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LETTER

Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs

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Abstract

The biodiversity–ecosystem functioning (BEF) relationship is central in community ecology. Its drivers in competitive systems (sampling effect and functional complementarity) are intuitive and elegant, but we lack an integrative understanding of these drivers in complex ecosystems. Because networks encompass two key components of the BEF relationship (species richness and biomass flow), they provide a key to identify these drivers, assuming that we have a meaningful measure of functional complementarity. In a network, diversity can be defined by species richness, the number of trophic levels, but perhaps more importantly, the diversity of interactions. In this paper, we define the concept of trophic complementarity (TC), which emerges through exploitative and apparent competition processes, and study its contribution to ecosystem functioning. Using a model of trophic community dynamics, we show that TC predicts various measures of ecosystem functioning, and generate a range of testable predictions. We find that, in addition to the number of species, the structure of their interactions needs to be accounted for to predict ecosystem productivity.

Keywords

Biodiversity–ecosystem functioning, food webs, trophic interactions.

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INTRODUCTION

Network theory is a staple of modern ecology (Dunne 2006). From early work on the structure of interspecific interactions, network studies moved to aspects of stability, resilience to perturbation and dynamics. Few attempts however have been made to draw explicit links between network structure and ecosystem functioning. This is surprising because the well-described effects of species richness are likely to be mediated by the structure of ecological interactions, and the position of species within the food web (Loreau 2010). In short, in a food web context, the identity of interacting species can be as important as other factors such as the overall number of species, functional diversity, evolutionary history or environmental conditions (Loreau *et al.* 2001; Hooper *et al.* 2005; Thompson *et al.* 2012). Yet, when the trophic structure is incorporated in empirical studies, the explanatory power of species richness tends to decrease (Duffy *et al.* 2007), indicating that trophic effects on ecosystem functioning are central and should be further understood.

Previous theoretical attempts to understand how diversity affects ecosystem functioning in a trophic context focused on extreme cases of network structure. Akin to classical biodiversity–ecosystem functioning (BEF) experiments, these studies increased species richness on a continuous scale and varied network properties only between two extremes, for example specialists and generalists (Thébault & Loreau 2003, 2005) or low and high connectance (Thébault *et al.* 2007). The inherent complexity of multiple species interactions revealed idiosyncratic BEF relationships in food webs, making any overarching theoretical approach difficult to achieve. Previous work also offered insights about why, in a network setting, the BEF relationship is not necessarily positive and linear (Duffy *et al.* 2007). However, these studies did not pinpoint a general mechanism explaining how trophic structure should act on ecosystem functioning (Loreau 2010). Ives *et al.* (2005) nonetheless showed that switching from one to two trophic levels did not require conceptually new mechanisms to link biodiversity to ecosystem functioning, which means that unifying network theory with BEF studies should be possible and worthwhile.

The absence of a general theoretical understanding of BEF in food webs is one of the possible explanations for inconsistent empirical findings over the last decade. Specifically, experimental studies agree that the impact of network structure on ecosystem functioning has synergistic effects with species richness and species-identity effects (Straub & Snyder 2006; Harvey *et al.* 2013). Niche partitioning among consumer species was proposed as a mechanism explaining productivity in communities (Finke & Snyder 2008); this would mirror the complementarity effect in non-trophic BEF studies, that is, each species brings a new function. However, accounting for the relative importance of each of these mechanisms has been so far a difficult task. This is in part due to the fact that experimental designs required to separate all the effects need to be factorial (Fox 2004), and because natural systems are affected by both species-identity variation (Montoya *et al.* 2003) and local environmental conditions (Tylianakis *et al.* 2008; Macfadyen *et al.* 2009). Notably, Dobson *et al.* (2006) showed that species identity can interact with predator richness, which makes the impact of food web structure on functioning difficult to measure. So far, we are left without an integrative mechanism to

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predict the impact of trophic structure on ecosystem functioning (Thompson *et al.* 2012). Because several aspects of network structure (e.g. trophic niche overlap) can be related to the key concept of functional complementarity/redundancy, we argue that the results of classical BEF analysis in a single trophic level can be revisited in a trophic context.

The BEF theory is essentially derived from niche theory and resource (exploitative) competition. Resource complementarity occurs when two focal species are specialised on different resources (Loreau 1998); similarly, predation complementarity occurs when the two focal species have different predators (Holt 1977). At the interaction between these two processes lies trophic complementarity, that is, the fact that species can functionally complement each other either through the use of different resources, being consumed by different predators, or both. In other words, we define trophic complementarity as the 'originality' of a species in a food web relative to the other ones, based on the identity of the species it interacts with. Even in the absence of resource competition, two species sharing a common enemy may interact via 'apparent' competition (Holt 1997), wherein an increase in the population size of one species will translate into higher enemy pressure for the other species. The current theory on BEF does not account for these indirect interactions and might therefore miss important elements for species complementarity.

In this article, through analysis of a mathematical model, we show that trophic complementarity is a general mechanism driving functioning of multi-trophic networks. Because it accounts for exploitative and apparent competition, it is analogous to the complementarity effect studied in classic BEF experiments, thus offering the perspective of re-analysing previous data. Starting with the mathematical analysis of a simple model, and scaling up to numerical experiments in complex communities, we show how increased complementarity results in increased functioning. We illustrate that the mechanism of trophic complementarity also translates to complex communities, and can be inferred based on simple knowledge of the trophic interactions. In the last part, we present numerical experiments of species extinctions to illustrate how our theoretical predictions could be tested experimentally.

