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Cascading extinctions, functional complementarity, and selection in two-trophic-level model communities: A trait-based mechanistic approach

Jurgis Sapijanskas [a,b,*], Michel Loreau [a]

[a] Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montreal, QC, Canada H3A 1B1
[b] AgroParisTech ENGREF, 19 avenue du Maine, 75015 Paris, France

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ABSTRACT

The influence of diversity on ecosystem functioning and ecosystem services is now well established. Yet predictive mechanistic models that link species traits and community-level processes remain scarce, particularly for multitrophic systems. Here we revisit MacArthur's classical consumer resource model and develop a trait-based approach to predict the effects of consumer diversity on cascading extinctions and aggregated ecosystem processes in a two-trophic-level system. We show that functionally redundant efficient consumers generate top-down cascading extinctions. This counterintuitive result reveals the limits of the functional redundancy concept to predict the consequences of species deletion. Our model also predicts that the biodiversity–ecosystem functioning relationship is different for different ecosystem processes and depends on the range of variation of consumer traits in the regional species pool, which determines the sign of selection effects. Lastly, competition among resources and consumer generalism both weaken complementarity effects, which suggests that selection effects may prevail at higher trophic levels. Our work emphasizes the potential of trait-based approaches for transforming biodiversity and ecosystem functioning research into a more predictive science.

1. Introduction

In the face of potential consequences of current biodiversity loss for the provisioning of ecosystem services, the relationship between biodiversity and ecosystem functioning (BEF hereafter) has emerged as one of the major scientific issues of our time (Loreau, 2010). Hundreds of experimental and theoretical studies have revealed that biological diversity influence numerous ecosystem processes (Balvanera et al., 2006; Cardinale et al., 2007). Despite initial disagreement over the interpretation of these results (Huston, 1997; Srivastava and Vellend, 2005), consensus emerged around two classes of complementary mechanisms: selection and complementarity (Loreau et al., 2001; Hooper et al., 2005). Complementarity encompasses both niche differentiation and facilitative interactions among species, as it is often difficult to distinguish which mechanism prevails in practice. Niche complementarity occurs when species differ in their resource requirements, which alleviates interspecific competition and leads to more complete resource use (Loreau, 1998). Facilitation is the result of species modifying the environment in a way that benefits co-occurring species (Vandermeer, 1989). Selection is a deterministic process that promotes dominance by species with particular traits. When competitive dominance is associated with high biomass productivity, selection effects contribute to the commonly observed positive effect of plant diversity on primary production (Cardinale et al., 2007).

Complementarity occurs when trait variation enables a permanent association of species that enhances overall performance. Trait variation also contributes to selection effects, by providing the range of possibilities necessary for the selective process to promote the most adapted species. Therefore, the main role of biodiversity in ecosystem functioning is to provide phenotypic trait variation. This conceptual clarification sparked recent interest in trait-based approaches, especially within the BEF literature (Naeem and Wright, 2003; Reiss et al., 2009). Trait-based approaches were originally developed for terrestrial plants (Lavorel and Garnier, 2002; Westoby and Wright, 2006), and are gaining increasing popularity in community ecology (McGill et al., 2006; Litchman and Klausmeier, 2008). They are thought to provide a framework to develop and test theories that integrate across life's domains, from micro- to macro-organisms (Green et al., 2008), while contributing to the coveted synthesis between community and ecosystem ecology (McGill et al., 2006).

Such optimism is motivated by the many advantages offered by trait-based approaches. In particular, they provide a mechanistic framework to address species redundancy (Reiss et al., 2009),

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* Corresponding author at: Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montreal, QC, Canada H3A 1B1.
Tel.: +1 514 398 6697; fax: +1 514 398 5069.
E-mail addresses: jurgis.sapijanskas@polytechnique.org (J. Sapijanskas), michel.loreau@mcgill.ca (M. Loreau).

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and they have the potential to link ecosystem functioning and environmental change (Norberg et al., 2001; Suding et al., 2008), link ecosystem functioning and evolutionary theory (Loeuille and Loreau, 2005; Litchman and Klausmeier, 2008), and incorporate intraspecific variation (Reiss et al., 2009). They can also reveal mechanistic trade-offs, suites of covarying traits or ecological strategies, which in turn allow multiple dimensions of diversity to be captured by a small number of easily measured variables at the organismal level (Lavorel and Garnier, 2002). Above all, the trait-based perspective seems to be a promising way to scale up from species or individual traits to ecosystem processes (Suding et al., 2008). The recent advances in quantitative trait-based approaches have led to the optimistic claim that they would help transform community ecology into a theoretically sound, predictive science (Webb et al., 2010). Yet, trait-based theoretical models remain scarce (Norberg et al., 2001; Pachepsky et al., 2001; Savage et al., 2007; Tanaka and Yoshino, 2009) and tend to focus on community responses to a changing environment, whereas BEF research is primarily concerned with the effects, rather than the responses, of diversity. Moreover, trait-based conceptual frameworks do not deal with ecological interactions in a satisfying way (Naeem and Wright, 2003; Suding et al., 2008), and models have yet to incorporate trophic complexity.

Positive effects of biodiversity on biomass within a trophic group have been reported frequently. Nevertheless, there is still debate on whether negative selection effects are frequent, especially for non-biomass functions (Jiang et al., 2008). Trait-based mechanistic models have proved useful in disentangling selection and complementarity effects and identifying key plant traits controlling the direction of selection effects (Loreau, 1998), but they have been restricted so far to systems with a single trophic level. The impact of biodiversity loss in systems with strong top-down control, such as many marine, freshwater and some terrestrial ecosystems, may depend more on the fate of consumers than that of primary producers (Duffy, 2002). An increasing number of theoretical studies have therefore examined BEF relationships in a multitrophic context (e.g., Thébault and Loreau, 2003, 2005; Ives et al., 2005). However, they have focused exclusively on biomass stocks and have not established a mechanistic link between species traits and ecosystem processes.

Cascading extinctions have also attracted attention recently due to their potential consequences for ecosystem functioning (Borrvall et al., 2000; Thébault et al., 2007; Srivastava and Bell, 2009). The extinction of one species can lead to secondary extinctions and cause large sudden changes in functional diversity (e.g., Paine, 1966). Although BEF relationships and coexistence mechanisms are intimately intertwined (Mouquet et al., 2002), trait-based coexistence has not been explicitly related to cascading extinctions.

Here we combine a multitrophic perspective and a trait-based approach to address multiple ecosystem processes while faithfully capturing ecological interactions and multiple dimensions of differentiation (Reiss et al., 2009). Revisiting MacArthur's classical consumer-resource model (MacArthur and Levins, 1967; MacArthur, 1972), we study the effects of consumer diversity on the stocks (resource biomass, consumer community size) and fluxes (total resource consumption by consumers) of ecosystems with two trophic levels. To cope with the unavoidable trade-off between realism and tractability, we examine four variants of MacArthur's model. These variants allow us to gradually derive analytical results linking species traits and ecosystem processes for a class of idealized communities. This reveals how the extinction of apparently redundant consumers can subsequently drive some resources to extinction, thus generating what we define as top-down extinction cascades. We then add interspecific variability along six trait axes in order to disentangle selection and complementarity effects with numerical simulations, using analytical results as mean trait approximations. Finally, we show how competition among resources can be incorporated into MacArthur's model, and we analyze the extent to which a third implicit trophic level affects our previous findings.

2. Models

2.1. Basic model with non-interacting resources

MacArthur's model has four main assumptions: (1) consumers have a linear functional response, which leads to exponential population growth with surplus energy (effective intake minus maintenance); (2) resources can be described by a linear axis z (e.g., foraging height, food particle size, or any stoichiometric gradient) of logistically growing independent types; (3) utilization curves $p_i(z)$ define consumer niches by describing the rates at which an individual of species i feeds on resources $R(z)$ of type z; (4) resource dynamics occurs at a significantly smaller time scale than that of consumers. The dynamics of the consumer-resource system are written as

$$\frac{dR(z)}{dt} = \rho(z)R(z)\left(1-\frac{R(z)}{\kappa_R(z)}\right)-\sum_{i=1}^{S} p_i(z)N_iR(z) \tag{1a}$$

$$\frac{dN_i}{dt} = N_ie_i\left(\int_{-\infty}^{+\infty} \varepsilon_i p_i(z)R(z)\,dz - d_i\right) \tag{1b}$$

where all symbols are defined in Table 1.

The full system can be reduced to S Lotka–Volterra-like equations for the consumers because of the hypothesis of time scale separation (Appendix A). However, the reduced model is valid only if no resource extinction occurs (Hsu and Hubbell, 1979). We assume that all resources coexist in our analytical work, but relax this assumption in our simulations, where we check for resource extinctions at each time step of the numerical integration and set $\kappa_R(z)$ to 0 whenever $R(z) \le 0$. If there is an internal equilibrium, it is a global attractor (Gatto, 1990). Therefore the outcome is not sensitive to initial conditions provided there is no extinction at $t = 0$.

We use the classical assumption that consumers have Gaussian utilization curves (e.g., May, 1974; Loeuille and

Table 1
Symbols used in the models.

Symbol	Description	Units
z	Resource gradient axis	
$R(z)$	Biomass of resource type z	[g]
$\rho(z)$	Maximum growth rate of resource type z	[s^{-1}]
$\kappa_R(z)$	Carrying capacity of resource type z	[g]
N_i	Population size of consumer species i	
$p_i(z)$	Utilization curve	[s^{-1}]
ε_i	Conversion efficiency from resource to energy	[$J\,g^{-1}$]
d_i	Energetic maintenance requirements	[$J\,s^{-1}$]
e_i	Conversion efficiency from surplus energy to offspring	[J^{-1}]
z_i	Niche center	
A_i	Total attack rate	[s^{-1}]
σ_{c_i}	Niche width	
Δ	Niche distance between two consecutive niche centers	
Θ_3	Theta Jacobi 3 function $\Theta_3(x) = \sum_{k=-\infty}^{+\infty} x^{k^2}$	
$n(z)$	Consumer community total density at point z	
$P_T(z)$	Consumer community total attack rate	[s^{-1}]
$C(z)$	Consumer community total consumption rate	[s^{-1}]
σ_α	Breadth of the competition kernel of the resources	
σ_R	Breadth of the resource gradient when Gaussian	

Subscript i refers to consumer species i.

