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Identity effects dominate the impacts of multiple species extinctions on the functioning of complex food webs

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Abstract. Understanding the impacts of species extinctions on the functioning of food webs is a challenging task because of the complexity of ecological interactions. We report the impacts of experimental species extinctions on the functioning of two food webs of freshwater and marine systems. We used a linear model to partition the variance among the multiple components of the diversity effect (linear group richness, nonlinear group richness, and identity). The identity of each functional group was the best explaining variable of ecosystem functioning for both systems. We assessed the contribution of each functional group in multifunctional space and found that, although the effect of functional group varied across ecosystem functions, some functional groups shared common effects on functions. This study is the first experimental demonstration that functional identity dominates the effects of extinctions on ecosystem functioning, suggesting that generalizations are possible despite the inherent complexity of interactions.

Key words: biodiversity; ecosystem functioning; food web; functional groups; marine and freshwater food webs; species extinctions; species identity; species interactions.

Introduction

There has been a great deal of effort over the past two decades to understand the impact of community structure on ecosystem functions (see reviews in Loreau et al. 2001, Cardinale et al. 2011). In spite of some controversies about interpretations of the data (e.g., Huston 1997), the vast number of experiments performed allowed quantitative analyses of the general trend (Balvanera et al. 2006, Cardinale et al. 2012, Naeem et al. 2012) and confirmed that a positive relationship between biodiversity and ecosystem functioning (BEF) emerges from simple and conceptually tractable mechanisms (i.e., selection effect and complementarity among species; Loreau and Hector 2001, Loreau 2010). Despite the impressive progress in that research area, there is still a wide array of crucial issues to resolve before we can provide satisfying recommendations for ecosystem management (Srivastava and Vellend 2005). Among them, the discipline must recognize the important complexity of natural ecosystems (Polis and Strong 1996, Duffy et al. 2007, Schmitz 2010) and, consequently, develop predictive tools to assess the impacts of species loss on ecosystem functioning.

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The incorporation of trophic interactions to the BEF theory clarified the importance of top-down and bottom-up constraints upon the diversity effect (see Duffy et al. 2007). For instance, in simple tri-trophic food webs, it is predicted that increasing predator diversity will increase primary producer biomass (Byrnes et al. 2006). Theoretical studies in relatively more complex systems have shown that many relations between ecosystem function and diversity could emerge from simple mechanisms (Duffy et al. 2007). The effect of adding plant species, for example, could either enhance (stoichiometric hypothesis; sensu DeMott 1998) or inhibit (resource dilution hypothesis; sensu Root 1973) consumption by herbivores, depending on the mechanism involved. Moreover, an ecosystem perspective explicitly integrating nutrient dynamics can strongly moderate simple predictions such as the effect of removing a predator on resource control by an herbivore (Schmitz 2008).

Moving forward in complexity from a food chain to a food web perspective remains a challenging task (Bascompte 2009) for both theoreticians and empiricists. Some theoretical studies of complex food webs suggested that the increasing number of ecological interactions (intraguild predation, omnivory, and indirect effects) with species richness promotes the emergence of diffuse and indeterminate reactions to disturbances (Polis and Strong 1996, Yodzis 2000, Berlow et al. 2009). Accordingly, results from experimental BEF studies in multitrophic communities revealed much higher variability between ecosystems and processes than in simpler

systems dominated by competitive interactions (Schmid et al. 2009). Consequently, in more complex trophic systems, BEF relationships are expected to be less predictable and nonlinear, in contrast to the monotonic relations observed in more simplified systems (Thébault and Loreau 2006). For instance, in seagrass beds, studies showed that the BEF relationship is dependent upon food chain length and that the plant richness effect on ecosystem functioning is dependent upon the richness of grazers (Duffy et al. 2003, 2005). These results suggest that species richness and trophic structure interactively influence ecosystem functions. Nonetheless, recent studies have suggested that the impacts of single species loss in complex food webs can be predicted with only a few variables (i.e., body size, trophic rank, and biomass ratios) even without an extensive knowledge of all of the ecological interactions within the system (Solan et al. 2004, Berlow et al. 2009). In diverse ecosystems, indirect positive and negative interactions may balance each other, leading to a dominance of direct and first-order interactions (species identity effect; Berlow et al. 2009).

Biodiversity and ecosystem function studies have usually considered ecosystem functions as independent from each other (Hector and Bagchi 2007). Nevertheless, ecosystems encompass many processes (functions) at the same time; thus, many empirical studies have suggested that considering multifunctionality increases the importance of species richness on the overall ecosystem functioning by reducing functional redundancy among species (Hector and Bagchi 2007, Gamfeldt et al. 2008). Further work by Mouillot et al. (2011) has suggested that the functional identity of species rather than species richness per se is the most important promoting factor of ecosystem multifunctionality. So far, these studies have all been carried out in competitive systems with plants and there is a need to test if predictions about multifunctionality would be observed in more complex and multitrophic ecosystems.