THE MODEL

We use a standard model of tri-trophic interactions as proposed by Chesson & Kuang (2008) to study coexistence of intermediate level consumers. Each trophic level can be made up of different populations/species, and feed upon the immediately inferior level. $\mathcal{R}$ species of resources (of population size R) are consumed by $\mathcal{N}$ consumers (N), themselves preyed upon by $\mathcal{P}$ predators (P). This model can translate to a wide number of canonical situations in community ecology, for example plants, herbivores and predators. The instantaneous changes in population when multiple species reside at each trophic level are given by the following system of equations:

$$\frac{1}{R_l}\frac{dR_l}{dt} = r_l^R(1-\alpha_l^R R_l) - \sum_j N_j \mathbf{C}_{jl}, \tag{1}$$

$$\frac{1}{N_j}\frac{dN_j}{dt} = \sum_l R_l \mathbf{C}_{jl} v_l - \sum_m P_m \mathbf{A}_{jm} - \mu_j, \tag{2}$$

$$\frac{1}{P_m}\frac{dP_m}{dt} = r_m^P(1-\alpha_m^P P_m) + \sum_j w N_j \mathbf{A}_{jm}. \tag{3}$$

A and **C** are interaction matrices representing, respectively, the bipartite networks for predation and resource consumption, in which the consuming organisms (predators and consumers respectively) are in rows, and the consumed organisms (consumers and resources respectively) are in columns. Values within these matrices are *per capita* interaction rates, and it is assumed that the functional response of each trophic level is linear. The remaining notation follows Chesson & Kuang (2008): r are intrinsic growth rates, α are intraspecific competition rates, w is the value of one unit of consumer biomass converted to predator biomass, v is the value of one unit of resource biomass converted to consumer biomass, and μ is the intrinsic mortality rate of consumers. Here, we assume r^P to be positive, that is, the predators can persist in the absence of the focal consumer; this assumption was proposed by Chesson & Kuang (2008) to focus on coexistence mechanisms at the intermediate trophic level. Predators only experience density-dependent mortality, in the form of the α^P *per capita* rate. In this article, these assumptions are conserved because they allow focusing on productivity, and as they promote coexistence, to do so in communities in which all species persist so that there are no complex, interactive effects of richness at each trophic level with network structure (Duffy *et al.* 2007). This situation can arise when predators have a large feeding niche, that is, will feed on prey that are outside the focal community of consumers studied here, or have the ability to temporarily switch to alternative prey when their preferred items are absent; these are fairly frequent situations in nature (Radloff & Du Toit 2004). This model explicitly accounts for intraspecific competition in predators and resource, making it explicit for these compartments, and phenomenological for the consumer level (intraspecific competition occurs through resource consumption and predator sensitivity). We define consumer productivity φ as the net production of biomass by consumers through resource exploitation, measured at ecological equilibrium (Loreau 1998; Loreau *et al.* 2001), that is,

$$\varphi = \sum_j \sum_l \mathbf{C}_{jl} v_l R_l^* N_j^*. \tag{4}$$

RESULTS

We use the model presented above to explore how manipulating trophic complementarity in scenarios of increasing complexity affects ecosystem functioning. Starting with (1) analytical results for a minimal food web, we expand this situation to the case where (2) resources and predators form a continuous niche axis. We then (3) measure the functioning of simulated complex food webs, and confront it to a measure of complementarity derived from the network analysis literature. We finally (4) present an application of our results; through simple simulations illustrative of species removal, we show how our results bear consequences for our capacity to predict the loss of function resulting from extinctions cascades. The predictions derived in this numerical experiment could easily be confronted to empirical results, by either selectively removing species or adding them like in a classical BEF experiment.

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Trophic complementarity predicts functioning in simple systems

Essentially, trophic complementarity is an extension of the concept of resource-use complementarity (Loreau 1998). It is tightly linked to conditions for coexistence, that is, to the fact that two coexisting species are specialised on different resources. In the simplest case of a trophic network with three discrete levels, complementarity in resource use among two consumer species is defined by the inverse of a measure of resource-use overlap, ρ_R (whose complete definition is given below – see eqn 8). Like resource-use complementarity, predation complementarity, is defined by the overlap in their predators, ρ_P (i.e. the fact that two consumers are preyed upon by a different set of predators – see below). These two measures are a decomposition of an all-inclusive single value ρ of niche overlap that we name here trophic complementarity. It tells how much consumers in a tri-trophic systems are exhibiting different strategies. In addition to being complementary because they do not overlap in resource consumption, consumers can increase their complementarity in a trophic context by not having the same set of predators (Fig. 1). Thus, a food web with maximal complementarity is made entirely of unconnected linear food chains, while a set of overlapping generalists result in a functionally redundant food web (Thébault & Loreau 2003, 2005).