Loreau, 2005; Scheffer and van Nes, 2006):

$$p_i(z) = \frac{A_i}{\sqrt{2\pi}\sigma_{c_i}} \exp\left(-\frac{(z-z_i)^2}{2\sigma_{c_i}^2}\right)$$

Six traits are considered in this study: each consumer species i is described by its total attack rate $A_i = \int p_i(z)\,dz$, niche center z_i, niche breadth σ_{c_i}, energetic maintenance requirements d_i, conversion coefficient from resource to energy ε_i, and conversion coefficient from surplus energy to offspring e_i. We study several variants of this basic model, which we name after their main assumptions: uniform (Ug) or non-uniform (NUg) resource gradient, absence or presence (Cr) of competition among resources, and number of traits that characterize consumers (1 or 6, i.e., either consumers differ only along the resource partitioning axis z or they differ in all six traits).

2.2. Ug1: uniform resource gradient, one trait varies

The Ug1 model assumes that an infinite number of equivalent consumer species feed on an infinite and uniform resource gradient. More precisely, for all z: $\rho(z) \equiv \rho$ and $\kappa_R(z) \equiv \kappa_R$. Consumers share the same trait values except for their niche centers, which are evenly spaced and separated by a distance Δ. These are common assumptions in the theoretical literature (e.g., May, 1974; Tanaka and Yoshino, 2009). Niche distance Δ is inversely related to consumer diversity: it is infinite when Δ is zero and zero when Δ is infinite. Because niches are evenly spread along the entire resource gradient, the consumer community exhibits the highest possible levels of niche complementarity for a given diversity. By varying Δ, complementary consumer communities of various levels of diversity can thus be compared. No competitive exclusion and hence no ecological selection occur since consumers have equivalent competitive abilities. Thus, the Ug1 model is designed to study pure complementarity effects (no selection effect) on BEF relationships by using niche distance Δ as a continuous measure of diversity.

2.3. NUg1: non-uniform resource gradient, one trait varies

To investigate more general BEF relationships driven by complementarity, consumers still differ in their niche center only but we implicitly allow resources to have different traits by relaxing the assumptions of infinity and uniformity of the resource gradient. For this class of communities, we derive a *local approximation* for all aggregate processes at equilibrium, based on the Ug1 model. This approximation assumes that the equilibrium population size of each species is most influenced by the resources within its niche and the competitive effects of its neighbors, and is hence primarily determined *locally*. More precisely, if the resource gradient is smooth enough, i.e., if $\rho(z)$ and $\kappa_R(z)$ do not vary drastically over a few niches widths σ_c, equilibrium community properties at any point z_0 of the gradient should be close to what they would have been if the gradient were infinite and uniform (Ug1 model) with the corresponding local values $\rho(z) \equiv \rho(z_0)$ and $\kappa_R(z) \equiv \kappa_R(z_0)$.

2.4. NUg6: non-uniform resource gradient, six traits vary

In this model, coexisting species are allowed to persist after species sorting. Communities are thus selected subsets of a larger and more diverse regional species pool. The six traits, which all except e_i affect competitive ability, differ among species; they have a normal distribution at the regional scale. We run simulations for randomly sampled species from the regional pool and compare their outcome to that of the NUg1 model. Using the *local approximation* of NUg1 as a null model of pure complementarity, selection effects due to differing competitive abilities can then be distinguished from the complementarity effects caused by resource partitioning. Poor competitors are excluded by species sorting so that, at the community level, mean trait values shift towards higher competitive abilities. Using the analytical expressions obtained from the Ug1 model, we study the impact of an infinitesimal shift of trait values towards stronger competitors on ecosystem processes. This allows predicting the direction of selection effects in the NUg6 model and unveiling their underlying ecological mechanisms.

2.5. NUgCr1 and NUgCr6: competing resources

A key limitation of MacArthur's model is the absence of interaction among resources, which should ideally be included to obtain realistic conclusions for multitrophic systems. We investigate the effects of introducing a Gaussian competition kernel among resources, which can be interpreted as the result of consumptive interspecific competition. Resource dynamics then obeys the equation

$$\frac{dR(z)}{dt} = \rho(z)R(z)\left(1 - \frac{\int \alpha(z,y)R(y)dy}{\kappa_R(z)} - \sum_{i=1}^{S} N_i \frac{p_i(z)}{\rho(z)}\right) \quad (2)$$

where $\alpha(z_1,z_2) = \exp(-(z_1-z_2)^2/2\sigma_\alpha^2)$ is the Gaussian competition kernel corresponding to resources feeding on an implicit lower trophic level with a niche breadth of $\sigma_\alpha/\sqrt{2}$. Assuming once again time scale separation and the absence of basal resource extinction, Lotka–Volterra-like equations for the dynamics of the full system can be derived using Fourier transforms (Appendix D).

Competition within a continuous spectrum strongly restricts the parameter space allowing global coexistence. Roughgarden (1979) showed that a Gaussian carrying capacity κ_R enabled the coexistence of a continuum, but Gyllenberg and Meszéna (2005), Szabó and Meszéna (2006) and Barabas and Meszéna (2009) recently rejected this example as being non-robust. It is indeed always possible to find an arbitrarily small perturbation of κ_R that leads to the competitive exclusion of parts of the spectrum. But this perturbation must be of a very specific form: it has to be constant and very localized or, more generally, of a high frequency relatively to the gradient axis z. The smaller the perturbation's magnitude, the higher its frequency must be to prevent global coexistence. Such constant, small-scale perturbations along a resource gradient may not be particularly realistic. Therefore, while keeping these restrictions in mind, we consider Gaussian resource gradients as a case worth studying and consequently assume $\kappa_R(z) = \kappa_{R_0}\exp(-(z^2/2\sigma R^2))$ and $\rho(z) = \rho_0\exp(-(z^2/2\sigma R^2))$ in the following NU$_g$Cr1 and NU$_g$Cr6 models. Apart from the added interactions between resources, these models share the same assumptions as the NUg1 and NUg6 models, respectively.

2.6. NUgCr1: non-uniform resource gradient, competing resources, one trait varies

As with the NUg1 model, a *local approximation* is derived with competing resources when consumer species share the same traits except for their evenly spaced niche centers.

2.7. NUgCr6: non-uniform resource gradient, competing resources, six traits vary

As with models with non-interacting resources, we use the pure complementarity case NUgCr1 as a null model to detect the selection effects captured by the NUgCr6 model in which consumers are sampled from a diverse regional pool.

3. Results

We first present analytical results derived for the Ug1, NUg1 and NUg1Cr models, which form the basis for subsequent simulation studies (NUg6, NUg6Cr). We then show how these combined models provide mechanistic insights into BEF relationships, in particular the causes of cascading extinctions, and complementarity and selection effects.

3.1. Analytical results

*Ug*1: Given the symmetry of this model, all consumers reach the same population size $N_i = N^*$ at equilibrium. As we are interested in ecosystem processes and total consumer community size is meaningless in an infinite system, we study instead consumer density per length unit of the resource gradient at point z, $n(z)$. The density is here uniform $n = N^*/\Delta$. Solving Eqs. (1) at equilibrium yields (Appendix B)

$$n = n_{max}/\Theta_3\left[\exp\left(-\frac{4\pi^2\sigma_c^2}{\Delta^2}\right)\right] \tag{3a}$$

$$n_{max} = \frac{\rho}{A}\left(1-\frac{d}{\varepsilon A\kappa_R}\right) \tag{3b}$$

where $\Theta_3(x) = \sum_{k=-\infty}^{+\infty} x^{k^2}$ denotes Jacobi Theta 3 function and n_{max} is the maximum possible consumer density given resource gradient parameters and consumer traits related to energy needs and acquisition. The ratio of energetic requirements to maximum potential effective intake $d/\varepsilon A\kappa_R$, hereafter called *requirement ratio*, is an important community-level property. The requirement ratio is always positive and, because intake must exceed requirements to prevent extinction, $d/\varepsilon A\kappa_R < 1$ is a necessary condition for consumer persistence (Eq. (3b)).

All aggregate ecosystem properties are analytic and Δ−periodic, therefore the total consumer community attack rate $P_T = \sum N_i p_i$ can be decomposed into Fourier series. Resource equilibrium levels R and total consumption rate C are then calculated at each point z from Eqs. (1) and (3) (Appendix B):

$$P_T(z) = nA\left(1+2\sum_{k=1}^{\infty} e^{-2\sigma_c^2\pi^2k^2/\Delta^2}\cos\left(\frac{2\pi kz}{\Delta}\right)\right) \tag{4a}$$

$$R(z) = \kappa_R\left(1-\frac{P_T(z)}{\rho}\right) \tag{4b}$$

$$C(z) = P_T(z)R(z) \tag{4c}$$

As we are interested in aggregate ecosystem properties rather than in variations within a period, we also derive mean consumer population size $\langle N\rangle$, mean resource biomass $\langle R\rangle$ and mean consumption rate $\langle C\rangle$ over a period at equilibrium (Appendix B):

$$\langle N\rangle = n \tag{5a}$$

$$\langle R\rangle = \kappa_R\left(1-\frac{An}{\rho}\right) \tag{5b}$$

$$\langle C\rangle = \frac{d}{\varepsilon}n \tag{5c}$$

It is noteworthy that the conversion coefficient from surplus energy to offspring e has no effect at equilibrium and only contributes to increase the consumers' maximum growth rates (Appendix A).

*NUg*1: Our *local approximation* assumes that the non-uniform gradient case is well approximated at each point z by Eqs. (3) and (4) (Ug1 model) after substitution of the constants ρ and κ_R for their local value $\rho(z)$ and $\kappa_R(z)$. It follows that, at any point z:

$$n(z) = \max\left(\frac{\rho(z)}{A}\frac{1-\dfrac{d}{\varepsilon A\kappa_R(z)}}{\Theta_3\left[\exp\left(-\dfrac{4\pi^2\sigma_c^2}{\Delta^2}\right)\right]},0\right) \tag{6a}$$

$$P_T(z) = n(z)A\left(1+2\sum_{k=1}^{\infty} e^{-2\sigma_c^2\pi^2k^2/\Delta^2}\cos\frac{2\pi kz}{\Delta}\right) \tag{6b}$$

$$R(z) = \max\left(\kappa_R(z)\left(1-\frac{P_T(z)}{\rho(z)}\right),0\right) \tag{6c}$$

$$C(z) = P_T(z)R(z) \tag{6d}$$

The corresponding aggregated stocks and fluxes are easily obtained by integrating these expressions over the entire resource gradient.

