Intermediate predation pressure leads to maximal complexity in food webs

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Responses of ecosystems to modifications of their environmental conditions are usually considered in terms of biodiversity or function. Maybe because they represent a hidden part of ecosystems, responses of ecological interactions are rarely studied. A more comprehensive view of the processes underlying the restructuring of food webs under environmental gradients appears crucial to understand how ecosystems functionalities are altered. We address this general issue in an experiment where trophic interactions are reorganized under a gradient of top–down effects (predation pressure) and bottom–up effects (nutrient availability). Unimodal relationships of species diversity are pervasive in ecology; we extend this principle to food-web topology: in our study, most topological descriptor values peak at intermediate predation intensity. The same unimodal pattern holds for network complexity, measured by entropy and scaled entropy (a measure independent of species diversity). Moreover, food web complexity is maximized at higher fish abundance when nutrient availability is increased. We infer that whereas in absence of top predators, a mechanism of competitive exclusion takes place, and indirect facilitation process underlies systems with a moderate predation pressure. These results highlight the importance of the dynamic reorganization of trophic links in response to bottom–up and top–down effects. Interaction between bottom–up and top–down forces argue for multifactorial studies of ecological effects.

Understanding the response of ecosystems to biotic forces (e.g. invasive species, species deletion, increase in predator abundance) or abiotic ones (e.g. global warming, resource enrichment) is a central issue in ecology. Most approaches have focused on biodiversity loss, functional properties, or relationships between biodiversity and ecosystem functioning. However, the cryptic modifications of ecological interactions, which underlie all ecosystem processes, are rarely addressed (Estes et al. 2011). We address this issue by analysing the response of trophic interactions – here the topology of an aquatic food web – to nutrient enrichment (bottom–up effect) and predation pressure (top–down effect).

Several experimental studies have explored changes in species diversity or functional diversity, such as production and biomass control across trophic levels or functional groups, in response to interactions between bottom–up and top–down forces (Brett and Goldman 1997, Hulot et al. 2000, 2014, Gruner et al. 2008, Nicolle et al. 2011). Moderate levels of grazing or primary productivity can increase species diversity (Hutchinson 1961, Kassen et al. 2000). A moderate predation pressure tends to maintain populations of competitively superior species under their carrying capacity, preventing competitive exclusion. Even if

several theoretical limitations have been presented (Chesson 2000, Fox 2013), some empirical results tend to show that these mechanisms hold in aquatic systems (Gliwicz et al. 2010). Modification of population size structure or niche breadth variation (MacArthur and Levins 1967, Gliwicz et al. 2010) can increase species coexistence. These results suggest the existence of unimodal relationships between diversity and environmental factors, though patterns of diversity–disturbance relationships can be more complex (Hughes et al. 2007, Miller et al. 2011). A few theoretical (Kondoh 2001) and experimental (Worm et al. 2002) papers underlined that complex patterns could emerge when taking into account several factors simultaneously. For example, the peak of the unimodal relationship should move toward higher levels of predation when increasing nutrient load (Kondoh 2001).

As these studies have mostly focused on response of species diversity or functional processes, the impact of bottom–up and top–down forces acting simultaneously on network topology remains elusive. In a similar way, models exploring the effects of trophic cascades on food webs rarely address the reorganization of trophic links in response to top–predator changes, despite impressive examples of cascading effects occurring in nature (Estes et al. 2011). Most

theoretical models consider the impact of ecological gradients on static food webs characterized by invariant trophic links, or eventually on networks only differing by the addition or deletion of a consumer species (Hulot et al. 2000). As species are connected in complex trophic networks, we expect that changes in bottom–up and top–down forces will not only affect species richness and composition, but will also reshape the topology of food webs. Some results about the topological impact of biotic (Woodward and Hildrew 2001, Lazzaro et al. 2009) or abiotic (Tylianakis et al. 2007) forces strongly support this hypothesis. For example, productivity gradients have been shown to be a key structuring pattern for food webs (Vermaat et al. 2009, Coll et al. 2011).

Species diversity has a clear impact on ecosystem functioning. Accordingly, changes in diversity associated with manipulations of nutrient resources and consumer pressure affect important ecosystem functions, such as carbon storage and nutrient retention (Worm et al. 2002). Moreover, several studies have predicted that changes in topological features should affect ecosystem properties. For example, connectance is known to affect food-web robustness and stability (Dunne et al. 2002b, Allesina and Tang 2012), and omnivory (i.e. feeding on multiple trophic levels) is predicted to be stabilizing, provided that interactions are prevalently weak (Fussmann and Heber 2002) or top-predator mortality is very low (Namba et al. 2008). The impact of changes of environmental conditions on food-web topology is rarely addressed, despite clear consequences on ecosystem properties and functioning (Worm and Duffy 2003, Estes et al. 2011).