In this study, we experimentally simulated multiple extinctions with freshwater and marine mesocosms. The design consisted of communities of up to 10 functional groups, sharing common features of complex food webs such as intraguild predation, omnivory, and cannibalism. It is often argued that the BEF in food webs is critically dependent on the topology of interactions and species traits (Loreau 2010), preventing any general theoretical prediction (Duffy et al. 2007). Consequently, we hypothesized that (1) BEF relationships will be variable across our two ecosystems and functions. Despite this indeterminacy, it has been suggested that the impacts of single-species loss in food webs can be predicted with only few variables, putting foremost the functional identity of species (Solan et al. 2004, Berlow et al. 2009). Therefore, we also hypothesized that (2) the effects of functional group extinctions on EF will be better explained by functional identity than by functional group richness. Ecosystems are supported by multiple ecological processes (functions) and functional groups are likely to have different impacts on them. Therefore, we also hypothesized (3) that the contribution of each functional group will differ between ecosystem functions. Moreover, because some functional groups can share some traits (i.e., body size, trophic ranks), we hypothesized (4) that some groups will share similar effects in the multifunctional space.

Materials and Methods

Experimental design

We ran the same experimental design in freshwater (from a pool of ten functional groups) and marine (from a pool of nine functional groups) ecosystems. Functional groups correspond to the taxonomic level of organization at which differences in feeding habits can be determined according to existing literature and expert knowledge (i.e., families for the freshwater ecosystem and species for the marine ecosystem). Thus, functional groups in this study are easily tractable and biologically relevant units based on natural history, but are not completely exclusive in their diet (i.e., there is overlap in feeding habits). It is noteworthy that periphyton and phytoplankton were not considered in the pool of functional groups and thus subjected to deletion, but instead were considered as a response variable. Starting from the full assemblage (10 and 9 functional groups), we removed 1, 2, and 4 groups and 1, 3, and 6 groups for the freshwater and marine ecosystems, respectively. We ran 10 and 9 removal sequences, respectively, for each ecosystem, which produced 30 (3 removal treatments $\times$ 10 assemblages) and 27 unique functional group compositions, respectively. A removal sequence corresponded to the progressive random removal of 1 to n functional groups. We constrained the sequences so that each functional group was removed at first position (1 group removed) one time. For the other richness levels, the removed functional group was randomly selected from the functional group pool without replacement. With this design, each functional group was equally represented over all assemblage sequences, allowing the partitioning of variance among identity, linear, and nonlinear group richness effects (Bell et al. 2009). For comparison, we also considered a reference treatment with all functional groups excluded. Each assemblage sequence was replicated three times in both experiments.

The life cycles of most of the functional groups used in our experiments were on a longer timescale than the duration of the experiments; consequently, there were few compensatory dynamics. Most BEF experiments impose compensatory readjustment within trophic levels in simple food webs (e.g., O'Connor and Crowe 2005; but see McGrady-Steed et al. 1997). However, this is not feasible in more complex food webs because (1) it would have required us to hypothesize how to distribute biomass among the remaining groups; and (2) organisms are discrete units and, in many cases, we would have to add fractions of organisms in order to adjust biomass. The lack of compensatory adjustment

of biomass could introduce a bias because it is not possible to know if the effect of a group removal treatment is caused by a group richness effect per se or by lowered total biomass or density. The experiments must therefore be interpreted as an instantaneous "picture" of the effect of functional group removal on ecosystem functioning, before reaching a new equilibrium. The ecosystem functions that we measured are therefore the results of structural changes in communities induced by functional group removals.

Freshwater ecosystem

The freshwater experiment took place at the Lac Macpès Research Station (Rimouski, Canada). The assemblages were maintained in 60-L capacity plastic containers during the course of the experiment. The assembling of communities took place on 6 July 2010 and the experiment ran for 8 weeks. One week prior to the start of the experiment, mesocosms were filled with 40 L of filtered water (20-μm nylon tissue) sampled from a neighboring lake. One pre-incubated (2 weeks in a lake) Hester-Dendy plate (periphyton substrate; NKY Environmental Supply, Florence, Kentucky, USA) was added in each mesocosm to allow for phytoplankton and periphyton to settle. Ten assemblage sequences of 1, 2, and 4 functional groups removed and 0 and 10 functional group removal treatments were replicated three times, for a total of 96 mesocosms. A 1-mm mesh screen was placed over each mesocosm to prevent emigration or immigration of organisms and detritus.

The communities consisted of seven benthic and two planktonic invertebrate groups and one fish (Fig. 1a). For logistical convenience and because body size has been previously correlated with the zooplankton feeding guild (Matthews and Mazumder 2007), zooplankton was split into two functional groups with respect to body size, using sieves (Fig. 1a). The first group consisted of small zooplankton (0.063–0.5 mm, dominated by copepods and small-sized cladocerans) and the second group of larger individuals (>0.5 mm, dominated by cladocerans). The other functional groups, with taxonomic resolution at the family level (after Merritt and Cummins 1996), consisted of: Hyalellidae (amphipods), Dystiscidae (water beetles), Coenagrionidae (larval damselflies), Corixidae (water boatmen), Gerridae (water spiders), Planorbidae and Lymnaeidae (gastropods), and Cyprinidae (cyprinid fishes). Densities were adjusted to correspond to recorded densities in lakes where organisms were sampled (after C. Normand, C. Nozais, A. Caron, and D. Pillay, *unpublished manuscript*).