Classical BEF studies, notably in plants (Schmid *et al.* 2008), are concerned by transgressive overyielding (TO), that is, the fact that a pair (or mixture) of species will reach a higher cumulative population size at equilibrium than the species with the higher carrying capacity. Loreau (2004) showed that, in a competitive Lotka–Volterra model in which two focal species compete at rates of resp. α_{21} and α_{12}, transgressive overyielding occurs when

$$(1-\alpha_{21})(1-x\times\alpha_{12})>0, \tag{5}$$

with $x=K_2/K_1$, that is, the ratio of carrying capacities. Given that K_1 and K_2 are, respectively, $1/\alpha_{11}$ and $1/\alpha_{22}$ (i.e. the inverse of intraspecific competition rates), we have $x=\alpha_{11}/\alpha_{22}$. We integrate this theory to recent extensions of the niche theory to trophic interactions. Chesson & Kuang (2008) show that for two consumer species i and j, once competition for resources and predation are incorporated into the model, $\alpha_{ii}=s_i/\kappa_i$, $\alpha_{jj}=s_j/\kappa_j$, and $\alpha_{ij}=\rho s_j/\kappa_i$, where s is the joint impact of competition and predation on fitness (i.e. how much the growth rate of a population is reduced through interactions with other species), κ is the species fitness (here measured by net natality), and ρ is the extent to which the trophic niches of i and j overlap.

After Chesson & Kuang (2008), s_j is defined by

$$s_j=\sqrt{\left(\sum_l\frac{\mathbf{C}_{jl}^2 v_l}{r_l^R\alpha_l^R}+\sum_m\frac{\mathbf{A}_{\mathbf{jm}}^{\mathbf{2}}\mathbf{w}}{r_m^p\alpha_m^p}\right)}, \tag{6}$$

κ is defined by

$$\kappa_j=\frac{1}{s_j}\left(\sum_l\frac{\mathbf{C}_{jl}v_l}{\alpha_l^R}-\sum_m\frac{\mathbf{A}_{jm}}{\alpha_m^p}-\mu_j\right), \tag{7}$$

and ρ is defined by

$$\rho=\frac{\sum_l\frac{\mathbf{C}_{jl}v_l\mathbf{C}_{kl}}{r_l^R\alpha_l^R}+\sum_m\frac{\mathbf{A}_{jm}w\mathbf{A}_{km}}{r_m^P\alpha_m^P}}{\sqrt{\left(\sum_l\frac{\mathbf{C}_{jl}^2v_l}{r_l^R\alpha_l^R}+\sum_m\frac{\mathbf{A}_{jm}^2w}{r_m^P\alpha_m^P}\right)\left(\sum_l\frac{\mathbf{C}_{kl}^2v_l}{r_l^R\alpha_l^R}+\sum_m\frac{\mathbf{A}_{km}^2w}{r_P^m\alpha_m^P}\right)}} \tag{8}$$

We substitute these values into eqn 5 and we find that transgressive overyielding occurs whenever

$$\left(1-\rho\frac{s_1}{\kappa_2}\right)\left(1-\rho\frac{s_1\kappa_2}{\kappa_1^2}\right)>0. \tag{9}$$

Transgressive overyielding requires coexistence between the two species, which occurs when

$$\rho<\frac{\kappa_1}{\kappa_2}<\frac{1}{\rho}. \tag{10}$$

This condition for the occurrence of transgressive overyielding as a function of ρ can furthermore be partitioned in ρ_R and ρ_P by setting, respectively, all predation-related and resource-related terms to 0. To understand under which conditions complementarity in the upper and lower trophic levels can affect transgressive overyielding, we adopt the following procedure. Consider the example of the

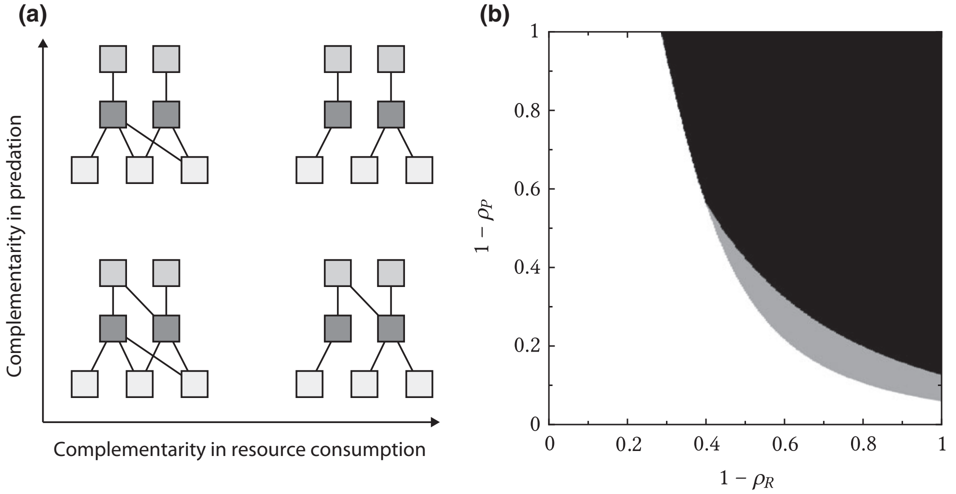

Figure 1 Left panel: in a system with three trophic levels, similarity in exploitation by predators, or similarity in resource exploitation, can be inferred by link distribution respectively to and from the focal level (here called consumers). Systems in which few focal species share links are highly dissimilar, that is complementary. Right panel: analytical results stemming from the derivation in the first paragraph of the results (eq. 10), in a system with $\mathcal{N}=\mathcal{R}=\mathcal{P}=2$. The grey area indicates coexistence but no transgressive overyielding, and the black area indicates coexistence and transgressive overyielding. Note that the axes correspond to $1-\rho_R$ and $1-\rho_P$, that is, increasing values indicates increasing complementarity in either consumption or sensitivity to predation.