In this study, we address how top-predator density and nutrient load affect food-web topology. We use an experiment in freshwater mesocosms manipulating four levels of fish density and two levels of nutrient load. 'Instantaneous' food webs describing trophic interactions in each mesocosm and on each date of observation were constructed, and their topology was analysed using 20 descriptors. Our results highlight that an intermediate level of consumer pressure maximizes several major topological features of food webs. Moreover, the simultaneous consideration of top–down and bottom–up forces reveals that the stock of top predators maximizing complexity depends upon bottom–up effects (even when the contribution of diversity to complexity is disregarded). Our study confirms that, by maintaining network at similar resolution levels (i.e. ensuring network comparability), experimental approaches provide an insightful contribution to theoretical advances regarding relationships between environmental changes and food-web topology.

Material and methods

Experimental protocol

Field design
We re-analysed the results of a 10-week factorial experiment, previously conducted (15 June – 23 August 1990) in Lake Créteil (suburbs of Paris, France), to assess the bottom–up and top–down interaction effects on the organization of aquatic communities. The balanced factorial design crossed two levels of nutrients with four levels of zooplank-

tivorous fish, with three replicates for each treatment. The experiment was run in 9.5-m³ enclosures ($1.5 \times 1.5 \times 4.3$ m deep) open to the atmosphere and sealed at the bottom. Enclosures were fertilized three times a week with soluble phosphorus (KH_2PO_4) and soluble nitrogen (NH_4NO_3) at two concentrations, N_1 and N_2, which corresponded respectively to phosphorus loading rates of 3.16 µg l^{-1} d^{-1} and 31.6 µg l^{-1} d^{-1} (N:P mass ratio = 20:1). At the beginning of the experiment, two-month-old cyprinids (mean total length: 30.0 ± 0.3 mm SE, mean wet weight: 0.25 ± 0.01 g SE), mainly roach *Rutilus rutilus* (88% of individuals) and a few breams *Abramis brama* (12% of individuals)*,* which are both filter feeders, were introduced to obtain a density gradient of four levels, $F_0 = 0$, $F_1 = 10$, $F_2 = 20$ and $F_3 = 40$ individuals per enclosure. The mortality rate of fish was very low (95.8% of fish individuals were recovered) and both species were present in all treatments throughout the length of the experiment. Moreover, we did not find any significant difference (p = 0.75) in the proportion of each fish species between treatments at the end of the experiment. Further information on the experimental protocol and results can be found elsewhere (Lacroix and Lescher-Moutoué 1991, Borcic et al. 1998, Hulot et al. 2000).

Sampling of organisms
Samples were collected on the 3rd and 8th weeks. For each sampling event, 24 litres of water were collected in each enclosure, from the surface to the bottom with a 2-litre Friedinger bottle for capturing planktonic taxa. The occurrence of larvae of chironomids (e.g. midges) on the mesocosm walls was recorded visually, using a nominal scale (chironomid tubs absent or rare, and moderately to highly abundant).

Network construction

Identification of trophic compartments
When possible, taxa were identified at the species or genus level. In most cases, organisms identified at the genus level belonged to only one non-determined species, with the exception of the phytoplankton genera *Coelastrum* and *Crucigenia*, for which several congeneric species were probably present but were not distinguished. A few complex groups (bacteria, small undetermined planktonic unicells, biofilm, Bdelloid rotifers, nauplii of calanoida, and nauplii of Cyclopoida, Chironomidae larvae) were also considered as trophic compartments. Detritus were assimilated to a basal compartment. The resulting 67 compartments were: basal species (n = 26), bacteria (n = 1), invertebrate consumers (n = 38), and fish (n = 2).

Identification of trophic links
Trophic links were determined mainly from detailed knowledge of the literature. In absence of specific information, we used allometric relationships between filter feeders and their prey (Burns 1968), as in Lazzaro et al. (2009). Remaining missing information where estimated through taxonomical similarities (species from similar genera were assumed to have similar diets, or only slight modification due to size effects). To take into account the diet differences between the successive ontogenic stages of Copepods, we splitted Calanoids and Cyclopoids taxa into two trophic species: nauplii on

one hand, and copepodites and adults on the other hand. Cannibalism potentially exists within Copepods. However, Copepods usually show a clear preference for small-sized prey (Brandl 2005). Thus, we only took into account predation of copepodites and adults on nauplii and we considered that the cannibalism within copepodite and adult stages was negligible. The presence of fish strongly impacts the size of some taxa, in particular cladoceran species. For example, the size of *Daphnia galeata* is reduced by 1/4 to 1/3 in presence of fish (Borcic et al. 1998). This reduces the diet size range of Cladocera, which is strongly dependent upon grazer body size (Burns 1968). Thus, we considered two different interaction networks: one for fishless enclosures and one for fish enclosures. Food webs were represented by binary matrices with predators listed as columns and prey as rows. Intersection elements of the matrices were either 0 (no consumption) or 1 (consumption).

Mesocosm food webs

By cumulating taxa from all enclosures on the two sampling dates we observed 67 trophic species. As indicated above, two cumulated matrices were constructed: one representing all potential interactions in fishless enclosures, and one representing all potential interactions in fish enclosures (Supplementary material Appendix 1, 2). We then constructed 48 instantaneous food webs corresponding to each treatment (2 nutrient levels $\times$ 4 fish modalities $\times$ 3 replicates $\times$ 2 dates) as subnets of the cumulated matrices without or with fish). These instantaneous food webs reflect the reorganization of species and their trophic links according to treatment.