Ecosystem properties were recorded as proxies of functioning at the end of the experiment. Phytoplankton biomass was determined from 150-mL water samples filtered onto Whatman GF/F filters and extracted for 24 h in 90% acetone, at 5°C in the dark (Parsons and Maita 1984). Concentrations of chlorophyll *a* and phaeopigments (non-photosynthetic degradation products of chlorophyll *a*) were calculated using equations from Holm-Hansen et al. (1965), after measuring fluorescence before and after acidification (HCl, 1 mol/L) in a 10-AU fluorometer (Turner Designs, Sunnyvale, California, USA). Periphyton dry mass was assessed from a 1×1 cm sample from each Hester-Dendy plate (24 h at 60°C). Bacterial abundance was measured using standard flow cytometric analysis. Samples for bacteria abundance determination were fixed with glutaraldehyde (0.1% final concentration) and stored at −80°C until flow cytometric analysis following Belzile et al. (2008). Total nitrogen (TN) and total phosphorus (TP) were measured using the copper-cadmium standard reduction method for autoanalyzers after alkaline persulfate digestion (Grasshoff et al. 1983).

Marine ecosystem

The marine experiment took place in the wet lab facilities of the Marine Research Institute (ISMER-UQAR) in Rimouski, Canada (see Plate 1). Assemblages were established on 18 October 2010 and the experiment ran for 6 weeks. Mesocosms were maintained in 21-L plastic containers. Mesocosms were randomly distributed on shelves. A unique tank supplied all of the mesocosms with surface water of the Lower St. Lawrence estuary at a flow rate of 14 L/h (accuracy ±3 L/h). Each mesocosm had its own water input and output to prevent water circulation between mesocosms. Lighting was held under a constant 12 h/12 h light/dark cycle. Mesocosms were filled with water from the St. Lawrence estuary and were filtered on sand filter one week prior to the start of the experiment to allow for periphyton to colonize.

The species pool consisted of nine representative species of the Lower St. Lawrence estuary (Canada) sublittoral zone (0–3 m depth; Fig. 1b): *Cancer irroratus* (rock crab), *Strongylocentrotus droebachiensis* (green sea urchin), *Mytilus edulis* (blue mussel), *Nucella lapillus* (dogwhelk), *Littorina littorea* (common periwinkle), *Gammarus* spp. (side swimmer), *Testudinalia testudinalis* (limpet), *Semibalanus balanoides* (barnacle), and *Littorina* spp. (*Littorina saxatilis* and *L. obtusata*, rough periwinkle and yellow periwinkle). The densities used were within the natural range observed at a small spatial scale in the study area (Griffin et al. 2009). Nine independent assemblage sequences of 1, 3, and 6 functional groups removed, in addition to 0 and 9 group treatments were replicated three times, for a total of 87 mesocosms.

Three ecosystem properties were recorded as proxies of ecosystem function at the end of the experiment. Periphyton biomass was measured as described for the freshwater system. Macroalgae biomass consumption was measured by weighing the residual biomass from the 100 g of the brown algae *Fucus distichus edendatus*, placed in each of the mesocosms at the beginning of the experiment. Encrusted algae biomass was measured