NUgCr 1: When resources interact with a Gaussian competition kernel, the local approximation becomes, at any point z (see Appendix D):

$$n(z) = \max\left[0,\frac{\rho_0}{A}\left[\sigma_R\frac{e^{-z^2/2(\sigma_c^2+\sigma_R^2-\sigma_\alpha^2)}}{\sqrt{\sigma_c^2+\sigma_R^2-\sigma_\alpha^2}}-\frac{d\sqrt{2\pi}\sigma_\alpha}{\varepsilon A\kappa_{R_0}}\right]\Big/\Theta_3\left[e^{-\frac{(4\sigma_c^2-2\sigma_\alpha^2)\pi^2}{\Delta^2}}\right]\right] \tag{7a}$$

$$P_T(z) = n(z)A\left(1+2\sum_{k=1}^{\infty} e^{-2\sigma_c^2\pi^2k^2/\Delta^2}\cos\frac{2\pi kz}{\Delta}\right) \tag{7b}$$

$$R(z) = \max\left[0,\frac{\kappa_{R_0}\sigma_R}{\sqrt{2\pi}\sigma_\alpha}\left[\frac{e^{-z^2/2(\sigma_R^2-\sigma_\alpha^2)}}{\sqrt{\sigma_R^2-\sigma_\alpha^2}}-\frac{n(z)A}{\rho_0\sigma_R}\left(1+2\sum_{k=1}^{\infty} e^{-2(\sigma_c^2-\sigma_\alpha^2)\pi^2k^2/\Delta^2}\cos\frac{2\pi kz}{\Delta}\right)\right]\right] \tag{7c}$$

$$C(z) = P_T(z)R(z) \tag{7d}$$

A necessary, but not sufficient, condition for global coexistence is $\sigma_c > \sigma_\alpha$, that is, niche breadth has to increase by a factor of at least $\sqrt{2}$ with trophic position (Appendix D). When $\sigma_c < \sigma_\alpha$, resources that are far enough from consumers' niche center gain a sufficient competitive advantage to exclude the more heavily preyed upon resources located at niche centers.

3.2. Cascading extinctions

*Ug*1: Our analytical results hold only if there is no resource extinction. A condition on consumers' requirement ratio and niche overlap can be derived for the global persistence of resources (Appendix B, Fig. 2a):

$$\forall z, R(z) > 0 \Leftrightarrow \frac{d}{\varepsilon A\kappa_R} > 1-\frac{\Theta_3\left[\exp\left(-\dfrac{\Delta^2}{4\sigma_c^2}\right)\right]}{\sqrt{2}\Theta_3\left[\exp\left(-\dfrac{\Delta^2}{2\sigma_c^2}\right)\right]} \tag{8}$$

We recover the classical result that resources are more likely to go extinct as their carrying capacity increases, which might explain observed decreases in diversity at high levels of

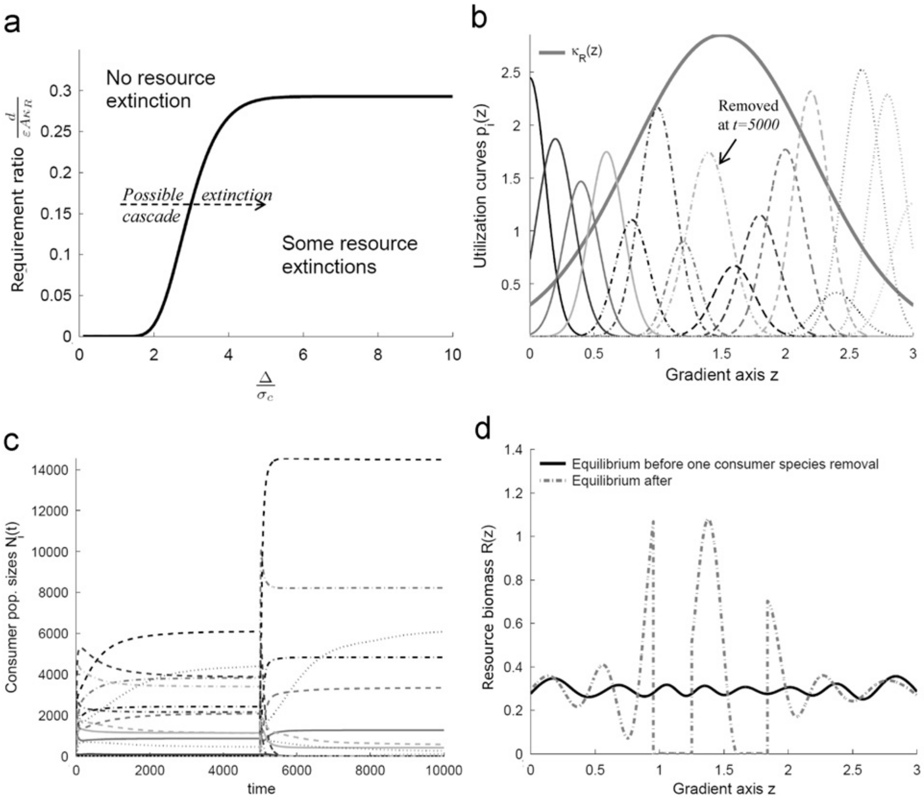

Fig. 1. Conditions for resource coexistence and consequent potential top-down extinction cascades. (a) Condition on the requirement ratio required for global persistence of all resources in the Ug1 model plotted against niche separation (niche distance scaled by niche width) Δ/σ_c (Eq. (8)). If $d/\varepsilon A\kappa_R$ falls above the curve there is no resource extinction, otherwise some resources are excluded. (b) utilization curves, (c) consumer dynamics and (d) resource equilibria for an extinction scenario of a single consumer species. (b) shows the utilization curves and the Gaussian resource gradient used, $\rho(z) = 10^4 e^{-(z-1.5)^2}$ and $\kappa_R(z) = 2.85e^{-(z-1.5)^2}$ restricted to [0, 3]. Niches centers z_i are evenly distributed along the resource gradient with a separation of $\Delta = 0.2$. Niche widths σ_{c_i} were drawn at random from a normal distribution with a mean of 0.15 and a 10% CV. A_i, e_i and ε_i were drawn at random in [0.1 , 1] assuming a uniform distribution and d_i was chosen both to allow coexistence and to achieve low requirement ratio values, i.e., $d_i = 0.29\varepsilon_i A_i$. (c) shows the temporal dynamics of the population sizes of consumers. Initial conditions are chosen so that there is no resource extinctions at $t=0$. One consumer species (with niche center at $z=1.4$) is removed at $t=5000$ by setting its population size to zero. (d) Equilibrium resource biomasses before and after the removal of one consumer species.

productivity (Abrams, 1995). Note that a higher carrying capacity here affects the *feasibility*, not the *stability* of the equilibrium, so this phenomenon is distinct from the paradox of enrichment (Rosenzweig, 1971). In addition, tightly packed communities of consumers (small Δ/σ_c) cannot overexploit resources, no matter how efficient or voracious they are (Fig. 1a).

Eq. (8) indeed proves that the most heavily consumed and extinction-prone resources are located at niche centers. With increased niche packing, more consumer species contribute to the aggregated attack rate, but their respective population sizes are reduced by stronger interspecific competition. At niche centers z_i, the shape of the Gaussian utilization curves gives a considerably larger weight to the corresponding consumer species i so that the effect of decreased population size prevails and the overall impact on $R(z_i)$ declines with niche overlap. The removal of consumer species in a tightly packed community with low requirement ratios can lead to top-down extinction cascades, i.e., to secondary extinctions of some resources, by increasing Δ, at least locally (Fig. 1a).

*NUg*6: Contradicting the intuitive prediction that tightly packed consumers are redundant and that their extinction should have no effect, simulations (Fig. 1b–d) confirm that top-down extinction cascades can occur even when consumer species differ slightly in all trait values. In the example shown in Fig. 1, by strongly reducing interspecific competition, the removal of one consumer species ($i = 8$, Fig. 1b) allows its direct neighbors ($i-1$ and $i+1$) to reach high enough populations sizes (Fig. 1c) to overexploit resources within their niches (Fig. 1d).

NUgCr 1 *and NUgCr*6: Top-down cascades of secondary extinctions are even more likely when resources compete directly. Resources freed from predation can indeed gain enough competitive advantage to exclude adjacent resources.

3.3. Complementarity effect

*Ug*1: The Θ_3 term in Eq. (3), which depends on the degree of niche overlap σ_c/Δ, reflects interspecific competition, thus capturing the "interaction milieu" (McGill et al., 2006) and lowering the overall density of the consumer community. Consumer density n, and consequently consumer total biomass, increases up to a plateau with increasing niche overlap (σ_c/Δ), i.e., with increasing diversity (smaller Δ) or decreasing specialization (larger σ_c) of consumer species (Fig. 2a). Numerically solving $n > 0.99n_{max}$ gives the approximate saturation point $\Delta \lesssim 2.7\sigma_c$, which is substantially less restrictive than thresholds obtained for limiting similarity (see Abrams, 1975 for a discussion on the $\Delta = \sigma_c$ limit). For a given niche breadth σ_c, the n_{max} saturation level is determined by the balance between two opposing phenomena: higher niche overlap (σ_c/Δ) means higher interspecific competition and lower population size of each species, but smaller niche distances (Δ) mean that more species contribute to the aggregate community size. When niche overlap is small ($\Delta > 2.7\sigma_c$), the effect of increased diversity overcomes the reduction of individual population sizes because of low interspecific competition. As shown by Eqs. (5), the dependencies of total