Food-web descriptors

Network topological descriptors were computed for all instantaneous matrices. They can be split into four categories.

Species properties

We analysed the total species richness, S, and the species richness of phytoplankton and invertebrate species. Invertebrates were split into either detritivores and herbivores (thereafter referred as 'herbivorous invertebrates') or partly carnivorous species (thereafter referred as 'omnivorous invertebrates'). Calanoids, which are typically considered as herbivorous, were considered as omnivorous since they are able to consume small planktonic animals such as rotifers (Brandl 2005). Note also that most herbivores are in fact omnivorous as they are able to eat bacteria, which are consumer species.

Network properties

The link density is the ratio of the number L of trophic links to the overall species richness, S. Connectance C is the number of links over the number of possible links, $C = L/S^2$. We defined a chain as a path linking a basal species to a non-basal species, and chain length as the number of links in the chain (our food webs did not contain cycles). The number of chains was the total number of paths linking basal species to non-basal species. Mean chain length was the total number of links in these paths divided by their total number. We also computed the mean length of maximal chains (paths linking basal species to top-consumers). The predator–prey ratio was the ratio between the number of consumer species and consumed species.

Trophic height of species

In a chain, the trophic level of a species is the number of species below it. Basal species have a trophic level of 0. The trophic height of a non-basal species is the average of its trophic level over all chains leading to it. The average of the trophic heights of all species, and of omnivorous invertebrate species, give the mean height of the food web, and of omnivorous invertebrates, respectively.

Generalism and omnivory properties

The generalism index of a trophic species is the number of species it consumes. The food-web generalism index is the mean value of the generalism indices of all consumer species. We computed the generalism index of consumers, of herbivorous invertebrates and of omnivorous invertebrates. The omnivory index of a species is the standard deviation of the trophic height of all its prey, and the food-web omnivory index is the mean value of the omnivory indices of all consumer species. We also computed the omnivory index of all consumers, and of omnivorous invertebrates.

Food-web complexity

We characterized food-web complexity using entropy, according to the Kolmogorov–Sinai definition (Billingsley 1965). In this context, entropy measures the diversity of pathways of energy flow between species in the trophic network. To account for the circulation of energy, we used the method of Allesina and Pascual (2009): a root node is attached to the network with links pointing to all the primary producers, and links are added from all species to the root node. This procedure ensures that the network matrix is irreducible (we furthermore checked that all our matrices were aperiodic, hence primitive). For a primitive binary matrix, entropy is the logarithm of the dominant eigenvalue of the matrix, $H = \ln (\lambda)$. Entropy increases with species richness S, and maximal entropy is obtained when all matrix entries are 1, in which case the value is $\ln (S)$. To disentangle complexity coming from an increase in species richness and from the very structure of the network, we also measured complexity using scaled entropy $H' = \ln (\lambda) / \ln (S)$. Network entropy is also a quantitative measure of its robustness (Demetrius and Manke 2005), that is its capacity to remain functional in the face of random perturbations.