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interaction matrices (**A** for predation sensibility and **C** for resource consumption respectively)

$$\mathbf{A} = \begin{pmatrix} 1 & 0 \\ a_{21} & 1 \end{pmatrix}, \tag{11}$$

$$\mathbf{C} = \begin{pmatrix} 0 & 1 \\ 1 & c_{22} \end{pmatrix}. \tag{12}$$

By changing a_{21} and c_{22} between 0 and 1, we can vary the values of ρ_C and ρ_P independently. The system is then analysed to see if the conditions for coexistence of the two consumers and transgressive overyielding are satisfied. We find that both resource-use and predation complementarity are important to accurately predict the occurrence of a positive effect of biodiversity on ecosystem functioning (TO, Fig. 2).

The TO is an important phenomenon to consider, as it can be measured experimentally [designs where the carrying capacity of each monoculture and each mixture are recorded are relatively tractable in a range of systems including bacteria (Gravel *et al.* 2011), plants (Schmid *et al.* 2008), insects and parasites (Tylianakis *et al.* 2007), plankton (Fox 2004), and animals (Duffy 2002)]. The left panel of Fig. 1 represents extreme situations with specialist and generalist food webs. An analytical solution of TO is tedious for more realistic communities and therefore we simulate a tri-trophic system to separate the effect of ρ_P and ρ_R on transgressive overyielding. The results of this analysis are presented in the right panel of Fig. 1. We find a clear positive effect of increasing trophic complementarity on the occurrence of TO. Predation complementarity is, in addition to resource-use complementarity, a determinant of TO. Trophic complementarity, being the integration of these two factors, has thus the potential to be a synthetic mechanism to explain the BEF relationship in food webs. It is worth noting that only in a narrow range of the parameter space coexistence occurred without resulting in TO.

Trophic complementarity predicts functioning in more complex systems

In the previous section, we derived a mathematical argument from niche theory to reveal how complementarity acts on functioning in a simple system, but two reasons make scaling up to more complex systems necessary. First, it is difficult to extrapolate these results to more diverse communities, for which there can be complex interactions both between and within trophic levels; second, it does not predict consumer productivity, which due to its ease of measurement, is one of the most frequently assessed outcomes of empirical BEF studies. To address these questions, we conduct numerical simulations of this system with 20 resources, 2 focal species of consumers and 20 predators, using a range of parameters for which coexistence occurs for all values of niche overlap considered. Keeping two consumers allows us to remain within the range of situations for which ρ, the index of complementarity derived by Chesson & Kuang (2008), can be used, while still examining the effect of increased complexity by increasing richness of the adjacent trophic levels. Resources and predators are evenly spaced along a continuous niche axis, according to the following procedure. The same logic pertains to resources and predators, so we illustrate only the former. Each resource l is given a position on the niche axis, ranging from $z_1 = 0$ to $z_{20} = 2$. The niche optimum of consumer species N_2 on the axis is fixed, with a trait value of $n_2 = 1.4$. The trait value of consumer species N_1 is varied from $n_1 = 0.3$ to $n_1 = n_2$ (100 steps of even size are done on each axis, so figures represent a total of 10^4 simulations). The values were chosen so that we explore the $0 \leq \rho_C \leq 1$ range, and for any value of n_1, $\sum_l f(n_2, z_l) = \sum_l f(n_1, z_l)$, that is, the cumulative impact of predation on N_1 and N_2 are equal. This last precaution is necessary, as it ensures that all else being equal (i.e. in the absence of competitive effects), the fitnesses of the two focal consumer species are equal. The link strength of consumer j with resource l, that is, $\mathbf{C}_{jl} = f(n_j, z_l)$, is given by a Gaussian function

$$\mathbf{C}_{jl} = \exp\left[-\frac{(n_j - z_l)^2}{2 \times \xi^2}\right], \tag{13}$$

in which ξ is the niche breadth, fixed equal for all species and trophic levels so as to simplify the analysis.

In this numerical experiment, we record two values: productivity, as defined in eqn 4, and the intensity of TO. Loreau (2004) defined the criteria for TO as $N_1^* + N_2^* > \max(K_1, K_2)$, with K being the

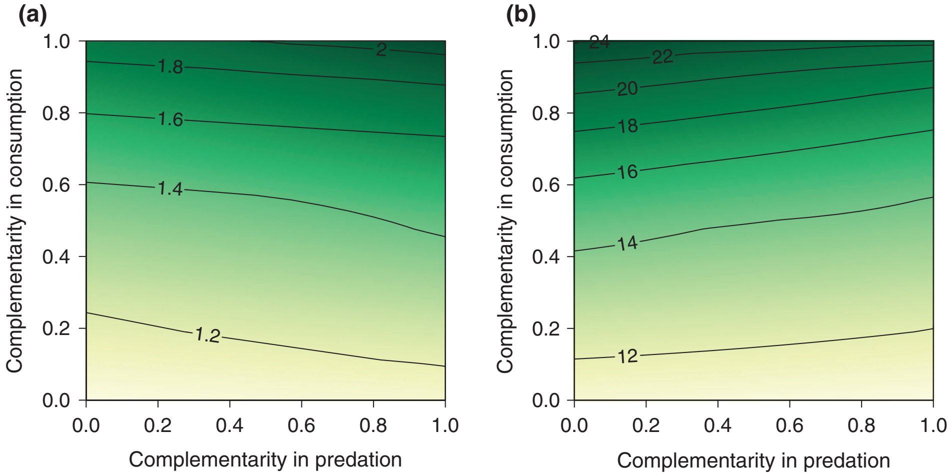

Figure 2 Consequences of varying complementarity (as measured by ρ_R and ρ_P) on transgressive overyielding (left) and productivity (right). Increasing the complementarity of both consumption and predation led to an increase in both TO and consumer productivity. However, while high complementarity in predation increases the intensity of TO, it decreases the productivity at equilibrium (for a fixed level of consumption complementarity). The lines (and colours) represent isoclines of productivity.