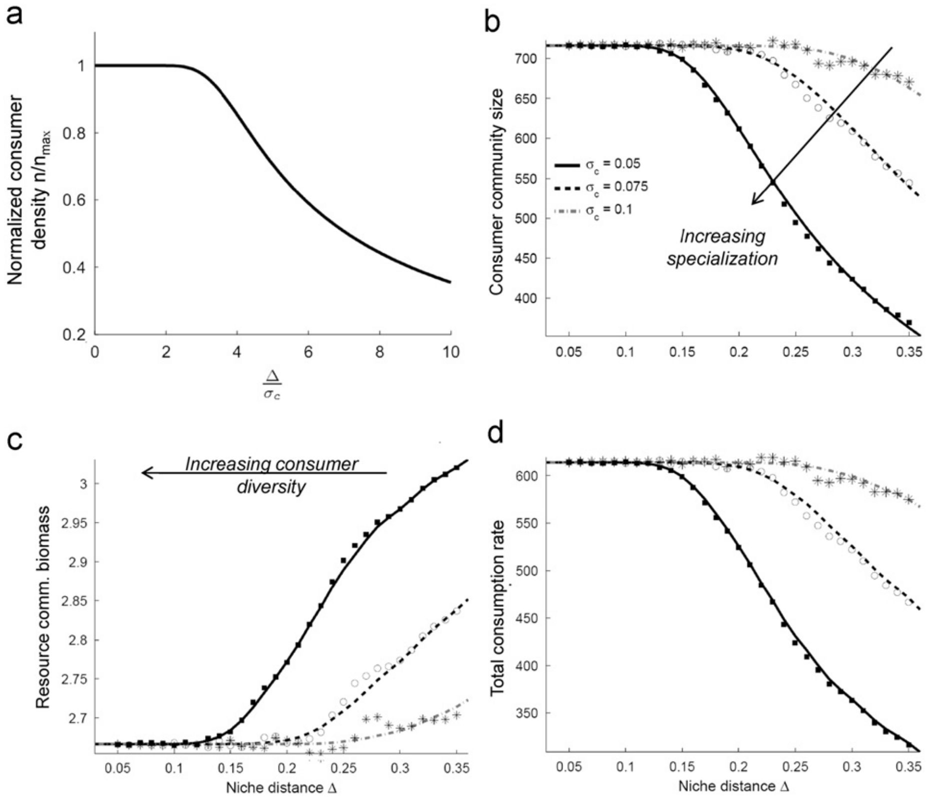

Fig. 2. Complementarity effect. (a) Total normalized n/n_{max} consumer density at each point z of the resource gradient plotted against niche separation Δ/σ_c in the Ug1 model (Eq. (3a)). Increasing niche overlap, i.e., smaller Δ/σ_c, can result from higher consumer diversity (smaller niche distance Δ) or lesser specialization of consumer species (larger niche breadth σ_c). (b) Consumer community size, (c) resource community biomass and (d) total consumption rate as functions of niche distance Δ for the NUg1 model. Symbols represent simulation results at equilibrium for different degree of consumer specialization: $\sigma_c = 0.05$ (■), $\sigma_c = 0.075$ (◦) and $\sigma_c = 0.1$ (*). Lines show the corresponding NUg1 local approximation. The gradient is multimodal with $\rho(z) = 1000(e^{-(z-1.5)^2} + e^{-(z-1)^2/0.1})$ and $\kappa_R(z) = 1.5(e^{-(z-1.5)^2} + e^{-(z-0.8)^2/0.1})$ restricted to [0, 3]. Trait values are A=0.7, e=0.1, d=6 and ε=7.

resource stock and total consumption rate on Δ are driven entirely by consumer population size. With decreasing niche distances, resource levels decline, whereas total consumption increases up to a plateau when $n = n_{max}$. It is noteworthy that the saturation levels of all ecosystem processes are independent of the degree of consumer specialization (Fig. 2).

*NUg*1: Simulations for various resource gradient shapes validate both the preceding qualitative results and the quantitative approximation (Eqs. (6)). Fig. 2 shows an example of a multimodal gradient with slightly different peaks for ρ and κ_R. The shape of the BEF relationship is independent of the shape of the resource gradient and is determined entirely by the interaction term Θ_3, as predicted by Eqs. (6). Comparing different levels of specialization (Fig. 2b–d) confirms that communities composed of specialist consumers require smaller niche distances, i.e., higher levels of diversity, to reach the saturation point in the BEF relationship.

*NUgCr*1: The preceding qualitative conclusions also hold for Eqs. (7). When complementarity alone is considered, competition among resources does not alter the direction of the BEF relationships and their shapes remain entirely driven by ecological interactions. However, competition at both trophic levels affects these shapes via σ_c and σ_α. A wider resource competition kernel strengthens the relative role of functional complementarity among consumers. Saturation of consumer density now requires $\Delta \lesssim 2.7\sqrt{\sigma_c^2 - \sigma_\alpha^2/2}$, and the latter expression decreases with σ_α. Thus, a higher diversity is needed to reach saturation of consumer density, and the latter increases faster with diversity relative to its saturation level (Fig. 3a). But at the same time the absolute value of all aggregate stocks and fluxes, including their saturation level, decreases with σ_α, yielding flatter BEF relationships (Fig. 3b–d) and smaller complementary effects in absolute terms.

*NUg*6 *and NUgCr*6: These models are inappropriate for studying complementarity alone but are instrumental in disentangling selection and complementarity effects when they occur simultaneously (see below).

3.4. Selection effect

*Ug*1: Table 2 displays the directions of changes in stocks and fluxes when there is an infinitesimal shift in trait values towards stronger competitors, i.e., when either A or ε increases or d decreases (Appendix C for proof). Recall that e has no effect at equilibrium. While such shifts always reduce resource levels, their impact on consumer population sizes and total consumption greatly depends on the magnitude of the requirement ratio. When consumers are relatively inefficient (requirement ratio $> \frac{1}{2}$) any gain in efficiency has a positive effect on total consumption and total consumer stock. However, if the requirement ratio is less than $\frac{1}{2}$, any gain in efficiency decreases total consumption. Finally, while a decrease in maintenance requirements d or an improvement in the conversion coefficient ε always increases consumer population sizes, an increase in total attack rate A can have either a positive or a negative effect. For efficient consumers, a larger A can lead to a reduction in resource biomass to such low levels that consumer community size also drops.

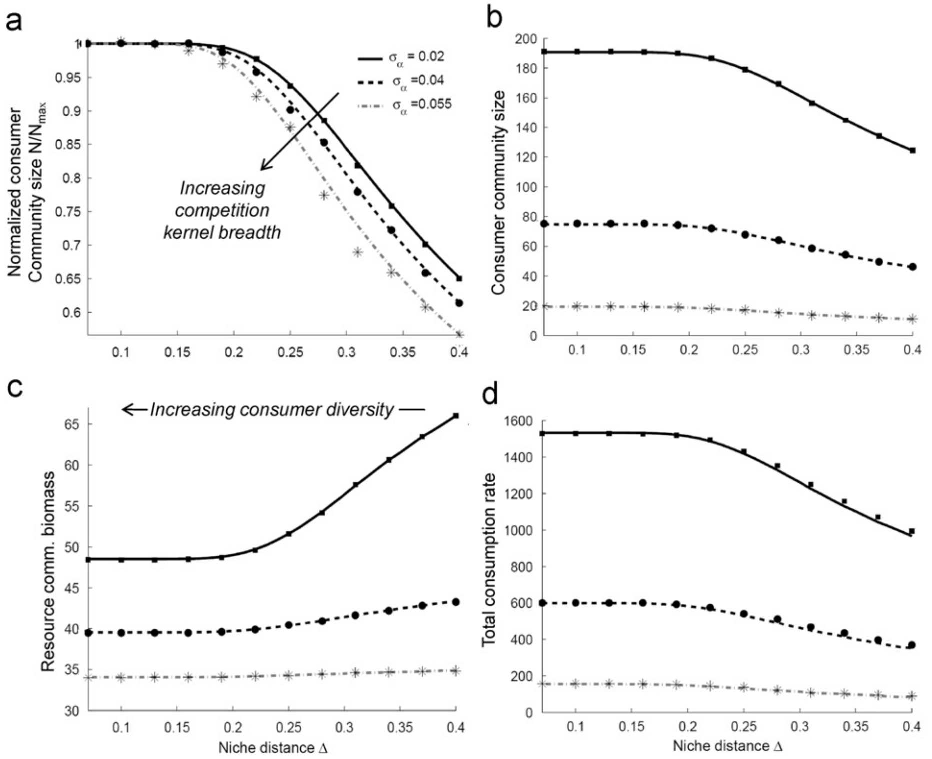

Fig. 3. Effects of resource competition on consumer complementarity. (a) Consumer community size relative to its saturated magnitude, (b) consumer community size, (c) resource community biomass and (d) total consumption rate plotted against niche distance Δ for the NUgCr1 model. Symbols represent simulation results at equilibrium for different breadth of the resource competition kernel: $\sigma_\alpha = 0.02$ (■), $\sigma_\alpha = 0.04$ (•) and $\sigma_\alpha = 0.055$ (*). Lines show the corresponding NUg1Cr local approximation (Eqs. (7)). The gradient is Gaussian with $\rho(z) = 100e^{-(z-2.5)^2}$ and $\kappa_R(z) = 2e^{-(z-2.5)^2}$ restricted to [0, 5]. Trait values are A=0.66, e=0.5, d=8, $\varepsilon = 1$ and $\sigma_c = 0.075$.

Table 2
Qualitative effects on community level processes at equilibrium of infinitesimal shifts in common trait values.

		if d ↘	if ε ↗	if A ↗
Consumer community size	if $\frac{d}{\varepsilon A \kappa_R} > \frac{1}{2}$	↗	↗	↗
	if $\frac{d}{\varepsilon A \kappa_R} < \frac{1}{2}$			↘
Resource community biomass		↘	↘	↘
Total consumption rate	if $\frac{d}{\varepsilon A \kappa_R} > \frac{1}{2}$	↗	↗	↗
	if $\frac{d}{\varepsilon A \kappa_R} < \frac{1}{2}$	↘	↘	↘

Changes in e have no effect at equilibrium.