Statistical analyses

We first tested the impact of fish and nutrient load on network structure using multivariate analysis of variance with permutation tests (PerMANOVA). Nutrient load was defined as a categorical variable, and fish effect was analysed by defining this variable as continuous and using a second-order polynomial regression for detecting a possible unimodal response to fish abundance. Time was considered as a random effect. In a second step, we analysed each response variable separately. We analysed the main effects of fish abundance using a second order regression (F and F²), of nutrient loading (N), and their interaction effects (F $\times$ N) using repeated-measures ANCOVA, with time as a random effect. In order to disentangle the impact of variation of species richness on that
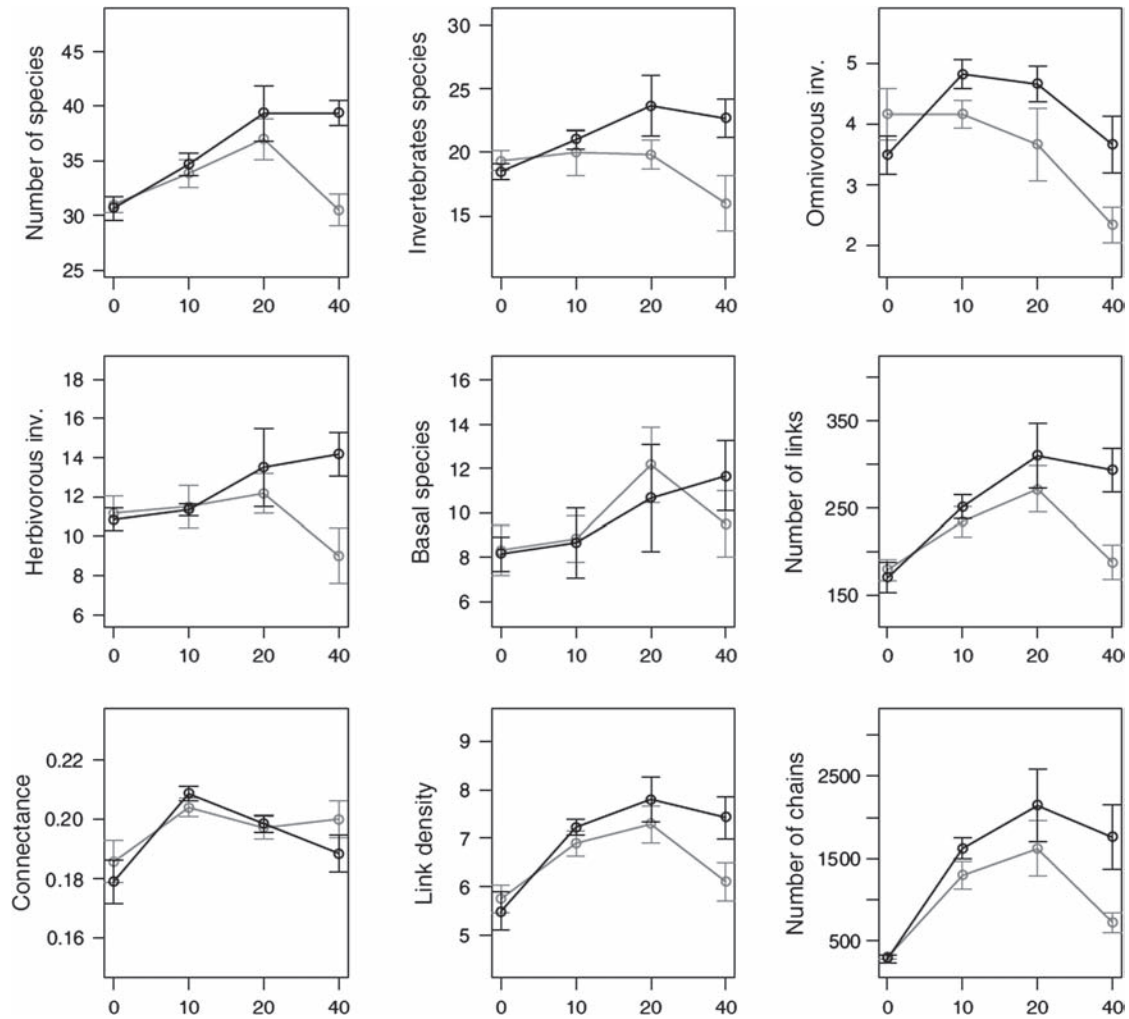
Figure 1. Responses of topological descriptors associated with species richness, trophic categories, and trophic links, to the nutrient and fish treatments (averaged over the two dates). Number of fish per enclosure in abscissa (F_0, F_1, F_2, F_3). Black lines represent the high level of nutrient load treatment, grey ones the low level. Error bars set $\pm$ SE.

of other descriptors, we also performed statistical analyses with species richness as a fixed effect for all descriptors but the number of invertebrates, omnivorous, herbivorous and basal species, as these descriptors are parts of species richness. All statistical tests were performed using the R software (ver. 2.11.0 < www.r-project.org >) on non-transformed data. In order to correct for the risk of finding randomly significant results through multiple testing, statistical significance was inferred using the false discovery rate controlling procedure (FDR) (Benjamini and Hochberg 1995), with a significant initial threshold of 0.05.

When the quadratic effect F^2 was significant, we also tested if model prediction of fish densities maximising descriptor values were impacted by nutrient load. We randomly associated replicates along the fish abundance gradient. As our experiment was based on three replicates, for each random association, three different trajectories were obtained for each nutrient level (as there were two nutrient levels, in total we obtained six trajectories). All of these trajectories were fitted using a quadratic polynomial, predicting levels of fish abundances maximizing descriptors values for the different nutrient loads (three values for both N_1 and N_2 treatments).

Mean comparison test were performed on this data, assessing whether the maximum descriptor values were obtained at higher fish abundances in N_2 than in N_1. We then made a permutation test in which replicates were randomly reattributed, and checked if mean comparison tests were significant in more than 95% of associations (10 000 replicates).