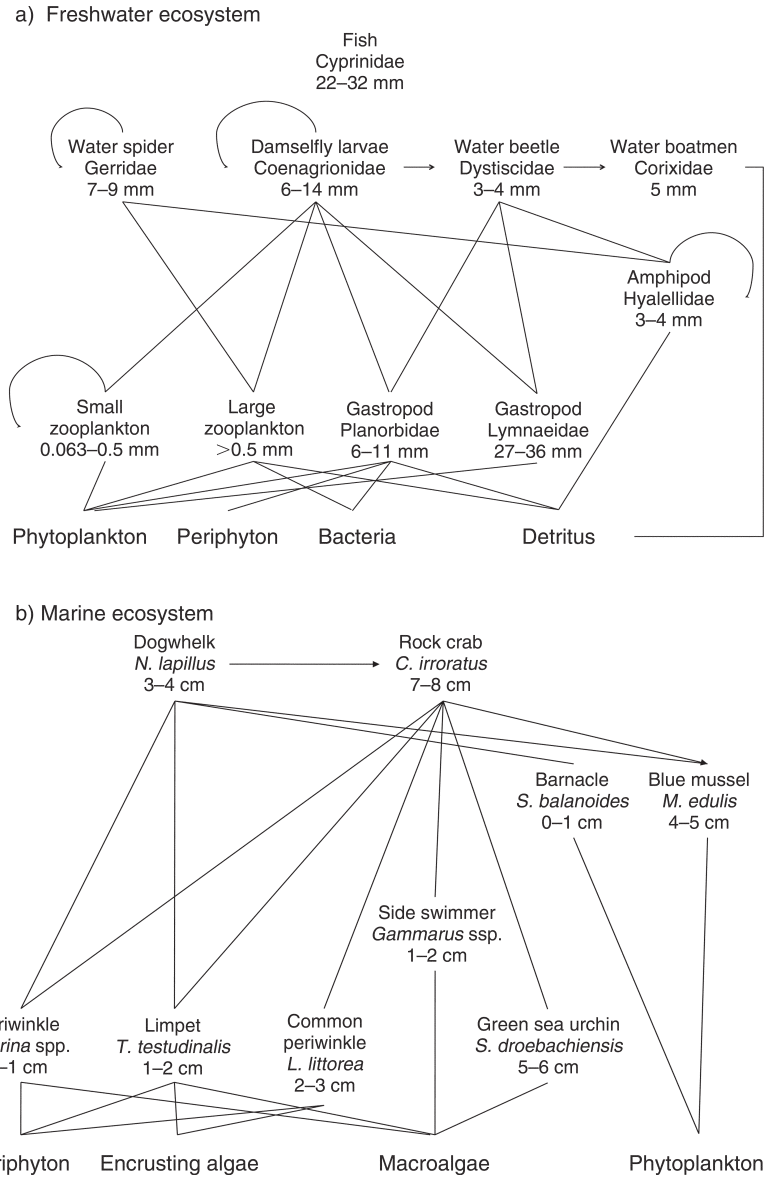

FIG. 1. Simplified schematic representation of the (a) freshwater and (b) marine ecosystems studied near Rimouski, Quebec, Canada. The nine marine species are: *Cancer irroratus*, *Strongylocentrotus droebachiensis*, *Mytilus edulis*, *Nucella lapillus*, *Littorina littorea*, *Gammarus* spp., *Testudinalia testudinalis*, *Semibalanus balanoides*, and *Littorina* spp. (*Littorina saxatilis* and *L. obtusata*, rough periwinkle and yellow periwinkle).

using the image-processing program ImageJ version 1.44 (National Institutes of Health 2011) to calculate the cover of *Raftsia verrucosa* present on a single rock placed in each mesocosm at the beginning of the experiment. Because all rocks differed in size and shape, algae cover was calculated in square centimeters instead of percent cover to allow comparison between treatments regardless of the dimensions of the rocks.

Statistical analyses

Impacts of functional group richness on single ecosystem functions.—The effect of functional group richness on ecosystem functioning was first analyzed using ANOVAs, with functional group composition nested within functional group richness (hypothesis 1).

We expected an inconsistent BEF relationship because of the complexity of the community structures; consequently, we used a set of linear models to partition the variance among different diversity properties (hypothesis 2): functional group identity, linear functional group richness (additive richness effect), nonlinear functional group richness (effect of functional group interactions), and composition (effect of a particular assemblage of functional groups). We used a modified nested linear model developed by Bell et al. (2009) to partition the variance of ecosystem functions. The model is as

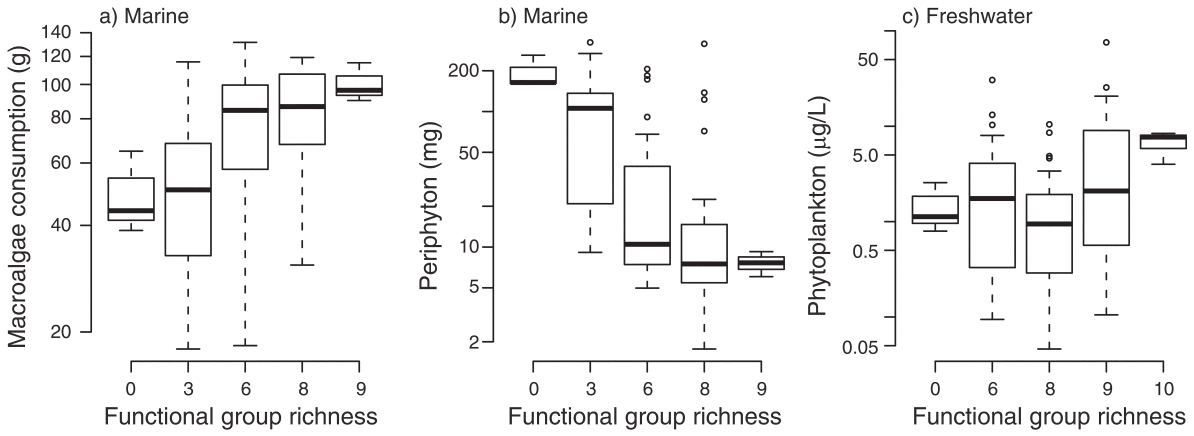

FIG. 2. Response of (a, b) marine and (c) freshwater ecosystem functions to functional group richness (number of functional groups). Boxplots indicate interquartile variance among richness treatments, with the bold line indicating the median, ends of the dashed line indicating minimum and maximum values, and black dots indicating outliers. Only significant functions are shown.

follows:

$$y = \beta_0 + \beta_{LR}x_{LR} + \beta_{NLR}x_{NLR} + \left(\sum_i^S \beta_i x_i\right) + \beta_M x_M + e \quad (1)$$

where y is the response variable; β_0 is the intercept (average value of the ecosystem function when richness is 0); $\beta_{LR}x_{LR}$ (with corresponding sum of squares SS_{LR}; df = 1, and error term $e = SS_M$) is the effect of linear functional group richness (additive effect of richness, owing to perfect complementarity); and $\beta_{NLR}x_{NLR}$ (SS_{NLR}; df = functional group richness levels − 2; $e = SS_M$) is the nonlinear effect of functional group richness (presumed to result from interactions among functional groups). The effect of functional group identity $\sum_i^S \beta_i x_i$ (with associated SS_i; df = number of functional groups − 1; $e = SS_M$) accounts for the contribution of each functional group, independently of the effect of functional group richness per se. The effect of each functional group composition is $\beta_M x_M$ (SS_M; df = number of unique composition − number of functional group − 1; e = residuals). For further details, see Bell et al. (2009).