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carrying capacity in the presence of predators. If TO occurs when this situation is satisfied, then it straightforwardly comes that the intensity Φ of TO can be quantified by

$$\Phi = \sum_j N_j^* / \max(K_j). \tag{14}$$

The numerator of eqn 14 is the total biomass or carrying capacity in mixture, and the denominator is the highest carrying capacity over the range of monocultures. The difference between this and the previous result is that we are focusing on how strong TO is when it occurs: transgressive overyielding occurs when values of Φ are above unity, and values largely above unity reflect strong TO. We choose simulation conditions that ensure that $\max(K_j)$ is fixed by keeping the sum of the values of $\mathbf{A}$ and $\mathbf{C}$ (i.e. the interaction matrices) constant and equal. This ensures that the total biomass of consumers is linearly related to the strength of TO (and hence, is not shown).

As shown in the left panel of Fig. 2, we find that increasing complementarity either in predation or consumption resulted in stronger TO. While increasing complementarity in consumption increases ecosystem productivity at equilibrium, all else being equal, increasing complementarity in predation decreases it. This is indicative of a strong top-down control of productivity. Productivity and strength of TO reflect two really different though complementary views of ecosystem functioning: TO reflects the ability of an ecosystem to produce more biomass than what could be inferred based on the carrying capacity of the best monoculture, while productivity gives insights about the intensity of energy flows into consumers at ecological equilibrium. In other words, TO strength is a relative measure of the biomass production, while productivity reflects the turnover of this biomass. In a system of intermediate complexity (several producers and predators, two consumers at the focal trophic level), we thus find that trophic complementarity is a good predictor of ecosystem functioning.

Influence of complex network structure on ecosystem functioning

In this section, we test the predictions made in the previous parts in a more complex system, with 12 species at each trophic level. We alleviate the assumption of fixed niche breadth made in the previous section, and keep the connectance (number of interactions relative to the number of species) of the upper and lower bipartite networks constant ($Co = 0.48$), but vary topologies (i.e. the way the interactions are distributed within the networks). This means that each network has an equal number of interactions, but species within networks do not. Supplementary section 1 presents results showing that the predictive power of complementarity is maximised for intermediate connectance values.

To analyse the effects of network structure on the productivity of the system, we keep the number of species at each trophic level (network size) and number of links in each bipartite network (connectance) constant. We simulate 5×10^4 random networks of size 12 by 12, with 69 interactions. To do so, a vector of 69 ones and 75 zeros was shuffled, then folded into a 12 by 12 bipartite adjacency matrix. Only unique networks for which all species had a degree (number of interactions) of at least 1 were retained. Out of these networks, we selected 100, which represents an evenly spaced continuum of functional diversities (here measured by nestedness, that is, the fact that specialist species exploit of subset of the niche of more generalist species). To do so, we generated a regularly spaced series of values of nestedness, ranging from the lower to the upper value found in the dataset, of size 100. For each of these values, the random network showing the closest value of nestedness was added to the final set. Each network was only added once. We simulated the system for all potential combinations of networks (10^4 combinations in total), and recorded the combinations $[\mathbf{A},\mathbf{C}]$ for which all species persisted at a stable density for 10^4 time steps after equilibrium was reached. Preliminary numerical experiments showed that for a network of size 12^2, the strength of each interaction needed to be scaled down to a value of λ inferior to unity in order for the system to be stable (i.e. at least one species of each level remained in all the simulations) – a value of $\lambda = 10^{-1}$ was used in the simulations presented here.

One hundred and nineteen different combinations of interaction matrices $\mathbf{A}$ and $\mathbf{C}$ were retained at the end of the screening process described in the previous paragraph. Consumer productivity was recorded once ecological equilibrium (i.e. the size of each population varied less than 10^{-2} over 1000 time steps) was reached. While it is theoretically possible to measure the intensity of TO, the relevance of doing so is arguable. Eqn 14 requires to know the carrying capacity of each monoculture. Experimentally, this would imply to put each single consumer in the presence of the full trophic network, which would be extremely difficult to accomplish for most but the simplest systems which we previously highlighted. In contrast, productivity is directly measurable in experimental and field settings, and reacts clearly to changes in complementarity.

Expanding our approach to networks with a realistic level of diversity requires a measure of complementarity specifically designed to accommodate these data as input (Fig. 3). This is where network approaches come into play. First, we computed an average measure of trophic overlap. For each of ρ, ρ_R and ρ_P, we measure the average overlap (resp. ρ^*, ρ_R^* and ρ_P^*), such that

$$\rho^* = \sum_{j=1}^{\mathcal{N}-1} \sum_{l=j}^{\mathcal{N}} \frac{\rho_{jl}}{(\mathcal{N}-1)(\mathcal{N}-2)}, \tag{15}$$