Results

Globally, we observed a clear effect of fish abundance (top–down effect) on topological descriptors, with 70% of the studied descriptors responding significantly in a linear or unimodal way. (Fig. 1, 2). The unimodal response was more often significant than the linear one (Table 1). The effect of nutrient load (bottom–up effect) was less pronounced, with 45% of the descriptors significantly affected. In both cases the PerMANOVA test was significant, with the exception of the interaction between nutrient and the fish quadratic term (F, F^2 and N: $p < 0.001$, $F \times N$: $p = 0.0032$, $F^2 \times N$: 0.46). Quadratic parameters were significantly negative for 65% of the descriptors, highlighting unimodal variations of these
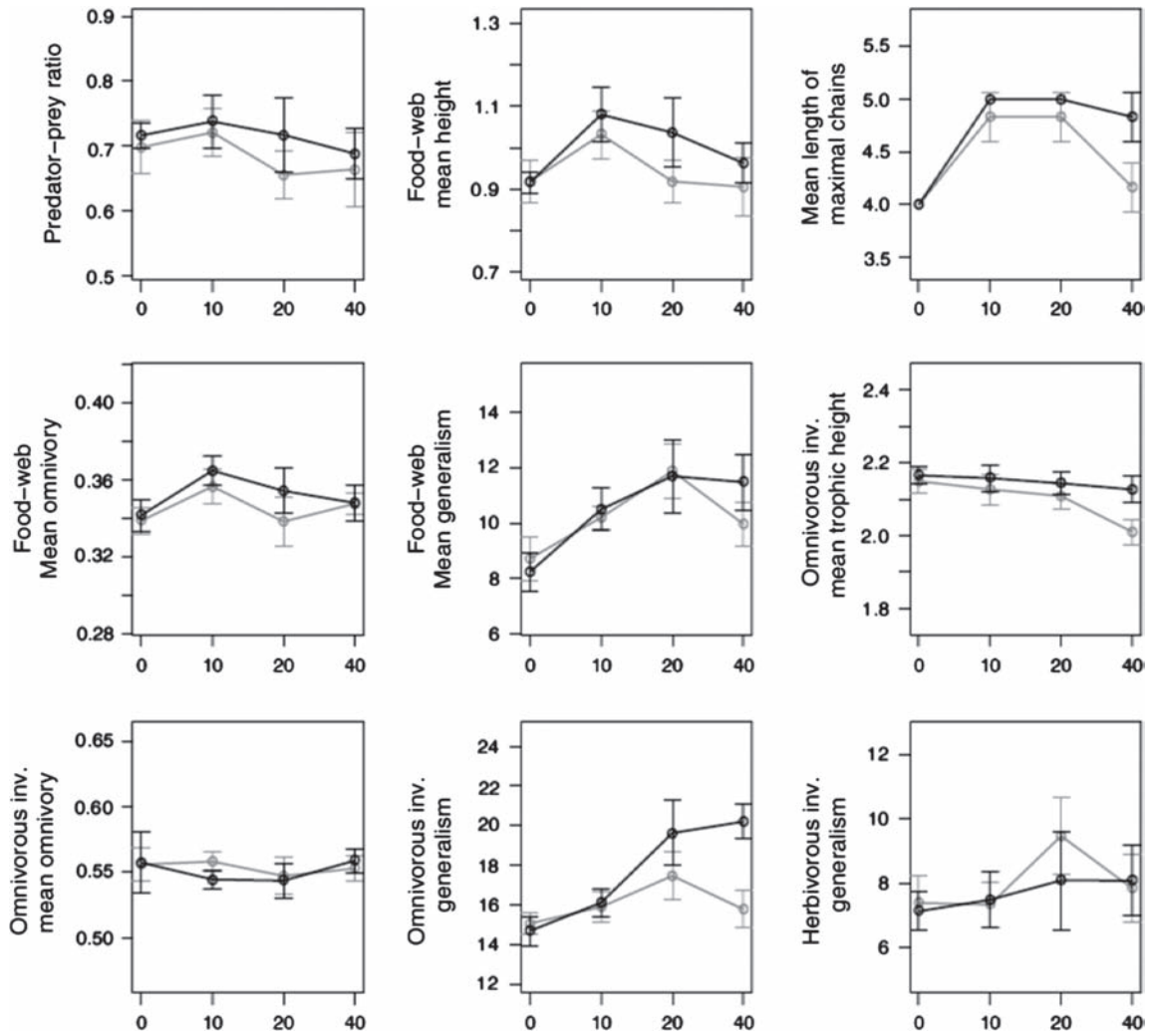
Figure 2. Responses of topological descriptors associated with species generalism and omnivory, and food-chain length, to nutrient and fish treatments (averaged over the two dates). Legends as in Fig. 1.

Table 1. Statistical effects of treatments on studied descriptors. p-values are not corrected; tests remaining significant after the FDR procedure are in bold. F and F^2 set the linear and quadratic fish effects N the nutrient effect, and $F \times N$ the interaction effect.

	F	F^2	N	$F \times N$
No. species	**0.006**	**<0.001**	**0.005**	**0.005**
No. invertebrates	0.839	**0.01**	**0.002**	**0.005**
No. omnivores	**0.003**	**0.004**	**0.02**	**0.015**
No. herbivores	0.425	0.09	**0.023**	**0.009**
No. basal species	**0.023**	0.119	0.915	0.236
No. links	**0.004**	**<0.001**	**0.009**	**0.017**
Connectance	0.167	**<0.001**	0.328	**0.008**
Link density	**0.002**	**<0.001**	**0.019**	0.025
No. chains	**0.002**	**<0.001**	**0.008**	0.077
Predator-prey ratio	0.155	0.772	0.165	0.453
Mean height	0.557	**0.017**	0.073	0.048
Chain length	**0.014**	**<0.001**	**0.008**	**0.005**
Food-web omnivory	0.819	0.137	0.17	0.049
Generalism	**0.003**	**0.001**	0.521	0.337
Height of omnivores	**0.001**	0.55	**0.012**	0.184
Omnivory of omnivores	0.976	0.207	0.712	0.869
Generalism of omnivores	**<0.001**	**0.016**	**0.009**	**0.006**
Generalism of herbivores	0.236	0.161	0.549	0.422
Entropy	**0.002**	**<0.001**	0.152	0.124
Scaled entropy	**0.015**	**0.014**	0.471	0.926

descriptors (60% with a significant linear response, 50% with both quadratic and linear parameters significant), with maximal values obtained at intermediate fish densities.