The original model by Bell et al. (2009) included a term $\beta_Q x_Q$ for the effect of the different partitioning of the species pool (SS_Q; df = number of partitioning − number of functional group; e = residuals). This model has been developed for a particular experimental design where every species richness treatment is a factor of the species pool. For instance, for a given species pool of size 10 there would be 5 different independent assemblages of 2 species, and these together would make one partition of the species pool. However, our design did not enable us to directly calculate this source of variation because our species deletion treatments are not all multiples of our sampled species pool. Nevertheless, because of the original sequential formulation of the model, we were able to remove the term $\beta_Q x_Q$ without any adverse effects. The term $\beta_Q x_Q$ was originally included in the degree of freedom calculation for SS_M and the residuals and has SS_M as the error term. The removal of $\beta_Q x_Q$ from the model thus leads to an increase of both degrees of freedom for $\beta_M x_M$ and residuals terms and to an increase of SS_M value. The overall effect is an overestimation of all F values (higher Type I error). Because reported F values for all terms were either highly significant ($P < 0.002$) or not significant, this increase in Type I error did not impair our capacity to interpret results, but still advises some caution.

Functional group contributions and ecosystem multifunctionality.—We hypothesized that functional groups would not have the same magnitude of effect on each ecosystem function. One major advantage of the linear model that we used (Eq. 1) is that it provides functional group-specific coefficients (β_i) describing the contribution of each functional group to an ecosystem function relative to the average contribution of all functional groups. We thus obtained a matrix of β_i coefficients × ecosystem functions by performing the linear model for all functions. We subsequently performed a principal component analysis (PCA) on this matrix to assess the relative position of the different functional groups in the multifunctional space.

All statistical analyses were carried out using R software (2.11.1 version; R Development Core Team 2010) and the "ade4" package for PCA (Chessel et al. 2012).

RESULTS

Effects of functional group richness on ecosystem functions

The effect of functional group richness on ecosystem functions varied across ecosystems and functions (Fig.

TABLE 1. Summary table of the effect of functional group richness on the different ecosystem functions studied in marine and freshwater ecosystems near Rimouski, Quebec, Canada.

	Factor				
	Group richness		Composition		Residuals
Ecosystem and functional group	df	*F*	df	*F*	df
Marine ecosystem					
Macroalgae	2	11.590***	24	2.2863**	54
Periphyton	2	35.438***	24	5.001***	54
Encrusted algae	2	1.034	24	2.131*	54
Freshwater ecosystem					
Total phosphorus (TP)	2	0.873	27	0.602	60
Phytoplankton	2	5.830**	27	2.659**	60
Bacteria	2	0.232	27	1.119	60
Periphyton	2	0.245	27	1.622	60
Total N (TN)	2	0.331	27	0.912	60

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

2). For the marine ecosystem, consumed macroalgae biomass increased significantly with group richness ($F_{2,54} = 11.6$, $P < 0.001$; Fig. 2a), whereas periphyton biomass decreased significantly ($F_{2,54} = 35.4$, $P < 0.001$; Fig 2b). Both functions saturated with increasing functional group richness (Fig. 2a, b). It is noteworthy that functional group composition also played a significant role in macroalgae consumption ($F_{24,54} = 2.3$, $P < 0.01$; Table 1) and periphyton biomass ($F_{24,54} = 5.0$ $P < 0\,001$; Table 1). For the freshwater ecosystem, phytoplankton biomass varied significantly with functional group richness ($F_{2,60} = 5.8$, $P < 0.01$; Fig. 2c), but this variation was not monotonic. The phytoplankton biomass was higher at 0 and 10 functional group treatments ($F_{1,4} = 14.2$, $P < 0.05$) and there was a depression at 8 groups ($P < 0.05$; Fig. 2), giving the relationship a "V" shape. The effect of functional group composition was also significant for phytoplankton ($F_{2,60} = 2.5$, $P < 0.01$; Table 1). Other freshwater (TP, bacteria abundance, periphyton, and TN) and marine (encrusted algae) functions that were measured did not show any statistically significant relationships with functional group richness (Table 1).

Partitioning effects of functional group richness

The overall performance of the ANOVAs was low and inconsistent because a great proportion of the freshwater functions and one marine function did not respond significantly to the functional group richness effect. We therefore partitioned the variance of the different ecosystem functions among functional group identity and linear and nonlinear group richness, which significantly improved the models (Table 2). The functional group identity effect was systematically the most important factor for ecosystem functioning, over all functions and ecosystems (see Table 2). For the marine ecosystem, macroalgae consumption and periphyton biomass, respectively, were also largely affected by linear group richness ($F_{1,17} = 22.45$, $P < 0.001$; $F_{1,17} = 45.69$, $P < 0.001$), in coherence with the ANOVAs. Phytoplankton biomass in the freshwater system was also affected significantly by the nonlinear diversity

TABLE 2. Linear models partitioning the variance between linear group richness, nonlinear group richness, identity effects, and composition effects.

