

# Size-based predictions of food web patterns

Lai Zhang · Martin Hartvig ·  
Kim Knudsen · Ken H. Andersen

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**Abstract** We employ size-based theoretical arguments to derive simple analytic predictions of ecological patterns and properties of natural communities: size-spectrum exponent, maximum trophic level, and susceptibility to invasive species. The predictions are brought about by assuming that an infinite number of species are continuously distributed on a size–trait axis. It is, however, an open question whether such predictions are valid for a food web with a finite number of species embedded in a network structure. We address this question by comparing the size-based predictions to results from dynamic food web simulations with varying species richness. To this end, we develop a new size- and trait-based food web model that can be simplified into an

analytically solvable size-based model. We confirm existing solutions for the size distribution and derive novel predictions for maximum trophic level and invasion resistance. Our results show that the predicted size-spectrum exponent is borne out in the simulated food webs even with few species, albeit with a systematic bias. The predicted maximum trophic level turns out to be an upper limit since simulated food webs may have a lower number of trophic levels, especially for low species richness, due to structural constraints. The size-based model possesses an evolutionary stable state and is therefore un-invadable. In contrast, the food web simulations show that all communities, irrespective of number of species, are equally open to invasions. We use these results to discuss the validity of size-based predictions in the light of the structural constraints imposed by food webs.

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L. Zhang · K. Knudsen  
Department of Applied Mathematics and Computer Science,  
Technical University of Denmark,  
Matematiktorvet 303B, 2800 Kgs. Lyngby, Denmark

M. Hartvig  
National Institute of Aquatic Resources,  
Technical University of Denmark, Charlottenlund Slot,  
Jægersborg Allé 1, 2910 Charlottenlund, Denmark

M. Hartvig  
Center for Macroecology, Evolution and Climate,  
University of Copenhagen,  
Universitetsparken 15, 2100 Copenhagen Ø, Denmark

K. H. Andersen (✉)  
Center for Ocean Life, National Institute of Aquatic Resources,  
Technical University of Denmark,  
Jægersborg Allé 1, 2910 Charlottenlund, Denmark  
e-mail: kha@aqu.dtu.dk

*Present Address:*

L. Zhang  
Department of Mathematics and Mathematical Statistics,  
Umeå University, 90187 Umeå, Sweden

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## Introduction

Dynamic food webs are a common modeling framework for simulating complete communities (Loeuille and Loreau 2005; Brose et al. 2006a; Rossberg et al. 2008; Boit et al. 2012; Gomez-Canchong et al. 2012). A food web model is constructed from a set of species represented as nodes in a network where each species is characterized by its biomass. An alternative representation of a community is through the abundance distribution of individuals as a function of their body size, the size spectrum (Sheldon et al. 1972; Reuman et al. 2008). This approach has been most successfully applied to aquatic ecosystems. The most celebrated

result of size-based theory is that the size spectrum follows a power law with an exponent such that the biomass in logarithmic size groups is approximately constant (Sheldon et al. 1977; Benoît and Rochet 2004; Andersen and Beyer 2006). Besides the size-spectrum exponent, it is possible to derive trophic and individual efficiencies (Borgmann 1987; Andersen et al. 2009) and, as we will demonstrate, maximum trophic level and resistance towards invasions. The predictions of size-based models are all achieved by ignoring the specifics of the species and the topological structure of the underlying food web through the assumption of a continuum of species or an “infinite diversity.” The question is whether these predictions are relevant for situations where the diversity is not infinite but instead characterized by a finite number of species. The aim of this work is to examine how well results based on the continuous size-based representations of communities correspond with simulation of food webs with a finite number of species. This aim will further contribute to a unification of size-based theory and food web theory.

To this end, we develop a trait-based food web model where each species is characterized by two traits: body size and spatial habitat preference. Body size is used to scale vital rates (Yodzis and Innes 1992), while the habitat trait is used to characterize a population’s distribution in space which is motivated by the classic niche model for species competition (MacArthur and Levins 1967). The strength of predator–prey interactions is jointly determined by both traits of prey and predator. By ignoring the trait for spatial habitat preference, the model becomes purely size-based, and we can derive analytic and semi-analytic predictions for the size-spectrum exponent, maximum trophic level, and resistance to species invasions into the established food webs.

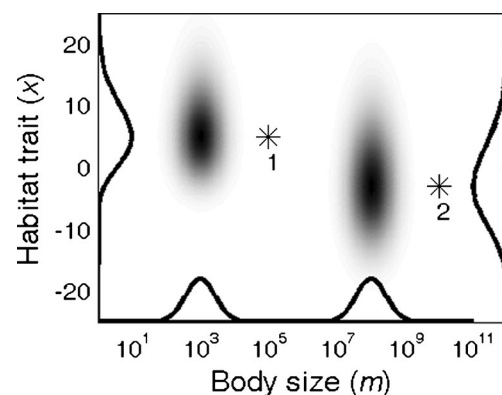
Food webs are constructed using community assembly. This process mimics the natural assembly of communities by building food webs through sequential additions of species picked from an external species pool (Post and Pimm 1983; Taylor 1988; Drake 1990). Early methods of community assembly provided invading species with random interactions to the other species, while recent approaches have added more mechanistic procedures where species interactions are partly determined by predator–prey body mass ratios (Virgo et al. 2006; Lewis and Law 2007). This approach serves as a starting point for the trait-based assembly model where the size trait is supplemented by an additional habitat trait and where the interaction is determined entirely by the traits. Food webs are assembled from species sampled from a two-dimensional species pool spanned by the two traits. From each realized food web, we can calculate size-spectrum exponent and the maximum trophic level. Further, the trait-based approach enables us to use concepts from evolutionary ecology to explore the