Interaction effects were significant for the number of species, the number of invertebrate, omnivorous and basal species, the number of links, the number of chains, the mean chain length, the generalism of omnivorous species and entropy. These interaction effects mean that differences between low and high nutrient load increased with the fish effect. Indeed, differences between the two nutrient levels were larger at high fish biomass levels (F_2, F_3) than at zero or low fish biomass levels (F_0, F_1). A closer examination of the species present in the enclosures indicates that large omnivorous invertebrates dominated in fishless enclosures, small ones dominated when fish were abundant, and both coexisted in enclosures characterized by intermediate fish densities.

When species richness was considered as a covariate in order to disentangle effects of species richness S on descriptors, results were quite similar for the quadratic response to fish abundance. The negative quadratic effect only disappeared for the food-web mean generalism. We found similar results on entropy measures (Fig. 3): quadratic fish effect was significant for entropy and scaled entropy, that is indepen-

dent of species richness. For these two descriptors no interacting effects were found.

Fish abundances maximising descriptors values were higher (p < 0.001) in mesocosms with high nutrient load than with low nutrient load when the quadratic effect was significant. It indicates that the predation intensity maximising food-web complexity increases with nutrient availability.

Discussion

The alteration of ecosystem functioning under global change is a central question (Loreau et al. 2001, Hooper et al. 2005). The role of food-web structure and the importance of top–down and bottom–up control on the relation between species diversity and ecosystem functioning has been demonstrated (Worm et al. 2002, Hooper et al. 2005). We focus here on the role of top–down (fish density) and bottom–up (nutrient load) forces on the topology of experimental aquatic food webs, and on the ecological mechanisms underlying network topology in response to bottom–up and top–down gradients. We found clear top–down effects but less systematic (although frequently significant) bottom–up effects on topological descriptors (Table 1, Fig. 1, 2). Globally, our results demonstrate that not only species diversity, but also network topology, are strongly dependent upon top–down and bottom–up forces, with two main results (Fig. 3): 1) an intermediate level of consumer pressure maximizes the topological complexity of food webs, even when the contribution of the number of species to complexity is disregarded. 2) the addition of resources increases the stock of top predators maximizing food-web complexity.

We now analyse separately the responses observed in mesocosm with different fish densities, using previous results on this experiment (Lacroix and Lescher-Moutoué 1991, Lacroix et al. 1996, Borcic et al. 1998, Bertolo et al. 1999, Hulot et al. 2000). The ecological consequences of the three cases (no fish, moderate fish density, high fish density) are illustrated in Fig. 4.

Fishless condition – competitive exclusion and invertebrate predation

In absence of fish, zooplankton communities in the enclosures were dominated by large (mainly adults) cladocerans and copepods (Lacroix and Lescher-Moutoué 1991, Borcic et al. 1998). Phytoplankton species were maintained at very low levels by the intense grazing pressure exerted by highly efficient generalist filter feeders (Lacroix et al. 1996). In such a context, small algae, able to compensate high grazing loss rates by a rapid turnover, prevailed within the phytoplankton community (Borcic et al. 1998). Small invertebrates, such as rotifers, were probably excluded by competition (Gliwicz et al. 2010) with large cladocerans that dominated the zooplankton community (Borcic et al. 1998), or by predation exerted by large omnivorous invertebrates (Brandl 2005). Overall, in absence of apex vertebrate consumers, the community was driven by a few large and competitively dominant invertebrate species exerting a strong top–down control on their prey (Fig. 4A).

Moderate fish stock – indirect facilitation and intermediate predation pressure

As predicted by Gliwicz et al. (2010), a moderate fish stock increased species richness. The introduction of a moderate density of roach decreased the abundance of large cladocerans, such as Daphnidae (Borcic et al. 1998). It provided a niche opportunity for smaller, less efficient herbivorous species such as rotifers and small cladocerans whose species richness significantly increased with fish density (p < 0.0228). This global reduction of herbivore size and the partial control of large cladocera by fish strongly reduced their grazing capacity (Bertolo et al. 1999), favouring the development of phytoplankton species. Moderate fish stocks increased the diversity of omnivorous invertebrates, probably because they were able to benefit from the observed higher abundances of resources, such as larger algae and small herbivores (Hulot et al. 2000), and to escape partly from invertebrate and fish consumers (Lacroix et al. 1996). This positive effect of fish on omnivorous invertebrates corresponds to an indirect facilitation process (Levine 1976). By modifying the selective forces on intermediate species, an intermediate predation pressure seems to be the first step towards the establishment of an indirect facilitation process. Thus, when kept at moderate densities, apex vertebrate consumers typically act as a keystone trophic group, preventing the most efficient consumers from reaching too high density and monopolizing food resources (Fig. 4B).