and similarly for ρ_R^* and ρ_P^*. This measure sums up the overlap between all consumers, in terms of joint sensitivity to predation and competition, competition alone, and predation alone. Because this measure is focused on the central trophic level (i.e. consumers), and requires a quantitative knowledge of numerous demographic parameters for all species in the food web, it can be difficult to apply it to more complex systems. For this reason, we also consider NODF (Almeida-Neto *et al.* 2008), a measure of nestedness in bipartite interactions that is negatively related to trophic complementarity (Fig. 3). High nestedness indicates that niches of the generalists overlap with niches of the most specialists species, and is as such negatively related to complementarity [nestedness is also tied to network stability (Okuyama & Holland 2008) and its temporal persistence (Olesen *et al.* 2008), making it an ecologically informative metric]. So as to facilitate the interpretation of this measure, we define trophic complementarity of a network as being $\mathcal{C} = (100 - NODF)/100$. Thus, values of $\mathcal{C}$ range from 0 (no complementarity) to 1 (maximal complementarity). Variance partitioning through comparison of the R^2 of ANOVAs reveals that complementarity of each network, but not the overlap measured by ρ and its components, predicts consumer productivity (Table 1). Systems in which complementarity in either the predation or resource consumption bipartite network, or both, is high, have a

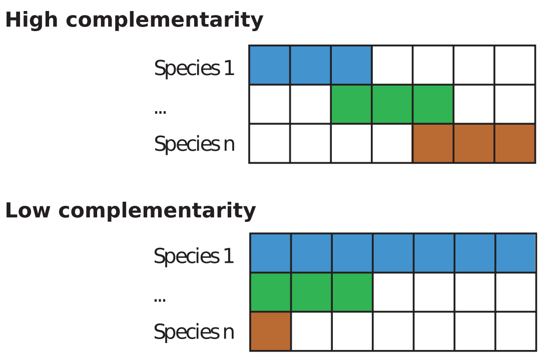

Figure 3 Trophic complementarity ($\mathcal{C}$) and its relationship to niche overlap and interaction matrices. In the upper diagram, $\mathcal{C}$ is high, as only a subset of the niche space is shared by two or more species (species are complementary). This corresponds to low nestedness. In the lower diagram, $\mathcal{C}$ is low, as the more specialist species (brown and green) niches are both a subset of the niche of the generalist (blue) species. In this later case, nestedness is high.

Table 1 Summary of ANOVA results. In the 'Parameter' column, × is the interaction between the two terms. Niche overlap as measured by ρ has no impact on productivity in complex systems. Trophic complementarity $\mathcal{C}$ measured through nestedness, however, has a strong and significant impact

Model	Parameter	*F* value	*P* value
1	$\mathcal{C}_A$	37.72	1×10^{-8}
$R^2 = 0.39$	$\mathcal{C}_C$	35.75	2×10^{-8}
d.f. = 113	$\mathcal{C}_A \times \mathcal{C}_C$	1.40	—
2	ρ_C	1.27	—
$R^2 = 0.05$	ρ_P	2.64	—
d.f. = 113	$\rho_C \times \rho_P$	3×10^{-4}	—

higher productivity at equilibrium than systems with a low complementarity (Fig. 4). Nestedness is known to be related to the degree distribution of species (Fortuna *et al.* 2010), as a nested network implies high variance in species degree. In supplementary section 2, we provide more information about the importance of degree distribution on our results. We show that increased nestedness increases linearly the variance of the degree distribution, meaning that for this particular analysis, the latter is not introducing any bias, and nestedness is an adequate measure of trophic complementarity. Similarly, adding the variance of the degree distribution in the linear model did not increased the predictive power compared to nestedness alone (data not shown).

Application: influence of species removal and extinction cascades on ecosystem functioning

In this section, we simulate species removal experiments to provide testable predictions. For each of the 119 networks used in the previous section, we remove at random 1–10 predators (the number being drawn randomly at each of the 100 trials done), or 1–10 consumers. We then simulate this less diverse system until a new equilibrium is reached. The complexity of this analysis stems from the fact that the removal of one species can trigger complex extinction cascades across all trophic levels (Solé & Montoya 2001), which can lead to the whole system collapsing. For this reason, our analysis was limited to networks with at least two species remaining in each trophic level (as expected, the number of systems which satisfied this criterion decreased with the increase in numbers of species removed). We measured the strength of extinction cascades as the proportion of remaining species ($\mathcal{R}'$, $\mathcal{N}'$, $\mathcal{P}'$) at each trophic level, with $\varepsilon' = 1 - \mathcal{R}'/\mathcal{R}$, $\varepsilon'' = 1 - \mathcal{N}'/\mathcal{N}$, and $\varepsilon''' = 1 - \mathcal{P}'/\mathcal{P}$. High values of ε indicates that most of the species went extinct. We expect that removing species will affect productivity and ecosystem functioning, possibly through its impact on structural properties of the networks. To quantify this impact, for each of the productivity and consumer biomass at equilibrium, connectance and nestedness of both networks, we measure the variation as

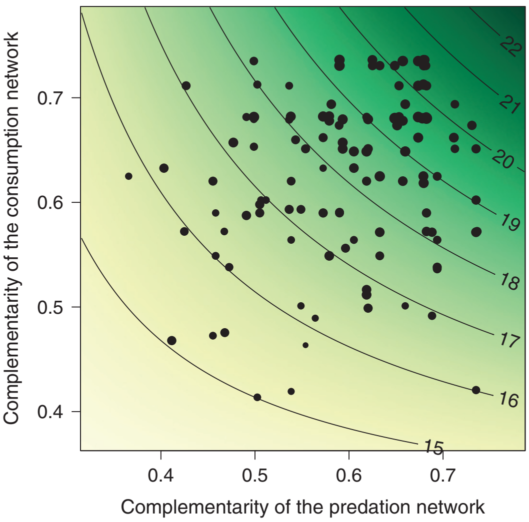

Figure 4 Trophic complementarity of the consumption (**C**) and predation (**A**) networks drive the productivity in the system. Each point of the graphic correspond to the simulation of one tri-trophic system as detailed in Table 1, and the width of the point increases with productivity. The background and contour line were predicted using the generalised linear model of Table 1 with a Gaussian response. The lines are isoclines of predicted productivity.

$$\Delta_X = \log_{10}(X'/X), \tag{16}$$

where X is the value of the metric before species removal, and X' is the value after it. A Δ_X value of 0 indicates that there were no changes following species extinctions, while $\Delta_X > 0$ means the metric increased following removal.