*NUg*6: Fig. 4 compares communities sampled from regional species pools in which species differ slightly in all their trait values (NUg6, open circles and black squares), and communities of species sharing the same trait values except for their niche centers (NUg1, black lines). The shared trait values in the NUg1 model are taken to be equal to the mean trait values in the NUg6 model, so that any difference between the two models is due to initial trait variation and not to mean trait value. In Fig. 4, each square and circle corresponds to the average equilibrium value of 50 random replicate communities computed for a given initial mean niche distance Δ. The NUg1 local approximation (Eqs. (6)) proves to be accurate as long as niche overlap remains low (high Δ). When niche overlap is high, however, ecosystem properties deviate from these predictions because of competitive exclusion induced by limiting similarity, whereby species with different competitive abilities cannot coexist with nearly coinciding utilization curves. The mean trait values of surviving species tend towards higher efficiency (lower d, higher A and ε), driving community properties away from the values obtained with the local approximation when complementarity alone is considered. This selection effect thus prevents the BEF relationships from saturating, as observed in the Ug1 and NUg1 models. While enhanced functional diversity always leads to more complete resource depletion (Fig. 4b), selection can counteract consumer complementarity and produce humped-shaped BEF relationships for other ecosystem properties (e.g., Fig. 4a open circles, Fig. 4c).

The overall selection effect is able to drive consumer abundance both above and below values derived from the local approximation, while holding the resource spectrum and mean trait values in the regional species pool constant (Fig. 4a). The only difference between circles and squares in Fig. 4 is the relative variability of traits in the species pool. Squares depict communities sampled from species pools characterized by normal distributions with 5% CVs along the six trait axes, whereas for communities represented by circles, only σ_{c_i}, A_i and z_i differ among consumer species. $d_i/\varepsilon_i A_i$ was set such that $d_i/\varepsilon_i A_i \kappa_R(z_i) < \frac{1}{2}$ for species feeding where the resource gradient is most productive and can sustain large consumer populations. The dominant species in the community therefore have low requirement ratios. The Ug1 model predicts that shifts in values of A generated by species sorting reduce consumer population sizes, while shifts in d and ε increase it (Table 2). When the positive effects of shifts in d and ε overcome the negative effect of shifts in A, communities display a globally positive selection effect; otherwise the selection effect is negative. The example depicted in Fig. 4a demonstrates the important role of trait relative variability at the regional scale in determining the sign of the selection effect, and thus the BEF relationships within a community.

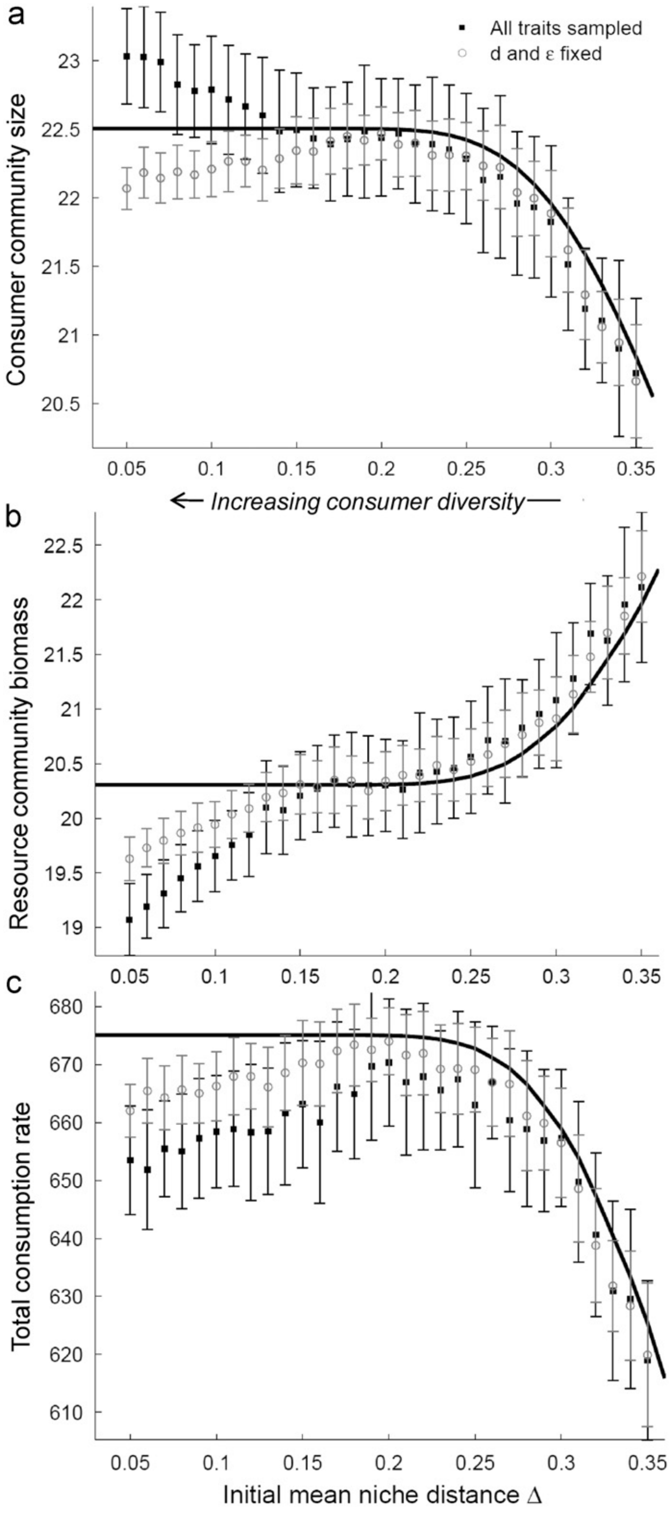

Fig. 4. Selection effect. Community level processes for communities randomly sampled from a diverse regional pool with non-interacting resources: (a) Consumer community size, (b) resource community biomass and (c) total consumption rate plotted against initial mean niche distance. Continuous lines correspond to the NUg1 local approximation when mean trait values at the regional scale are taken for the common trait values (Eqs. (6)). For each initial mean Δ, 50 replicate communities are sampled. Niche centers are given by $z_i = i\Delta + \beta_i$ where β_i is drawn from a normal distribution with a standard deviation of 0.05Δ. Symbols correspond to the mean community level process over the 50 replicates and error bars show the standard deviation. Comparison between a regional pool in which all six traits have normal distributions with CVs of 5% (■) and a regional pool in which all species share the same d and ε values while σ_c, A, e and z_i have normal distributions with 5% CVs (○). Mean values are $\sigma_c = 0.1$, $e = 0.5$, $A = 4$, $d = 15$, $\varepsilon = 0.5$. $\rho(z) = 100e^{-(z-1.5)^2}$ and $\kappa_R(z) = 25e^{-(z-1.5)^2}$ restricted to [0, 3].

NUgCr 1 *and NUgCr*6: Adding competition among resources does not qualitatively change the results regarding the selection effect (Appendix D).

4. Discussion

In this study, we have developed a series of mechanistic models that link species traits, species diversity, vulnerability to cascading extinction, three ecosystem processes, i.e., total consumer biomass, total resource biomass, and total consumption rate. These models provide new insights into the relationship between biodiversity and ecosystem functioning. In particular, they point to the limits of static approaches to functional redundancy in predicting the consequences of species deletion; they allow disentangling the mechanisms that yield different shapes of BEF relationships and emphasize the role of relative trait values and variability at the regional scale; and they suggest that the relative contributions of complementarity and selection in shaping BEF relationships may vary among trophic levels.

Our models reveal that communities of tightly packed consumers display counterintuitive properties. In particular, they can produce top-down cascades of secondary extinctions since the removal of a consumer species can generate subsequent resource extinctions. The mechanism that generates these extinction cascades is fundamentally different from that involved in species extinctions following loss of a keystone predator (Paine, 1966) because it occurs with non-interacting resources. Here, tight niche packing results in high levels of interspecific competition, which keep efficient consumers at low population sizes and thereby prevent them from over-exploiting their resources. Consumer species with strongly overlapping niches were found to be unable to drive their resources extinct regardless of their trait values or the shape of the resource gradient. By sharply reducing interspecific competition, the primary extinction of one consumer species allows efficient neighboring species to reach high enough population sizes and consequently drive some resources extinct within their niches. It is noteworthy that this result holds true for degrees of niche overlap consistent with the coexistence threshold imposed by limiting similarity. While the overall efficiencies of consumers need not be strictly identical, nonetheless they must be similar for consumers to coexist as described by Meszéna et al. (2006).

Our result seems to contradict the findings of Borrvall et al. (2000) and Ebenman et al. (2004), who showed that redundancy, defined as the number of species per trophic level, improved the resistance of tritrophic foodwebs to secondary extinctions in a deterministic context and in the absence of competition among basal species. Here, we investigated the mechanisms driving a particular class of extinction cascades, namely top-down cascades. While the proportions of randomly assembled communities that display secondary extinctions may well be reduced with increasing redundancy (Borrvall et al., 2000; Ebenman et al., 2004), we have found that top-down cascades are more likely in communities composed of tightly packed consumers. In fact, this result matches and provides a mechanistic basis for Ebenman et al.'s (2004) simulation work, which revealed that the proportion of secondary extinctions belonging to basal species increases with redundancy, while the proportion belonging to the top trophic level decreases. Furthermore, Borrvall et al.'s (2000) and Ebenman et al.'s (2004) simulations included direct intraspecific competition (e.g., interference competition) at the top and middle trophic levels. Thébault et al. (2007) showed that the number of secondary extinctions increases with redundancy in the absence of direct intraspecific competition at these trophic levels, while it decreases when present. Thus, the absence of intraspecific competition in forms other than purely consumptive may contribute to the top-down cascades we demonstrated with MacArthur's model. Nevertheless, Thébault et al. (2007) found that when primary extinctions take place at the top trophic level, the mean number of secondary extinctions always increases with redundancy, independently of the presence of direct intraspecific competition at the middle and top levels. Extinction cascades in communities of similar species show that the functional redundancy concept should be used cautiously. A static approach could readily suggest that consumers with high niche overlap are redundant, and lead to the erroneous prediction that their removal should have no effect. Caution is all the more recommendable since our models are deterministic and stochasticity can only increase the likelihood of extinction cascades. Stochasticity indeed proves to cancel out any deterministic benefit of redundancy for secondary extinctions (Ebenman et al., 2004) because redundancy reduces population sizes and small populations are more prone to stochastic extinctions (Lande, 1993). Unfortunately, a focus on functional traits related to the ecological niche does not directly lead to a definition of redundancy able to predict the consequences of species deletions.