High fish densities – predation pressure versus nutrient availability

At the highest fish density, network complexity decreased. A first explanation is that intermediate species collapsed as they became unable to support very high fish densities (Nicolle et al. 2011). A second explanation might be that the facilita-
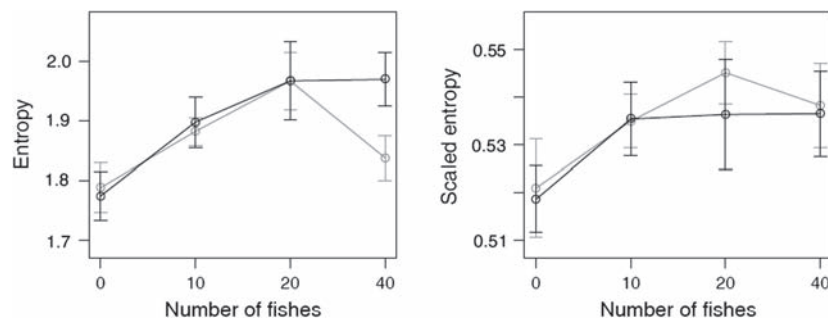

Figure 3. Responses of network complexity, measured by entropy and scaled entropy (independent of species richness), to nutrient and fish treatments (averaged over the two dates). Legends as in Fig. 1.
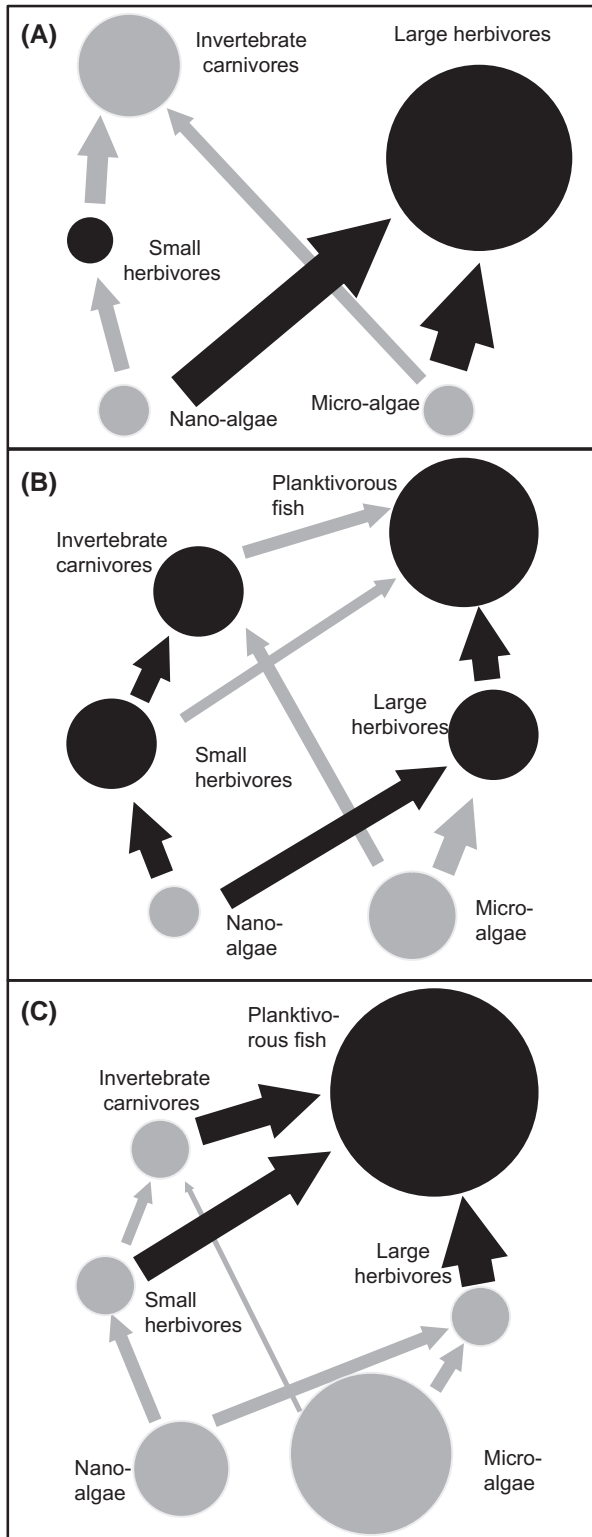
Figure 4. Illustrative food webs representing the hypothesis underlying three ecological situations: no fish (A), moderate fish abundance (B), and high fish abundance (C). Circles represent trophic groups and arrows represent trophic interactions: (A) exclusion of small herbivores by larger competitors or by large invertebrate carnivores, (B) facilitation mechanism between fish and invertebrate carnivores, and (C) over predation of intermediate species by fish. Grey colors represent trophic groups and interactions that are not involved in the above mechanisms. Symbol size illustrates trophic groups biomass (circles) and predation intensity (arrows).