stability of the food web towards invasions from alien species, i.e., species not belonging to the species pool.

We demonstrate how the size-spectrum exponent converges as the size of the species pool size is increased. We further demonstrate how the maximum trophic level is determined either by energetic constraints on the productivity of the resource when the species pool is densely packed or constrained by the topology of the emerging interaction matrix when the species pool is dilute. The maximum trophic level is therefore not determined by a single constraint. Finally, we demonstrate how the stability of the emerging food webs towards alien invasive species is independent of the species richness of the food web. We discuss how the trait-based food web model concept may be generalized to other traits.

### Food web model

A species  $i$  is characterized by two traits: body size  $m_i$  and habitat trait  $x_i$ . Size is given in terms of mass, and habitat is dimensionless. Body size is employed to scale vital rates of search volume and respiration. The habitat trait is used to characterize a population’s spatial location and distribution; for simplicity, a one-dimensional abstract representation of space is used (Hartvig 2011): each species is centered on a position in space, with a home range that increases with body size  $m_i$ . Predator–prey interactions between spatially co-occurring organisms take place through predation following the rule of “big-eat-small” (Cohen et al. 1993; Brose et al. 2006b; Barnes et al. 2010) (Fig. 1). Formally, this interaction is described by a size-selection kernel  $\phi(m_i/m_j)$  and a spatial interaction kernel  $\psi(x_i - x_j)$ . Together they



**Fig. 1** Illustration of how the prey preference depends on the size trait  $m$  and the habitat trait  $x$  for two species shown with asterisks. The prey preference (shaded areas) are constructed by multiplying the size selectivity, shown by the bell-shaped curves on the horizontal axis, with the habitat preference which are shown on the vertical axes. The two species have the same preferred predator–prey size ratio, but the habitat range is wider for the large species

determine when predation may occur and their product constitutes the interaction strength.

The size-selection kernel is a lognormal function (Ursin 1973), describing the preference of  $m_i$  sized predators to  $m_j$  sized prey:

$$\varphi(m_i/m_j) = \exp\left(-\left(\ln \frac{m_i}{\beta m_j}\right)^2 / (2\sigma_m^2)\right) \quad (1)$$

that peaks when  $m_i/m_j$  equals the preferred predator–prey mass ratio  $\beta$ . Thus, individuals with mass ratio far from  $\beta$  have negligible interactions. The range of prey sizes that a predator can consume is determined by the width of the selection function  $\sigma_m$ .

The spatial kernel  $\psi(x_i - x_j)$  describes the strength of the interaction which is given by the spatial overlap of the interacting populations. It is assumed that abundance  $N_i$  of a species  $i$  is normally distributed in space with a center at  $x_i$  (Hartvig 2011):

$$\psi(x_i - x_j) = \frac{1}{\sqrt{2\pi(\sigma_x^2(m_i) + \sigma_x^2(m_j))}} \times \exp\left(\frac{-(x_i - x_j)^2}{2(\sigma_x^2(m_i) + \sigma_x^2(m_j))}\right). \quad (2)$$

The width of the spatial distribution is determined by  $\sigma_x(m_i)$ , which is an increasing function of body size (Kramer and Chapman M 1999; Haskell et al. 2002; Jetz et al. 2004) and interpreted here as the home range of species  $i$ :

$$\sigma_x(m_i) = \sigma_0 + \frac{1}{2} \log_{10}(m_i/m_0),$$

where  $\sigma_0$  is the home range of  $m_0$  sized species.

Population dynamics of  $N_i$  is prescribed by the Yodzis and Innes (1992) model:

$$\frac{dN_i}{dt} \frac{1}{N_i} = \varepsilon(E_{R,i} + E_{C,i})m_i^{-1} - \tilde{k}m_i^{n-1} - \mu_i, \quad (3)$$

where the food encountered from the resource ( $E_{R,i}$ ) and other species ( $E_{C,i}$ ) is described using the interaction kernels (1) and (2):

$$E_{R,i} = \gamma m_i^q \int R(x) \varphi(m_i/m_0) \psi(x_i - x) dx,$$

$$E_{C,i} = \gamma m_i^q \sum_j m_j N_j \varphi(m_i/m_j) \psi(x_i - x_j),$$

where individuals within consumer species  $i$  obtain food from resources  $R(x)$  (hereafter denoted by  $R$ , but keep in mind that it is a density distribution of the habitat trait) and other smaller consumer species with a mass-dependent volumetric search rate  $\gamma m_i^q$  (Ware 1978). Intrinsic losses  $\tilde{k}m_i^{n-1}$  represents metabolic costs and mortality from other