We have showed that niche complementarity alone produces monotonic but saturating BEF relationships: total consumer biomass and consumption rate increase while total resource stock decreases with consumer diversity. As intuitive as it may be, this result seems to contradict Ives et al. (2005), who obtained a hump-shaped relationship between the stock of moderately specialized consumers and their species richness. This apparent inconsistency stems from slightly different coexistence mechanisms produced by the chosen community assembly rules. Ives et al. (2005) added consumer species sequentially, waiting for the system to equilibrate before any new introduction. In this study, we introduce all species simultaneously, as in Scheffer and van Nes (2006). This avoids the edge effects responsible for competitive exclusion of consumers and the extinction of overexploited resources described by Ives et al. (2005). Over many replicates, the total amount of resources is thus lower when more consumer species are introduced successively, which yields a hump-shaped BEF relationship. Neither of these assembly rules is completely realistic, but ours permits analysis of tightly packed communities, which cannot be generated from the procedure used by Ives et al. (2005). Such communities have been described in nature (Terborgh and Diamond, 1970; Schoener, 1974; Inger and Colwell, 1977), may arise from coevolution (Scheffer and van Nes, 2006) and have intriguing properties on their own. In particular, our work reveals that tightly packed communities show saturation of, and tight biotic control over, all ecosystem processes, and strong extinction cascades. Therefore, an important empirical question for BEF research would be to assess the level of species packing and saturation of ecosystem processes exhibited by natural communities to determine whether they fall in the steeper part of the BEF relationships where complementarity effects are strong and species extinctions are bound to alter ecosystem processes substantially (Figs. 2–4).

BEF relationships are shaped not only by niche complementarity, but also by selection effects (Cardinale et al., 2007), the direction of which is still debated (Jiang et al., 2008). Ives et al. (2005) already demonstrated that selection could either increase consumer density, if consumer species vary in assimilation efficiency, or reduce it, if consumers differ in capture rates. The situation is actually more complex. The overall selection effect is determined by the combined contributions of several traits, the sign and magnitude of which depend on relative trait values and variability at the regional scale and on the ecosystem function of interest. Variability among consumer species in conversion coefficient from surplus energy to offspring has no effect on any ecosystem properties. However, aggregate consumer stock is always positively affected by varying maintenance requirements d or conversion coefficient from resource to energy ε, while diversity of attack rates A has a negative effect on efficient consumers (low requirement ratio) and a positive one on inefficient ones. Selection effects on aggregated consumption rate are negative for these three traits (d, ε and A) when consumers are efficient, positive otherwise. For the aggregated consumer stock and consumption rate, the overall selection effect can then be positive, negative or even neutral. Taking complementarity into account, BEF relationships can then be monotonic (non-efficient consumers), hump-shaped (efficient ones) or saturating if the overall selection effect remains neutral. There is only one unconditional effect: higher consumer diversity always leads to more complete resource depletion. These results are consistent with those obtained by Thébault and Loreau (2003), who showed that mean total plant biomass always decreases upon herbivore addition but that negative selection effects and even hump-shaped relationships between herbivore diversity and total herbivore biomass can occur.

Our model also predicts possible shifts in the directions of selection effects along fertility gradients. The sign of selection effects was shown to depend on the value of the requirement ratio, and hence on the resources' carrying capacity. Therefore, if consumer traits are held constant, as for instance in a replicated experiment with the same consumers, selection effects on total resource consumption can be positive at low fertility and become negative at high fertility. Similar shifts in the direction of selection effects on total consumer biomass further require that selection effects be dominated by selection on consumer attack rates (Table 2). Thus, much like in systems with one trophic level (Loreau, 1998), across-site comparisons of consumer diversity effects should be interpreted with caution unless abiotic factors are closely controlled.

One of the main limitations of MacArthur's classical model was the absence of interaction among resources, which strongly limited its relevance to multitrophic systems. We showed how competition can be incorporated at the lower trophic level for a particular class of gradients while preserving analytical tractability. Our analysis reveals that an increase in the degree of generalization with trophic position is a necessary condition for global coexistence. But wider competition kernels at the next lower trophic level also weaken absolute complementarity effects induced by consumer diversity. Thus, in food webs structured by consumptive competition at each trophic level, the relative magnitude of selection effects compared to complementarity effects may increase with trophic position. Our model does not make it possible to predict the exact magnitude of selection effects, let alone their variation among trophic levels, without additional assumptions about the links between species traits, dispersal from the regional pool, and trophic levels. But we showed that, irrespective of the shape of the resource gradient and the presence or absence of competition between resources, consumer generalism makes complementarity effects saturate at a lower diversity. Moreover, when resources compete, BEF relationships driven by complementarity alone become flatter. Selection may therefore prevail at higher trophic levels where diet breadth tends to be larger, which would explain the reported paucity of transgressive overyielding (mixture performance exceeding the best monoculture) at higher trophic levels (Duffy et al., 2007).

The relative simplicity of our models enables a detailed analytical study at the community level without overly sacrificing species-level ecology, but it comes at the price of generality. Our results are based on near-symmetrical consumer communities with almost evenly spaced niche centers along a single niche axis. Examples of non-random and even regular organization patterns have been reported (Schoener, 1984; Dayan et al., 1990) and theoretical work initially supported this hypothesis (MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1974). Subsequent studies, however, produced contradictory results (Abrams, 1983), which led Abrams (1990) to conclude that there was little theoretical support for evenly spaced utilization curves. Nevertheless, such patterns have been observed and this assumption remains a classical starting point in theoretical studies (e.g., Ives et al., 2005; Tanaka and Yoshino, 2009). Moreover, we only studied equilibrium conditions, although transient dynamics can be remarkably long relative to generation times in tightly packed communities (Scheffer and van Nes, 2006). We also ignored plasticity, which can be of particular importance in trophic interactions, by inducing niche expansions, contractions or shifts and corollary modifications of the utilization curves (Duffy, 2002; Casula et al., 2006). We did not incorporate any a priori constraints on trait covariations in our model since we only looked at small deviations around mean values. The potential consequences of trade-offs should not be overlooked. They would indeed constrain relative trait values and variability, which would in turn alter the sign of selection effects and the shape of BEF relationships. For example, Thébault and Loreau (2003) showed that these relationships were substantially influenced by a trade-off between competitive capacity and resistance to herbivory among plants. BEF studies should therefore better incorporate the fundamental trade-offs identified by trait-based approaches (Westoby and Wright, 2006; Green et al., 2008). Most importantly, we only considered compartmentalized trophic levels, while diversity at different levels may be interdependent and experiments suggest that the high frequency of omnivory and intraguild predation has a major impact on diversity effects at higher trophic levels (Duffy et al., 2007).

The challenges are clear: BEF research must transform into a predictive science rather than simply confirm patterns while taking into account multiple ecosystem processes and the full complexity of biotic interactions (Naeem and Wright, 2003; Reiss et al., 2009). In the light of our results, we believe such a transformation could be achieved by incorporating trait-based approaches, which make it possible to address multiple traits and just as many dimensions of differentiation, while ostensibly providing a mechanistic way to scale up from organisms or species to populations, communities, and ecosystems.

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Appendix A. Quasi-steady state approximation

Assuming that resource dynamics take place at a small time scale compared to consumer dynamics, we can use a quasi-steady state approximation (setting Eq. (1a) to zero and substituting in Eq. (1b)) to recover a Volterra-like competition system (Gatto, 1990):

$$R(z) = \kappa_R(z)\left(1 - \sum_{i=1}^{S} \frac{p_i(z)N_i}{\rho(z)}\right) \tag{A1a}$$

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{\sum_{j=1}^{S} \alpha_{ij} N_j}{K_i}\right) \tag{A1b}$$

where

$$r_i = \int e_i \varepsilon_i \kappa_R(z) p_i(z)\, dz - e_i d_i \tag{A2a}$$

$$K_i = \frac{\int \kappa_R(z) p_i(z)\, dz - d_i/\varepsilon_i}{\int [\kappa_R(z)/\rho(z)] p_i^2(z)\, dz} \tag{A2b}$$

$$\alpha_{ij} = \frac{\int [\kappa_R(z)/\rho(z)] p_i(z) p_j(z)\, dz}{\int [\kappa_R(z)/\rho(z)] p_i^2(z)\, dz} \tag{A2c}$$

Throughout the study we assumed that ε_i was uniform $(\forall z, \varepsilon_i(z) = \varepsilon_i)$ because it seemed sensible as a first approach. From Eq. (A2), it is clear that changing the shape of $\varepsilon_i(z)$ is, for consumers, equivalent to changing the shape of $\kappa_R(z)$. This point requires in turn that all consumers share the same ε shape, that is have separable conversion efficiencies $\varepsilon_i(z) = \varepsilon_i w(z)$. The separability assumption is met when all consumers rank resources in the same order on an energetic basis, which does not appear to be too restrictive. The preferences reflected by the utilization curves are then related to other dimensions of food discrimination (e.g., foraging height or any micro-habitat, food size, stoichiometric balance gradient, etc.).

Appendix B. Ideal symmetrical communities: Ug1 model

This appendix gives the mathematical proof for the results described in the Ug1 sections. Let the resource gradient be infinite and uniform and have an infinite number of equivalent consumers with evenly spaced niche positions, $\forall i \in \mathbb{Z}, \forall z \in \mathbb{R}$:

$$\rho(z) \equiv \rho, \quad \kappa_R(z) \equiv \kappa_R, \quad e_i = e, \quad \varepsilon_i = \varepsilon, \quad d_i = d$$

$$p_i(z) = \frac{A}{\sqrt{2\pi}\sigma_c} \exp\left(-\frac{(z - i\Delta)^2}{2\sigma_c^2}\right)$$

It yields at the species level:

$$r_i = r = e(\varepsilon \kappa_R A - d)$$

$$K_i = K = 2\sqrt{\pi}\rho \frac{\sigma_c}{A}\left(1 - \frac{d}{\varepsilon A \kappa_R}\right)$$

$$\alpha_{ij} = \exp\left(-\frac{(i-j)^2 \Delta^2}{4\sigma_c^2}\right)$$

Hence a necessary condition for consumer persistence is $d/\varepsilon A \kappa_R < 1$.

Given the symmetry of the problem, all consumers will reach the same density at equilibrium N^* and Eq. (A1b) entails $N^* = K/\Theta_3[\exp(-\Delta^2/4\sigma_c^2)]$ where $\Theta_3(x) = \sum_{n=-\infty}^{\infty} x^{n^2}$ denotes theta Jacobi 3 function, defined and analytical on $]-1,1[$. Let n be the density of consumers at each point z on the gradient at equilibrium and refer to n/n_{max} as the normalized density. Using the identity $\sqrt{x}\Theta_3[\exp(-\pi x)] = \Theta_3[\exp(-\pi/x)]$ (Jacobi, 1828), Eqs. (3) follow.