tion hypothesis, which explains the coexistence of different guilds of consumers, ultimately depends upon the balance between bottom–up positive effects and top–down negative effects on invertebrate carnivores. In our mesocosms, the largest species of invertebrate carnivores, which had also the highest trophic height within invertebrate communities (*A. robustus* had a trophic height close to that of cyprinids in mesocosms), were also the first to disappear. Thus, the raise in fish density decreased the mean trophic height of the omnivorous invertebrate guild. The generalism index also decreased, since fish predation favoured small organisms, which typically have narrower diet breadths than large ones (Humphries 2007). By triggering all these community alterations, fish crowding induced a decrease in species richness of all non-basal species (except for herbivores in high nutrient conditions), in the number of chains, and in food-web connectivity (Fig. 4C). In this case, intermediate species appear as bottlenecks, limiting the energy flow within the food web (Allesina and Bodini 2004).

Interaction between top–down and bottom–up effects

The increase of nutrient load had no effect on food-web topology in absence of fish or at low fish density. Consumer communities were characterized by a few large and competitively dominant species in this case. These species were probably able to maintain their prey at threshold levels excluding potential competitors, despite nutrient enrichment. At the opposite, the increase of nutrient inputs led to marked topological differences at high top-predators density. This suggests that resource enrichment buffered against predation effects via food-web structure (Davis and Rosemond 2010). The simultaneous consideration of both top–down and bottom–up effects indicates that the documented impacts of productivity or nutrient availability on food-web topology (Coll et al. 2011) should depend on the ecology of the highest trophic levels. In our results, nutrient enrichment increased the level of top-predator abundance that maximized food-web complexity. This is in accordance with theoretical predictions on the effects of productivity and disturbance on species richness (Kondoh 2001), and with experimental results on the resource × consumer interaction effects on species diversity (Worm et al. 2002). However, we go one step further by highlighting the close link between diversity responses, the restructuring of trophic pathways, and ecological processes at the scale of the food web. This response of network topology and species traits to environmental gradients is supported by empirical studies (Coll et al. 2011).

Resources, intermediate predation pressure and food-web complexity

Our results support the hypothesis that an intermediate level of top-consumer pressure maximizes food-web complexity. This is in agreement with the response of diversity to consumer gradients (Worm et al. 2002) or to productivity gradients (Connell 1978). However, they bring a novel dimension by highlighting unimodal patterns of responses of food-web topology and complexity to increasing predation pressure. The different parts of the unimodal response are associated

with a dominance of different ecological processes: low, moderate and high levels of predation pressure lead to competitive exclusion, indirect facilitation and bottleneck effect respectively. These contrasting patterns are linked to changes in the abundance of the apex consumers impact food-web topology.

The mechanisms corresponding to various top-predator densities were described for different kinds of ecosystems, both aquatic and terrestrial, or using modelling approaches (Vandermeer 1980, Tilman 1990). In the same way, the generality of the mechanisms underlying transitions between the different situations, such as size-dependent interactions (Emmerson and Raffaelli 2004, Petchey et al. 2008, Vucic-Pestic et al. 2010) and consumption of dominant species, (i.e. functional response depending upon prey frequencies) argues in favour of the generality of our results.

Connectance and species richness are key determinants of structural patterns (Williams and Martinez 2000) and food-web robustness (Dunne et al. 2002a). They address the ability of food webs to resist to species loss in response to enrichment gradients (Coll et al. 2011, O'Gorman et al. 2012). The interaction effect observed between nutrient load and predation intensity on connectance and species richness (Table 1) validates a multifactorial approach to food-web robustness (Vermaat et al. 2009, O'Gorman et al. 2012), and their utility to disentangle the relative effects of environmental factors on food-web structure and robustness.

Conclusions

By considering the whole complexity of trophic interactions, food-web topology provided a unifying framework, and constituted a powerful tool for integrating and interpreting the effects of a large variety of interdependent trophic interactions on community structure. Complexity, as most of topological descriptors, was mainly affected by fish treatment, and more globally, we observed stronger responses of food-web topology to top–down effects (fish manipulation) than to bottom–up effects (nutrient load). In accordance with the synthesis of Estes et al. (2011) on the importance of apex species in ecosystems, we have shown that top species drives the reorganization of species interactions, hence of ecosystem functionalities. This does not mean that bottom–up forces are unimportant, as the stock of top consumers inducing maximal complexity appeared to be dependent upon nutrient load. In our experiment, the treatments with intermediate fish abundances that maximized entropy corresponded to fish densities frequently observed in natural systems (Lacroix and Lescher-Moutoué 1991), suggesting that species diversity and food-web complexity might be maximized in such standard conditions. These topological reorganisations in response to perturbations are usually not addressed in dynamical systems studies, where the presence/absence of trophic links is most of the time invariant.

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