	Factor								
	Richness, linear		Richness, nonlinear		Groups, identity		Composition		Residuals
Ecosystem and functional group	df	*F*	df	*F*	df	*F*	df	*F*	df
Marine ecosystem									
Macroalgae	1	22.454***	1	0.669	8	37.747***	17	0.816	44
Periphyton	1	45.697***	1	1.271	8	62.539***	17	1.229	44
Encrusted algae	1	0.049	1	1.170	8	13.128***	17	1.383	44
Freshwater ecosystem									
Total phosphorus (TP)	1	0.972	1	2.177	9	10.354***	19	0.969	49
Phytoplankton	1	1.231	1	10.016**	9	47.444***	19	0.846	49
Bacteria	1	0.047	1	0.588	9	22.405***	19	0.596	49
Periphyton	1	0.233	1	0.272	9	26.199***	19	0.791	49
Total N (TN)	1	0.806	1	0.037	9	12.380***	19	0.641	49

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

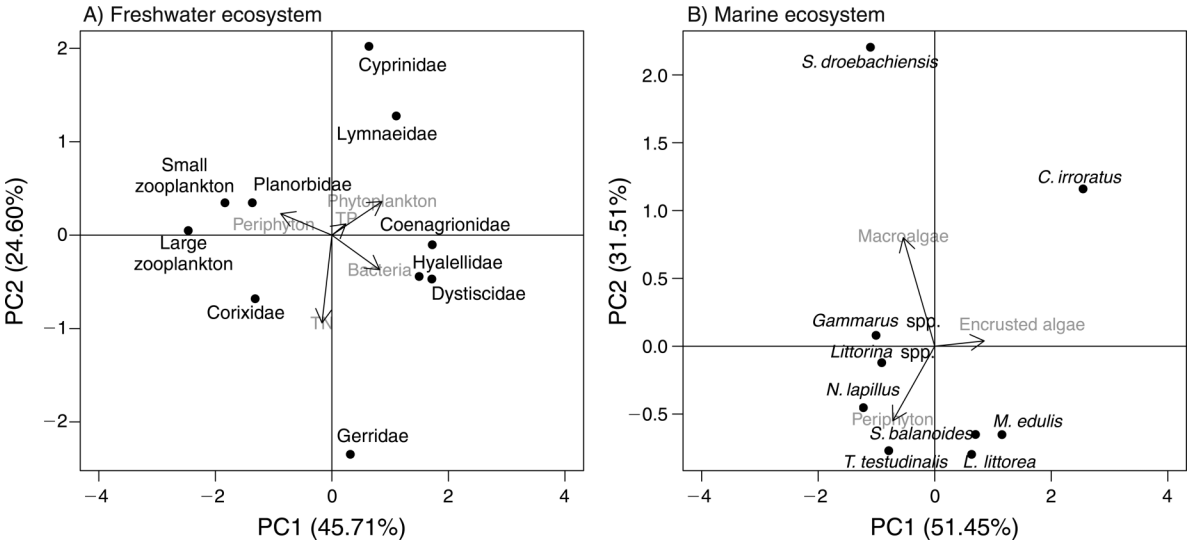

FIG. 3. Relationships between functional group individual contribution and ecosystem multifunctionality for the (a) freshwater and (b) marine ecosystem (first and second axes of the principal component analysis, PC1 and PC2). Groups are shown in black text and ecosystem functions in gray text. Values in parentheses in the axis labels are the percentages of variation explained.

effect (explaining the "V" shape reported in Fig. 2; $F_{1,19} = 10.01$, $P < 0.01$).

Functional group position in the multifunctional space

Because functional group identity effects are the main drivers of the freshwater ecosystem and among the most important for the marine ecosystem, we analyzed their relative position in the multidimensional space using PCA. Functional group effects varied greatly across functions (Fig. 3, Tables 3 and 4). A group of three grazers (i.e., small zooplankton, large zooplankton, and *Planorbidae*) showed a positive impact on periphyton biomass and a negative impact on phytoplankton biomass in the freshwater system (Fig. 3a). These grazers were also in complete opposition (i.e., strong negative impact) to bacterial abundance (Fig. 3a). In contrast, three functional groups of carnivores/omnivores (i.e., Coenagrionidae, Dystiscidae, and Hyalellidae) had a positive impact on bacterial abundance and phytoplankton biomass, and a strong negative impact on periphyton biomass (Fig. 3a). The functional groups corresponding to the two largest organisms (i.e., Cyprinidae and Lymnaeidae; Fig. 1), respectively a grazer and apex predator, showed an important impact on the overall system (Fig. 3a). These two functional groups shared a positive impact on phytoplankton and a negative impact on TN (Table 3). The Corixidae functional group, which consists of an intraguild predator and carnivore, showed a positive impact on TN, but was in complete opposition with phytoplankton biomass (Fig. 3a).

In the marine ecosystem, the effect of identity on ecosystem functioning was not linked to trophic rank as in the freshwater ecosystem (Table 4, Fig. 3a, b). A suspension-feeder group (*S. balanoides* and *M. edulis*; Fig. 1) and one grazer group (*L. littorea*; Fig. 1) shared a common negative effect on macroalgae consumption and a positive effect on encrusted algae biomass (Table 4, Fig. 3b). The *Gammarus* spp. group, which is omnivorous, and *Littorina* spp., a grazer group (Fig. 1), shared a common positive effect on macroalgae consumption and a negative effect on encrusted algae biomass (Table 4, Fig. 3b). The predator *N. lapillus* (Fig. 1), showed a negative impact on periphyton biomass and negative one on encrusted algae (Fig. 3b). As in the freshwater ecosystem, the functional groups corresponding to the largest organisms (*C. irroratus* and *S. droebachiensis*; Fig. 1), respectively predator and grazer, showed an important impact on the overall system (Fig. 3b). These two functional groups, however, shared only a negative impact on periphyton biomass (Table 4).