Total consumer community attack rate at point z, $P_T(z) = \sum_{i \in \mathbb{Z}} N_i p_i(z)$, is at equilibrium a continuous and Δ periodic function of z and can thus be decomposed into Fourier series:

$$P_T(z) = N^* \sum_{i \in \mathbb{Z}} p_i(z) = nA\left(1 + 2\sum_{k=1}^{\infty} e^{-2\sigma_c^2 \pi^2 k^2/\Delta^2} \cos\left(\frac{2\pi k z}{\Delta}\right)\right) \tag{B1, B2}$$

R given by Eq. (A1a) is a continuous and Δ periodic function of z and can thus be decomposed into Fourier series:

$$R(z) = \kappa_R\left[1 - \frac{AN^*}{\rho\Delta}\left(1 + 2\sum_{k=1}^{\infty} \exp\left(\frac{-2\sigma_c^2 \pi^2 k^2}{\Delta^2}\right) \cos\left(\frac{2\pi k z}{\Delta}\right)\right)\right] \tag{B3}$$

Eq. (B3) proves that the most depleted resources are at $z \in \{k\Delta,\ k \in \mathbb{Z}\}$ (centers of consumer niches) and provides the condition for global coexistence, equation (8), by solving $R(0) > 0$.

All community level properties are $\Delta-$periodic. As we are interested in total stocks and flux at the community level and not forcibly in variations within a period, we derive results at equilibrium for the means over a period of total consumer population size $\langle N \rangle$, resource biomass $\langle R \rangle$ and consumption rate $\langle C \rangle$. n being uniform yields $\langle N \rangle = n$. Mean resource follows:

$$\langle R \rangle = \frac{1}{\Delta}\int_0^{\Delta} R(z)\,dz = \kappa_R\left(1 - \frac{An}{\rho}\right) \tag{B4}$$

Mean consumption rate over a period is given by

$$\langle C \rangle = \frac{1}{\Delta}\int_0^{\Delta} \sum_{i \in \mathbb{Z}} N^* p_i(z) R(z)\,dz \tag{B5a}$$

$$= n\sum_{i \in \mathbb{Z}} \int_0^{\Delta} p_i(z) R(z)\,dz \tag{B5b}$$

$$= n\sum_{i \in \mathbb{Z}} \int_{-i\Delta}^{(1-i)\Delta} p_0(u) R(u + i\Delta)\,du \tag{B5c}$$

$$= n\sum_{i \in \mathbb{Z}} \int_{-i\Delta}^{(1-i)\Delta} p_0(u) R(u)\,du \tag{B5d}$$

$$= n\int_{-\infty}^{\infty} p_0(u) R(u)\,du \tag{B5e}$$

$$= \frac{d}{\varepsilon} n \tag{B5f}$$

where Eq. (B5d) and (B5f) use respectively the periodicity of R and Eq. (1b) at equilibrium with $i=0$.

Appendix C. Community level effects of shifts in consumer trait values

This appendix gives the mathematical proof for the directions, displayed in Table 2, of changes of both stocks and flux when an infinitesimal shift of common consumer trait values occurs. We use the elasticity $l_y^X = (y/X)\partial X/\partial y$ of a variable X to a parameter y. It is interpreted as the variation of X when y varies by 1%: $\delta X/X = l_y^X \delta y/y$. Elasticity can be positive or negative if, for example, an increase in y entails a decrease in X. The elasticities of the means of community level processes over a period to A, ε and d (Table C1) can be calculated for the Ug1 model. Elasticities to e are equal to zero, because e has no effect at equilibrium, and they are consequently not reported in Table C1. The signs of all elasticities are controlled by the value of l_d^N compared to 0 and $l1$ which depends solely on the requirement ratio value $d/\varepsilon A\kappa_R$. The qualitative impacts of an infinitesimal variation in trait value can thus be directly deduced from the requirement ratio value.

Table C1
Elasticities of community level processes over a period at equilibrium.

	Elasticity to d	to ε	to A
Consumer community size	$l_d^N = -\dfrac{d}{\varepsilon A\kappa_R - d}$	$l_\varepsilon^N = -l_d^N$	$l_A^N = -(1 + l_d^N)$
Resource community biomass	$l_d^R = -\dfrac{An}{\rho - An} l_d^N$	$l_\varepsilon^R = -l_d^R$	$l_A^R = -l_d^R$
Total consumption rate	$l_d^C = 1 + l_d^N$	$l_\varepsilon^C = -l_d^C$	$l_A^C = -l_d^C$

Appendix D. Competing resources

Let $\mathcal{F}(f)(\xi) = \int_{-\infty}^{\infty} f(x)e^{-i\xi x}\,dx$ denote the Fourier transform of f and $\mathcal{F}^{-1}(g)(x) = (1/2\pi)\int_{-\infty}^{\infty} g(\xi)e^{+i\xi x}\,d\xi$ be the inverse Fourier transform of g. For any competition kernel of the form $\alpha(z,y) = \alpha(z-y)$, Eq. (2) at equilibrium is equivalent to a convolution equation when no extinction occurs

$$\frac{dR(z)}{dt} = 0 \Leftrightarrow \int \alpha(z,y)R(y)\,dy = \kappa_R(z) - \sum_{i=1}^{S} N_i \frac{p_i(z)\kappa_R(z)}{\rho(z)} \tag{D1}$$

Taking the Fourier transform on each side, dividing by $\mathcal{F}(\alpha)(\xi)$ and taking the inverse Fourier transform yields

$$R^{eq}(z) = \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}(\kappa_R)}{\mathcal{F}(\alpha)}\right)\right](z) - \sum_{i=1}^{S} N_i \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}\left(\dfrac{p_i\kappa_R}{\rho}\right)}{\mathcal{F}(\alpha)}\right)\right](z) \tag{D2}$$

By substituting Eq. (D2) into Eq. (1b), we obtain LV-like equations for the dynamics of the full system:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{\sum_{j=1}^{S} \alpha_{ij} N_j}{K_i}\right) \tag{D3}$$

where

$$r_i = \int e_i \varepsilon_i p_i(z) \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}(\kappa_R)}{\mathcal{F}(\alpha)}\right)\right](z)\,dz - e_i d_i \tag{D4a}$$

$$K_i = r_i \Big/ \int e_i \varepsilon_i p_i(z) \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}\left(\dfrac{p_i\kappa_R}{\rho}\right)}{\mathcal{F}(\alpha)}\right)\right](z)\,dz \tag{D4b}$$

$$\alpha_{ij} = \frac{\int p_i(z) \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}\left(\dfrac{p_j\kappa_R}{\rho}\right)}{\mathcal{F}(\alpha)}\right)\right](z)\,dz}{\int p_i(z) \left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}\left(\dfrac{p_i\kappa_R}{\rho}\right)}{\mathcal{F}(\alpha)}\right)\right](z)dz} \tag{D4c}$$

From now on, we assume the competition kernel is Gaussian: $\alpha(z,z') = \exp(-(z-z')^2/2\sigma_\alpha^2)$. If ρ and κ_R are proportional, i.e., $\forall z\ \kappa_R(z) = k\rho(z)$, we have

$$\left[\mathcal{F}^{-1}\left(\frac{\mathcal{F}\left(\dfrac{p_i\kappa_R}{\rho}\right)}{\mathcal{F}(\alpha)}\right)\right](z) = k\frac{A_i}{2\pi\sigma_\alpha\sqrt{\sigma_{c_i}^2 - \sigma_\alpha^2}} e^{-(z-z_i)^2/2(\sigma_{c_i}^2 - \sigma_\alpha^2)}$$

Given Eq. (D2), $\sigma_c > \sigma_\alpha$ is a necessary condition for resources' coexistence when ρ and κ_R are proportional.

Idealized symmetrical communities: UgCr1 model. In the idealized symmetrical case with competing resources, the parameters of the LV-like systems become

$$r_i = r = e\left(\frac{\varepsilon A\kappa_R}{\sqrt{2\pi}\sigma_\alpha} - d\right) \tag{D5a}$$

$$K_i = K = \frac{\rho\sqrt{\pi}}{A}\sqrt{4\sigma_c^2 - 2\sigma_\alpha^2}\left(1 - \frac{d\sqrt{2\pi}\sigma_\alpha}{\varepsilon A\kappa_R}\right) \tag{D5b}$$

$$\alpha_{ij} = \exp\left(-\frac{(i-j)^2\Delta^2}{4\sigma_c^2 - 2\sigma_\alpha^2}\right) \tag{D5c}$$

This proves that $\sigma_c > \sigma_\alpha/\sqrt{2}$ is a necessary for consumers to exist at equilibrium. Community level processes are then calculated at each point z as before:

$$R(z)=\frac{\kappa_R}{\sqrt{2\pi}\sigma_\alpha}\left[1-\frac{nA}{\rho}\left(1+2\sum_{k=1}^{\infty}e^{-2(\sigma_c^2-\sigma_\alpha^2)\pi^2k^2/\Delta^2}\cos\left(\frac{2\pi kz}{\Delta}\right)\right)\right]\tag{D6a}$$

$$n(z)=\frac{\rho}{A}\left(1-\frac{d\sqrt{2\pi}\sigma_\alpha}{\varepsilon A\kappa_R}\right)\Big/\Theta_3[e^{-(4\sigma_c^2-2\sigma_\alpha^2)\pi^2/\Delta^2}]\tag{D6b}$$

$$P_T(z)=nA\left(1+2\sum_{k=1}^{\infty}e^{-2\sigma_c^2\pi^2k^2/\Delta^2}\cos\left(\frac{2\pi kz}{\Delta}\right)\right)\tag{D6c}$$

$$C(z)=P_T(z)R(z)\tag{D6d}$$

$\sigma_c>\sigma_\alpha$ is thus a necessary condition for global coexistence. If $\sigma_c<\sigma_\alpha$, resources which are far enough from the niche center of a consumer (as a rule of thumb: outside the central $2\sigma_c$ bandwidth) gain a sufficient competitive advantage from not being heavily preyed upon and exclude resources located at niche centers.

