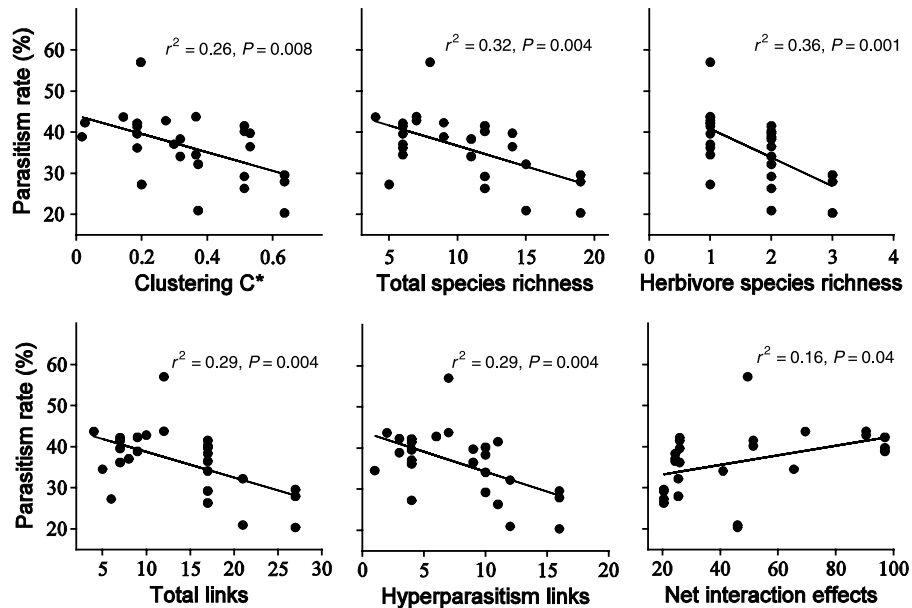


Figure 3 Individual associations between total parasitism rates (TPR) and measures of food web complexity using least-squares linear regression. TPR is not significantly correlated with parasitoid species richness of each subweb ($r = 0.128$; $P = 0.532$) and number of links of hyperparasitism of each subweb ($r = 0.2032$; $P = 0.319$).

Table 1 Summary of multiple regression model (forward introduction stepwise procedure). Independent contributions of each predictor variable to the prediction of TPR after controlling for all other independent variables are shown (β , or standardized regression coefficients). P -values are the significance of each predictor variable within the model that includes all three variables

Dependent variable	Predictor variables	Cumulative R^2	β	P
TPR	Richness of herbivores	0.361	-0.616 ± 0.142	0.0003
	Number of links of hyperparasitism in each subweb	0.481	0.404 ± 0.141	0.009
	Net interaction effect	0.592	0.345 ± 0.141	0.023

single trophic levels: as food web complexity increases, mortality rates on herbivores decrease.

Multiple regression analysis using step-forward variable selection resulted in a significant 3-factor model (Table 1), which explained almost 60% of the variance in TPR across communities:

$$\begin{aligned} \text{TPR} = & 0.362 - 0.072 (\text{Richness of herbivores}) \\ & + 0.016 (\text{Links of hyperparasitism in each subweb}) \\ & + 0.001 (\text{Net interaction effects}) \end{aligned}$$

Although multicollinearity exists among some independent variables, the three predictor variables are not significantly correlated with each other (Table 2). In addition, very little redundancy exists between each predictor variable and the rest of independent variables (tolerance values of 0.919, 0.931, and 0.933, respectively). This indicates that collinearity does not affect the explanatory power of our model (Sokal & Rohlf 1995; Legendre & Legendre 1998). This

model agrees with that obtained using backward elimination of variables. In this case, the percentage of variance explained is very similar (61%), and richness of herbivores is replaced with total number of links in the final model. Both variables are highly correlated ($r = 0.929$, $P < 0.001$), but we found more biological rationale for using richness of herbivores. That is, because total number of links increases with the number of herbivores present in the web. Furthermore, the variance explained by the full model ($R^2 = 0.633$) is very similar to that explained by our 3-factor model ($R^2 = 0.592$). We also tried different combinations of three predictor variables, and none of them resulted in higher explanatory power.

The regression model suggests that herbivores occurring in food webs with fewer other herbivore species and supporting more hyperparasitoids (specialists plus generalists) suffer higher parasitism rates. However, it is not that simple. In these highly compartmentalized food webs, the only way different

Table 2 Correlations between predictor variables

Predictor variable	Richness of herbivores	Number of links of hyperparasitism in each subweb	Net interaction effect
Richness of herbivores	1		
Number of links of hyperparasitism in each subweb	0.222 ($P = 0.27$)	1	
Net interaction effect	-0.216 ($P = 0.29$)	-0.184 ($P = 0.368$)	1

herbivores can belong to the same network is via generalist hyperparasitoids. These hyperparasitoids typically divide their foraging effort among the available victims (Dawah *et al.* 1995). Hence, they may reduce parasitism rates of herbivores embedded in more complex webs where herbivore richness is higher. This is supported by the negative relationship between the number of links of hyperparasitism in the whole food web and TPR on each herbivore species (Fig. 3, $r^2 = 0.29$, $P = 0.004$). Therefore, TPR increases if hyperparasitism increases on single herbivore species, but TPR decreases if generalist hyperparasitoids are present connecting different herbivore species (i.e. different subwebs). Albeit this complex interaction, hyperparasitism (a particular type of omnivory) in these food webs appears key to mediate ecosystem services in lower trophic levels.