DISCUSSION

Our approach highlighted that the typical BEF approach (i.e., using only the effect of functional group richness, per se) does not apply well to all food webs and functions. We found that the relationship was monotonic for two functions (i.e., macroalgae consumption and periphyton biomass) in the marine system, but in the freshwater system, it was unimodal for phytoplankton biomass and other functions were not significantly related to the number of removed groups. According to our hypothesis 1, the BEF relationship is known to be context dependent, showing great variation depending on the environments and functions being studied (Wojdak 2005). This variation would be mainly attributed to species identity (hypothesis 2), where one or several species have a dominant influence on ecosystem functioning (Griffin et al. 2010), and to

TABLE 3. Functional group contribution to freshwater ecosystem functions: a positive coefficient indicates that a species is contributing more to the given function than the average species; a negative coefficient indicates it is contributing less than average.

Taxon	Phytoplankton		Periphyton		Bacteria		TN		TP	
	β	SE	β	SE	β	SE	β	SE	β	SE
Small zooplankton	**−0.47**	0.16	0.27	0.14	−0.03	0.05	−0.05	0.07	−0.13	0.12
Large zooplankton	**−0.68**	0.15	**0.36**	0.13	−0.07	0.05	0.01	0.07	0.00	0.11
Dystiscidae	**0.36**	0.15	**−0.34**	0.14	0.05	0.05	0.02	0.07	−0.01	0.11
Hyalellidae	0.20	0.16	−0.06	0.14	**0.10**	0.05	0.01	0.07	0.07	0.12
Corixidae	−0.26	0.14	**0.26**	0.13	−0.04	0.05	0.10	0.06	0.09	0.11
Gerridae	−0.11	0.16	−0.16	0.14	0.06	0.05	**0.15**	0.07	−0.08	0.12
Coenagrionidae	0.23	0.16	**−0.38**	0.14	0.05	0.05	−0.03	0.07	0.01	0.12
Planorbidae	−0.23	0.15	0.06	0.13	**−0.11**	0.05	0.00	0.06	0.01	0.11
Lymnaeidae	0.26	0.15	−0.05	0.13	0.03	0.05	−0.10	0.06	0.08	0.11
Cyprinidae	**0.70**	0.14	0.05	0.13	−0.04	0.05	−0.12	0.06	−0.04	0.11

Note: Although global identity effect is significant for each functions (see Table 2), boldface values indicate significant coefficients (β_i) inside each linear model at the $P < 0.05$ level.

species interactions that are difficult to predict (Yodzis 2000).

The effect of species identity is often confounded with the effect of species richness. As synthesized by Ieno et al. (2006), a significant effect of diversity can be due to richness per se, species identity, and a combination of both effects. Not controlling for different components of species richness could lead to a misinterpretation of the effect of extinctions by masking the importance of species identity. In our experiments, although explained variation was high for the few significant ecosystem functions when we used only functional group richness and composition as explaining factors (R^2 for phytoplankton = 0.57, R^2 for macroalgae = 0.59, R^2 for periphyton = 0.78; Fig. 2), the partitioning of the diversity effect in marine and freshwater systems clearly improved our understanding of extinction effects and how functioning was modulated by functional group identity for all ecosystem functions (see Table 2).

Functional group richness per se played a substantial role in explaining the effects of functional group removal on ecosystem functions in the marine system. This result is the opposite of what was found in the freshwater ecosystem, where functional group identity seemed to be the sole important factor (Table 2). We hypothesize that this could be caused by differences in food web structure. The freshwater ecosystem contained more intraguild predation and cannibalism, and was also closed, all characteristics that are expected to cause less predictive and nonlinear responses to change in richness (Polis and Strong 1996, Thébault and Loreau 2006). These results are also in accordance with the hypothesis of Berlow et al. (2009) that in food webs having complex structures, trophic interactions may balance each other and lead to a dominance of identity effect. In the freshwater ecosystem, the functional group identity effect was very strong relative to linear functional group richness effect (e.g., for phytoplankton, $F(\text{identity})/F(\text{richness}) = 38.54$; Table 2). The results in the freshwater ecosystem also showed a lot of opposite, antagonistic identity effects between functional groups (Table 3). In such a system, we should not expect a monotonic linear relationship with functional group richness because antagonistic identity effects cancel each other out as richness increases. Our results thus are in agreement with expectations in a system where complementarity (i.e., linear functional group richness in our model) is very low compared to identity effect. It might explain why there was no BEF relationship for the freshwater system, presumably because the increasing

TABLE 4. Functional group contribution to marine ecosystem functions: a positive coefficient indicates that a species is contributing more to the given function than the average species; a negative coefficient indicates it is contributing less than average.