In our simulations, removing consumers yields complex effects (Table S1). Productivity is primarily impacted by changes in connectance, nestedness of resources, and declines with extinctions of consumers, but only after more than half of the original pool of consumers is removed (Fig. 5); this result is likely contingent upon the structure of each network. It suggests that trophic complementarity and the structure of links at the median trophic level are crucial to productivity. Changes in consumer biomass were explained by variation of connectance in the predation network, and nestedness in the consumption network (Table S1). This last result emphasises that consumer population size is regulated both by bottom-up (resource-use complementarity) and top-down (predation complementarity) effects. When removing predators, species and interaction loss are more important than changes of trophic complementarity (Table S1). Productivity quickly decreases with predator removal, but the equilibrium biomass of consumers increases (Fig. 5). This is congruent with a release from a strong top-down control

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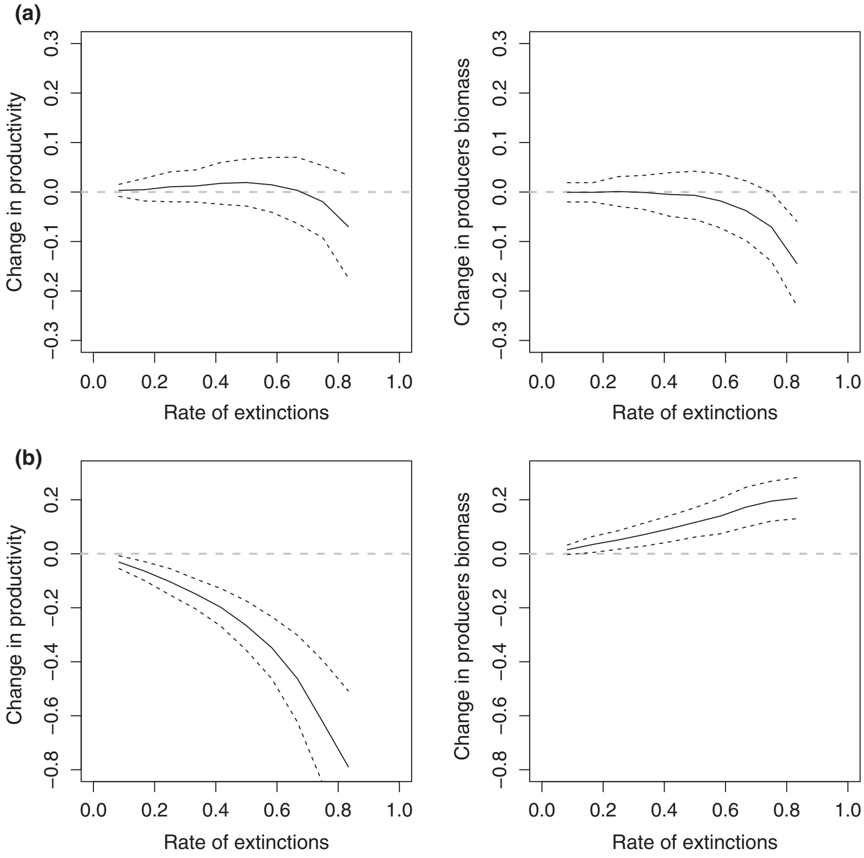

Figure 5 Impact or removing either consumers (top) or predators (bottom) on productivity (left) or consumers biomass (right). For each panel, the rate of extinctions it the one of the trophic levels for which organisms were removed (ε'' for consumers removal, and ε''' for predators removal). The mean (solid line) and one standard deviation (dashed lines) are represented.

of consumers by predators with their extinction. The potentially complex dynamics that are likely to arise when both bottom-up and top-down effect are acting (Narwani & Mazumder 2012) may explain the lower R^2 for the removal of consumers than for the removal of predators (Table S1).

DISCUSSION

Accounting for the structure of species interactions is a major step to scale up predictions of community ecology to complete ecosystems (Proulx *et al.* 2005). Here, we show that trophic complementarity, that is, the combined impact of exploitative and apparent competition, is a driver of ecosystem functioning in multi-trophic systems. Our results suggest that in addition to the number of species, the structure of their interactions needs to be accounted for so as to predict consumer productivity. Classical results in this field used transgressive overyielding as a measure of increased functioning. In the context of multi-trophic communities, this measure can be replaced by an index which is easier to assess outside of an experimental context, such as consumer productivity. We show a positive effect of increased trophic complementarity on transgressive over-yielding, and a positive effect of increasing resource-use complementarity on consumer productivity (Fig. 2). By simulating extinction cascades, we show that consumer productivity and equilibrium biomass are differently impacted. The strongest predictor of change in these values was connectance, that is, the number of links between predators and their prey, and prey and their resources. This suggests that in our model, trophic structure is extremely important in driving the function of complex ecosystems, and top-down control acts synergistically with trophic complementarity.