We observed that the patterning of interaction strengths also influences TPR. For example, mortality inflicted by hyperparasitoids on primary parasitoids (negative signs in Fig. 2) reduces NIEs on herbivores. Our model emphasizes that this reduction also diminish TPR on each herbivore.

DISCUSSION

Our results have implications for understanding the relationships between food web complexity and ecosystem services as well as for biological control practice. First, we find that both herbivore species richness and food web topology are associated with total parasitism rates. These results apparently contrast with that of Rodríguez & Hawkins (2000) who found no effect of increased richness on function in the same data set. However, these authors only investigated one aspect of community complexity (i.e. parasitoid species richness), whereas we have analysed additional characteristics of complexity across trophic levels. Interestingly, the explanatory variables of service supply included in the model reflect aspects of network configuration; namely, links of hyperparasitism in each subweb, NIEs, and herbivore species richness, the latest closely related to the levels of generalist hyperparasitism experienced by a particular web. On the one hand, this indicates that omnivores (i.e. species feeding on different trophic levels), here hyperparasitoids, are relevant for

ecosystem functioning. This aspect adds to the effect of omnivory on ecosystem stability as previously reported (Lawler & Morin 1993; Polis & Strong 1996) and predicted by recent food web theory (e.g. McCann & Hastings 1997 but see Pimm & Lawton 1977). On the other hand, our results show that indirect effects could be as important as direct effects for ecosystem functioning (Abrams *et al.* 1996). The indirect effects observed in plant-host-parasitoid food webs represent a good example of how trophic cascades influence functions at lower trophic levels. Hence, the linkage between biodiversity and ecosystem services may have more to do with how species interact with each other than with how many species constitute each particular community.

Second, we found a negative relationship between total parasitism rates and web complexity, which can be interpreted as reflecting that complexity is detrimental for the functioning of the system. This fuels the idea that parasitoids will be better control agents in simple systems than in complex ones, which is consistent with analyses of insect life tables and the historical record of biological control (Hawkins *et al.* 1999). These analyses basically show that biological control, when it occurs, is mainly due to a single parasitoid species, and it is more successful in simplified habitats than in more complex ones. More generally, our analysis is consistent with arguments that top-down control and trophic cascades are stronger in low-diversity webs (Strong 1992; Duffy 2002; Schmitz *et al.* 2000). Finally, our results are in agreement with the growing literature on multitrophic interactions (e.g. Tscharntke & Hawkins 2002), which has demonstrated many complex and unexpected feedbacks when more than one trophic level is considered. Thus, conclusions on diversity-ecosystem function relationships observed in communities of primary producers should be extrapolated to multitrophic systems with care (see also Raffaelli *et al.* 2002; Paine 2002).

High mortality rates of herbivores are considered positive for biological control practice (Hawkins *et al.* 1993), because this is the service we seek. Hence, the concept of ecosystem service includes us (the observers) as elements in the valuation process (Daly 1997). But this service can be viewed under a different perspective. The long-term persistence of plant-host-parasitoid communities explored here could depend on

the existence of herbivore populations large enough to maintain viable populations of parasitoids. The data showed that herbivores in more complex food webs have lower mortality (i.e. parasitism) rates, which can be interpreted as that complex communities had the potential to persist longer than the simpler ones (but see Vos *et al.* 2001). However, this seems unlikely. The natural food webs explored here have probably persisted for thousands of years, independently of their complexity, suggesting that herbivores can maintain viable populations of parasitoids both in complex and simple communities. Thus, there is no evidence that the most complex food webs are the most persistent, and hence parasitism rates are not likely related to the persistence of the community.

Even so, the general message derived from our analysis is that the preservation and management of functional ecosystems can benefit from adopting a food web perspective that considers more than species richness, including the topology, strength and indirect effects of higher-level interactions.

ACKNOWLEDGMENTS

The authors thank University of California at Irvine for their hospitality during the preparation of the first draft of the manuscript. The authors thank Jeremy Fox and two anonymous referees for valuable suggestions that greatly improved the clarity of the manuscript. This work was supported by Comunidad de Madrid FPI-4506/2000 (JMM).

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Editor, N. Huntly

Manuscript received 24 January 2003

First decision made 19 February 2003

Manuscript accepted 31 March 2003