Taxon	Periphyton		Macroalgae		Encrusted algae	
	β	SE	β	SE	β	SE
Cancer irroratus	**−0.69**	0.10	−0.04	0.05	0.06	0.04
Strongylocentrotus droebachiensis	−0.02	0.10	**0.25**	0.05	−0.00	0.03
Mytilus edulis	0.11	0.10	−0.06	0.05	**0.08**	0.04
Nucella lapillus	0.19	0.10	0.00	0.05	−0.06	0.04
Littorina littorea	0.07	0.11	−0.08	0.05	0.03	0.04
Testudinalia testudinalis	**0.30**	0.10	−0.01	0.05	−0.01	0.04
Gammarus spp.	−0.01	0.10	0.01	0.05	−0.07	0.04
Semibalanus balanoides	−0.05	0.11	−0.09	0.05	0.01	0.04
Littorina spp.	0.10	0.11	0.01	0.05	−0.05	0.04

Note: Although global identity effect is significant for each functions (see Table 2), boldface values indicate significant coefficients (β_i) inside each linear model at the $P < 0.05$ level.

PLATE 1. (Top) The marine design inside the wet lab facilities of the ISMER, with every plastic container being a mesocosm. (Bottom) Green sea urchins (*Strongylocentrotus droebachiensis*) and periwinkles (*Littorina saxatilis* and *Littorina obtusata*) grazing on benthic macroalgae (we used *Fucus distichus edentates* as benthic macroalgae in the current experiment). Photo credits: A. Séguin.

functional group richness leads to an averaging of all the positive and negative effects. In the marine ecosystem, however, the functional group richness effect was much stronger relative to the identity effect (e.g., for periphyton, F(identity)/F(richness) = 1.37; Table 2). It suggests that there was greater complementarity between groups and that most functional groups are contributing additively in the same direction on ecosystem functions (all positive or all negative; see Tables 3 and 4), generating a clear BEF relationship in this system (Fig. 2). The replication of our experimental design in two different ecosystems, which has been rarely undertaken at this scale, enables us to be confident about the generalization of our results on the importance of identity effects in food web response to extinctions.

Little attention has been devoted to studying the effects of food web diversity with a multifunctional perspective. Hector and Bagchi (2007) observed that the number of species needed to maintain ecosystem multifunctionality would be much higher than the expected number when looking at only a single function at a particular point in time and space (see also Gamfeldt et al. 2008, Isbell et al. 2011). These results imply that when considering the global functioning of an ecosystem, redundancy among species should be much lower, making ecosystems more susceptible to species losses than previously envisaged (Gamfeldt et al. 2008). These

studies, however, all have been carried in grasslands, at a single trophic level. Our results suggest that we have to be careful about extending these results to communities with multiple trophic levels. In the marine system, the complementarity between functional groups in their identity effect is high for each single ecosystem function; thus, increasing functional group richness should maximize the overall functioning. On the other hand, in the freshwater system, there is a lot of variation as well as antagonistic effects between functional groups on each single ecosystem function. In that case, increasing functional group richness does not necessarily lead to an increase in overall functioning. Rather, it is specific functional group assemblages that will lead to a maximization of multifunctioning. These results suggest that maximizing ecosystem functioning in a food web perspective might be dependent upon the interaction between functional group identity and the food web topology.

Our experimental results also showed that some functional groups have similar effects on ecosystem functioning, particularly in the freshwater system. For instance, the two groups of zooplankton and the family Planorbidae affected periphyton biomass and phytoplankton biomass, whereas the two largest functional groups, Cyprinidae and Lymnaeidae, shared a positive effect on phytoplankton biomass but a negative one on TN (see Fig. 3a). It seems that functional groups that shared common traits could also share common functions (Petchey et al. 2004, Solan et al. 2004, Berlow et al. 2009). For instance, body size could be a major driver of ecosystem functioning, as it captures many aspects of the ecology of a species and appears to be a useful surrogate measure of the niche (Williams et al. 2010). Solan et al. (2004) studied the covariance between functional traits such as stress sensitivity, body size, and rarity and the extinction risks of benthic organisms. They found that if sediment bioturbation decreased with the number of species extinctions, the magnitude and rapidity of the change varied with the trait that was under study. In the marine system, we also found functional groups that shared similar effects on ecosystem functions. However, we are not able to conclude that shared traits drive functioning, except for the two larger groups that were distantly located from every other group on the PCA (as in freshwater system). This discrepancy between the two systems may be explained again by the difference in the way each functional group contributed to ecosystem functions. In the freshwater ecosystem, trophic rank seemed to be the main trait linking functional groups that shared common effects on functioning. In marine ecosystem, however, because most of functional groups shared a complementary effect on functioning, it is not expected that particular assemblages of functional groups will share common effects, but rather that all functional groups will contribute more evenly to ecosystem functions and thus will be closer to each other in the multifunctional space (Fig. 3).

Conclusion

These two experiments showed that a mechanistic understanding of the effects of extinctions in complex ecosystems is possible, despite the absence of consistent BEF relationships. A great proportion of the observed variation in ecosystem functioning can be explained by identity effect, in both freshwater and marine systems. Our results also suggested that in food webs with strong antagonistic identity effects, maximizing one function may imply very specific assemblages. This study was also a first attempt to understand the effects of multiple extinctions on ecosystem multifunctionality within a food web perspective. We found that functional groups that shared common traits also shared commons effects on ecosystem functions for one ecosystem. These results warn us, however, about generalization from one food web to another, because the maximization of overall ecosystem functioning may be more influenced by the identity effects and food web topology than by richness per se.

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