Previous theoretical analyses of BEF in food webs faced the challenge of finding general mechanisms and predictions. It was concluded that our ability to predict the effect of species richness on ecosystem functioning is highly contingent on the particular structure of the food web under study (Loreau 2010). This interpretation was derived from the observation of different BEF relationships for different limiting food web configurations. Thébault & Loreau (2003), for instance, found various BEF relationships with the contrasted situations of a stacking of specialised plant-herbivores (positive linear BEF), generalist herbivores (hump-shaped BEF) and assemblages with a competitivity-resistance trade-off (hump-shaped, but almost negative BEF). The general understanding they reached from these examples was that the trophic position of the species being lost plays a critical role, just as the connectance of the overall food web. Loreau (2010) concluded that the BEF relationship is predictable, provided that the food web structure is already known.

The mechanism of trophic complementarity we propose here encompasses all these extreme situations, just as the intermediates between them. Trophic complementarity is a general mechanism derived from niche theory that allows us to predict the contribution of a single species addition (which would correspond to the derivative of the BEF relationship with respect to species richness – Berlow *et al.* 2009). This mechanism tells us that we would shift from an additive effect of species addition when trophic complementarity is high (no niche overlap, linear increase with species richness), to a non-additive effect when trophic complementarity is low (a saturating or even hump-shaped relationship). This approach is flexible enough to account for different shapes of BEF relationships. It also predicts ecosystem properties from aggregate network metrics such as nestedness, based on the topological structure of interactions. Such metrics are more useful than connectance alone since they go beyond the community-average description of interactions (akin to metrics of functional complementarity, such as trait dispersion, that go beyond species richness). Indeed, recent experimental work by Striebel *et al.* (2012) highlighted that 'trophic overyielding' (the increase of predator productivity in response to increased consumer diversity) can only be fully understood if different prey use by the predator, resource use by the prey, and their multiplicative effects, are accounted for. Our definition of trophic complementarity allows doing this, and will help further increase the predictive power in empirical studies. The generality of the mechanism also facilitates cross-ecosystem comparisons, and the approach could provide predictions for experiments where species richness is varied either simultaneously at both the plant and the herbivore levels, or independently.

We used the reciprocal of NODF as a measure of complementarity, because it is widely used in the context of networks analysis, but this is by no means the only possible measure of complementarity. For example there are variations of NODF which might be better suited to mutualistic systems (Bastolla *et al.* 2009). When quantitative data about interaction strength are available, or in complex food webs, standard overlap indices such as Horn-Morisita (Horn 1966) can alternatively be used. Devictor *et al.* (2010) similarly proposed that responsiveness and inconsistency (Bell 1990), two measures of functional diversity and complementarity, can be used in this context. One important avenue for future research is nonetheless to refine our understanding of different trophic complementarity measures, to assess their generality, and usability in cross-system comparison. NODF is still for the time being an interesting measure, as it requires only coarse knowledge of the system, namely the presence or absence of interactions. It becomes possible to forecast the impact of the arrival of a new species on ecosystem functioning, which can prove especially useful to assess the consequences of biological invasions on ecosystem services (Dobson *et al.* 2006; Macfadyen *et al.* 2009; Pejchar & Mooney 2009). Due to the low complexity of information needed to measure NODF, there is a tremendous opportunity in the form of a reanalysis of previous diversity-functioning experimental results in the light of trophic complementarity.

In keeping with this idea of expanding our results to more complex systems, special attention should be given to the diversity of biotic interactions. One common interaction missing from our model is omnivory, which is known to have important effects on interaction rates (Montoya *et al.* 2003). Using measures of complementarity incorporating this effect, which can, for example be based on species roles in different network motifs, will help refine our understanding of the importance of trophic complementarity on ecosystem functioning. Kéfi *et al.* (2012) emphasised the importance of non-trophic interactions, as non-feeding relationships can dramatically alter the equilibrium state and dynamics of complex ecosystems (Cardinale *et al.* 2002). To some extent, the non-trophic interactions can become more important than the trophic ones, through, for example protective symbioses (Jaenike & Brekke 2011; Kwiatkowski & Vorburger 2012) preventing interactions from occurring. Previous research demonstrated an impact of mutualistic symbiosis complementarity on productivity (Maestre *et al.* 2012), and integrating different types of interactions will refine our ability to predict and understand the functioning of empirical ecosystems. For example the functioning of grasslands and forest ecosystems is driven by complementarity between both pathogenic and mutualistic fungi (Schnitzer *et al.* 2011). In keeping with the integration of other type of interactions, we foresee the possibility of investigating the importance of trophic complementarity on ecosystem multi-functionality and other aspects of functioning, including for example nutrient cycling or decomposition, in addition to the production of biomass. Finally, we emphasise that our model, despite its simplicity, is testable experimentally. The simple dynamics we assumed fit particularly well the behaviour of emblematic experimental systems that can be raised in mesocosms, such as plankton (Striebel *et al.* 2012), or bacteria–phages (Weitz & Dushoff 2008). The latter were showed to display a strong gradient of nestedness (Weitz *et al.* 2013), making them ideally suited to test our predictions.

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AUTHORSHIP

Conceived the research TP, NM, DG; Implemented the model TP; Analytical results TP, DG; Numerical experiments TP; Analysed the results TP, DG; Wrote the manuscript all authors.

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