The means over a period Δ are

$$\langle n\rangle=n\tag{D7a}$$

$$\langle R\rangle=\frac{\kappa_R}{\sqrt{2\pi}\sigma_\alpha}\left(1-\frac{An}{\rho}\right)\tag{D7b}$$

$$\langle C\rangle=\frac{d}{\varepsilon}n\tag{D7c}$$

We recover the expression for non-interacting resources equations (B4) and (B5) simply by substituting $\kappa_R/2\pi\sigma_\alpha$ for κ_R and σ_c for $\sqrt{\sigma_c^2-\sigma_\alpha^2/2}$. The qualitative results regarding the impact of shifts in d, ε and A and the consequent selection effect are therefore not modified.

Gaussian resource gradient: NUgCr1 Model. Let $\kappa_R(z)=\kappa_{R_0}\exp(-z^2/2\sigma_R^2)$ and $\rho(z)=\rho_0\exp(-\frac{z^2}{2\sigma_R^2})$. It follows:

$$R(z)=\frac{\kappa_{R_0}}{\sqrt{2\pi}\sigma_\alpha}\left[\sigma_R\frac{\exp\left(-\frac{z^2}{2(\sigma_R^2-\sigma_\alpha^2)}\right)}{\sqrt{\sigma_R^2-\sigma_\alpha^2}}-\frac{1}{\sqrt{2\pi}\rho_0}\sum_{i=1}^{S}A_iN_i\frac{\exp\left(-\frac{(z-z_i)^2}{2(\sigma_c^2-\sigma_\alpha^2)}\right)}{\sqrt{\sigma_c^2-\sigma_\alpha^2}}\right]\tag{D8a}$$

$$r_i=e\left(\varepsilon A\kappa_{R_0}\frac{\sigma_R}{\sigma_\alpha}\frac{\exp\left(-\frac{z_i^2}{2(\sigma_c^2+\sigma_R^2-\sigma_\alpha^2)}\right)}{\sqrt{2\pi(\sigma_c^2+\sigma_R^2-\sigma_\alpha^2)}}-d\right)\tag{D8b}$$

$$\begin{aligned}K_i&=K(z_i)\\&=\rho_0\sqrt{2\sigma_c^2-\sigma_\alpha^2}\frac{\sqrt{2\pi}}{A}\left(\sigma_R\frac{\exp\left(-\frac{z_i^2}{2(\sigma_c^2+\sigma_R^2-\sigma_\alpha^2)}\right)}{\sqrt{\sigma_c^2+\sigma_R^2-\sigma_\alpha^2}}-\frac{d\sqrt{2\pi}\sigma_\alpha}{\varepsilon A\kappa_{R_0}}\right)\end{aligned}\tag{D8c}$$

$$\alpha_{ij}=\exp\left(-\frac{(i-j)^2\Delta^2}{4\sigma_c^2-2\sigma_\alpha^2}\right)\tag{D8d}$$

A *local approximation* can be derived by assuming that at each point of the gradient z_0, all aggregated properties are close to what they would have been if all parameters were uniform equal to their value at z_0. Starting with $n(z)\approx K(z)/[\Delta\Theta_3(e^{-(4\sigma_c^2-2\sigma_\alpha^2)\pi^2/\Delta^2})]$, the expressions shown in the main text follow.

References

Abrams, P., 1975. Limiting similarity and form of competition coefficient. Theoretical Population Biology 8 (3), 356–375.

Abrams, P., 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics 14, 359–376.

Abrams, P., 1990. Ecological vs evolutionary consequences of competition. Oikos 57 (1), 147–151.

Abrams, P., 1995. Monotonic or unimodal diversity productivity gradients—what does competition theory predict. Ecology 76 (7), 2019–2027.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9 (10), 1146–1156.

Barabas, G., Meszéna, G., 2009. When the exception becomes the rule: the disappearance of limiting similarity in the Lotka–Volterra model. Journal of Theoretical Biology 258 (1), 89–94.

Borrvall, C., Ebenman, B., Jonsson, T., 2000. Biodiversity lessens the risk of cascading extinction in model food webs. Ecology Letters 3 (2), 131–136.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences of the USA 104 (46), 18123–18128.

Casula, P., Wilby, A., Thomas, M.B., 2006. Understanding biodiversity effects on prey in multi-enemy systems. Ecology Letters 9 (9), 995–1004.

Dayan, T., Simberloff, D., Tchernov, E., Yomtov, Y., 1990. Feline canines—community-wide character displacement among the small cats of Israel. American Naturalist 136 (1), 39–60.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99 (2), 201–219.

Duffy, J.E., Carinale, B.J., France, K.E., McIntyre, P.B., Thebault, E., Loreau, M., 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology Letters 10 (6), 522–538.

Ebenman, B., Law, R., Borrvall, C., 2004. Community viability analysis: the response of ecological communities to species loss. Ecology 85 (9), 2591–2600.

Gatto, M., 1990. A general minimum principle for competing populations—some ecological and evolutionary consequences. Theoretical Population Biology 37 (3), 369–388.

Green, J.L., Bohannan, B.J.M., Whitaker, R.J., 2008. Microbial biogeography: from taxonomy to traits. Science 320 (5879), 1039–1043.

Gyllenberg, M., Meszéna, G., 2005. On the impossibility of coexistence of infinitely many strategies. Journal of Mathematical Biology 50 (2), 133–160.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75 (1), 3–35.

Hsu, S.B., Hubbell, S.P., 1979. 2 predators competing for 2 prey species—analysis of MacArthur model. Mathematical Biosciences 47 (3–4), 143–171.

Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110 (4), 449–460.

Inger, R.F., Colwell, R.K., 1977. Organization of contiguous communities of amphibians and reptiles in thailand. Ecological Monographs 47 (3), 229–253.

Ives, A.R., Cardinale, B.J., Snyder, W.E., 2005. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. Ecology Letters 8 (1), 102–116.

Jacobi, C.G.J., 1828. Suite des notices sur les fonctions elliptiques. J. Reine Angew. Math. 3, 303–310.

Jiang, L., Pu, Z., Nemergut, D.R., 2008. On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. Oikos 117 (4), 488–493.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142 (6), 911–927.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. Functional Ecology 16 (5), 545–556.

Litchman, E., Klausmeier, C.A., 2008. Trait-based community ecology of phytoplankton. Annual Review of Ecology Evolution and Systematics 39, 615–639.

Loeuille, N., Loreau, M., 2005. Evolutionary emergence of size-structured food webs. Proceedings of the National Academy of Sciences of the USA 102 (16), 5761–5766.

Loreau, M., 1998. Biodiversity and ecosystem functioning: a mechanistic model. Proceedings of the National Academy of Sciences of the USA 95 (10), 5632–5636.

Loreau, M., 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Philosophical Transactions of the Royal Society B-Biological Sciences 365 (1537), 49–60.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology—biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294 (5543), 804–808.

MacArthur, R., Levins, R., 1967. Limiting similarity convergence and divergence of coexisting species. American Naturalist 101 (921), 377–385.

MacArthur, R.H., 1972. Geographical Ecology; Patterns in the Distribution of Species. Harper & Row, New York.

May, R.M., 1974. On theory of niche overlap. Theoretical Population Biology 5 (3), 297–332.

May, R.M., MacArthur, R., 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences of the USA 69 (5), 1109–1113.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21 (4), 178–185.

Meszéna, G., Gyllenberg, M., Pásztor, L., Metz, J.A.J., 2006. Competitive exclusion and limiting similarity: a unified theory. Theoretical Population Biology 69 (1), 68–87.

Mouquet, N., Moore, J.L., Loreau, M., 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. Ecology Letters 5 (1), 56–65.

Naeem, S., Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6 (6), 567–579.

Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R., Levin, S.A., 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proceedings of the National Academy of Sciences of the USA 98 (20), 11376–11381.

Pachepsky, E., Crawford, J.W., Bown, J.L., Squire, G., 2001. Towards a general theory of biodiversity. Nature 410 (6831), 923–926.

Paine, R.T., 1966. Food web complexity and species diversity. American Naturalist 100 (910), 65–75.

Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology & Evolution 24 (9), 505–514.

Rosenzweig, M., 1971. Paradox of enrichment—destabilization of exploitation ecosystems in ecological time. Science 171 (3969), 385–387.

Roughgarden, J., 1979. Theory of Population Genetics and Evolutionary Ecology: An Introduction. Macmillan, New York.

Savage, V.M., Webb, C.T., Norberg, J., 2007. A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. Journal of Theoretical Biology 247 (2), 213–229.

Scheffer, M., van Nes, E.H., 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. Proceedings of the National Academy of Sciences of the USA 103 (16), 6230–6235.

Schoener, T., 1974. Resource partitioning in ecological communities. Science 185 (4145), 27–39.

Schoener, T., 1984. Size Differences Among Sympatric, Bird-eating Hawks: A Worldwide Survey. Princeton University Press, Princeton, pp. 254–281.

Srivastava, D.S., Bell, T., 2009. Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. Ecology Letters 12 (10), 1016–1028.

Srivastava, D.S., Vellend, M., 2005. Biodiversity–ecosystem function research: Is it relevant to conservation? Annual Review of Ecology Evolution and Systematics 36 267–294.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14 (5), 1125–1140.

Szabó, P., Meszéna, G., 2006. Limiting similarity revisited. Oikos 112 (3), 612–619.

Tanaka, Y., Yoshino, M., 2009. Predicting the phenotypic response of resource-competing communities to environmental change. Journal of Theoretical Biology 257 (4), 627–641.

Terborgh, J., Diamond, J.M., 1970. Niche overlap in feeding assemblages of new-guinea birds. Wilson Bulletin 82 (1), 29–52.

Thébault, E., Huber, V., Loreau, M., 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. Oikos 116 (1), 163–173.

Thébault, E., Loreau, M., 2003. Food-web constraints on biodiversity–ecosystem functioning relationships. Proceedings of the National Academy of Sciences of the USA 100 (25), 14949–14954.

Thébault, E., Loreau, M., 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. American Naturalist 166 (4), E95–E114.

Vandermeer, J.H., 1989. The Ecology of Intercropping. Cambridge University Press, Cambridge, New York.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I., Poff, N.L., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13 (3), 267–283.

Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology & Evolution 21 (5), 261–268.