sources than predation. Population abundance is regulated by predation from larger species with a mortality:

$$\mu_i = \sum_j \gamma m_j^q N_j \varphi(m_j/m_i) \psi(x_j - x_i)$$

Resource biomass density  $R$  is described using logistic growth and assumed to be continuously distributed along the spatial direction  $x$  with constant carrying capacity  $K$ :

$$\frac{dR}{dt} \frac{1}{R} = \underbrace{\tilde{r}m_0^{n-1} \left(1 - \frac{R}{K}\right)}_{\text{Intrinsic growth rate}} - \underbrace{\sum_j \gamma m_j^q N_j \varphi(m_j/m_0) \psi(x_j - x)}_{\text{Loss due to predation}}, \quad (4)$$

where the intrinsic growth rate is scaled with body size as  $\tilde{r}m_0^{n-1}$  (Savage et al. 2004).  $m_0$  is the resource body size as well as the smallest body size of consumer species. The right-hand side of (3) is the per capita growth rate of a species with trait values  $m_i$  and  $x_i$ . We use the per capita growth rate as a measure of the invasion fitness of an invading species, i.e., a species with negligible abundance, into an established community (Metz et al. 1992).

To avoid results that depend on the specific choices of  $m_0$  and  $\gamma$ , Eqs. (3) and (4) are scaled by setting  $\tau = t\gamma m_0^q$ ,  $w_j = m_j/m_0$ . The equations for biomass  $B_i = w_i N_i$  then become

$$\begin{aligned} \frac{dB_i}{d\tau} \frac{1}{B_i} = & \varepsilon w_i^{q-1} \left( \int R\varphi(w_i) \psi(x_i - x) dx \right. \\ & + \sum_j B_j \varphi(w_i/w_j) \psi(x_i - x_j) \Big) - k w_i^{n-1} \\ & - \sum_j w_j^{q-1} B_j \varphi(w_j/w_i) \psi(x_j - x_i), \end{aligned} \quad (5)$$

$$\frac{dR}{d\tau} \frac{1}{R} = r \left(1 - \frac{R}{K}\right) - \sum_j w_j^{q-1} B_j \varphi(w_j) \psi(x_j - x), \quad (6)$$

where  $r = \tilde{r}m_0^{n-q-1}/\gamma$  and  $k = \tilde{k}m_0^{n-q-1}/\gamma$ . Thus,  $\gamma$  and  $m_0$  disappear from the system, while two new parameters  $r$  and  $k$  emerge representing scaled productivity and intrinsic losses. Parameter values are given in Table 1.

### Analytic approximations

Three analytic and semi-analytic solutions to (5) are developed: size-spectrum exponent, maximum trophic level, and resistance to invasions. All analytic solutions rely on ignoring the habitat trait such that species are characterized only by their body size. The habitat trait will be considered in the full food web solution in Section “Community assembly”.

**Table 1** Model parameters

Parameter	Value	Interpretation
$\beta$	100	Preferred predator–prey mass ratio <sup>a</sup>
$\varepsilon$	0.2	Conversion efficiency <sup>b</sup>
$q$	0.75	Exponent of volumetric search rate <sup>c</sup>
$n$	0.75	Exponent of metabolic costs <sup>d</sup>
$k$	3.3	Prefactor for intrinsic mortality <sup>e</sup>
$\sigma_m$	1	Width of selection function <sup>a</sup>
$\sigma_0$	$\sqrt{2}/2$	Home range of $m_0$ sized species <sup>f</sup>
$\Delta x$	50	Ecosystem size <sup>g</sup>
$r$	30	Prefactor for the scaled resource generation rate <sup>e</sup>
$K$	$510m_0/\text{vol}$	Resource carrying capacity <sup>e</sup>

<sup>a</sup>Ursin (1973)<sup>b</sup>Rossberg et al. (2008)<sup>c</sup>Theoretically expected value is 0.8 (Andersen and Beyer 2006), but  $q = n$  is employed to ease analytic analysis<sup>d</sup>West et al. (1997)<sup>e</sup>Adjusted to produce up to five trophic levels above the resource<sup>f</sup>Hartvig (2011)<sup>g</sup>The total spatial size of the ecosystem is set to be  $\Delta x = 50 (\gg \sigma_x(w_{\max}))$  such that the largest species ( $w_{\max} \sim 10^{10}$ ) have sufficient room for roaming. We use periodic boundary condition in the niche direction when performing community assembly

### Size-spectrum solution

The relationship between body size and individual abundance can be derived from (5) under three assumptions: (1) no variation in the  $x$  direction, (2) that there is a continuum of species along the body size direction, and (3) that the range of body sizes spans the interval  $(0, \infty)$ . Assumptions 2 and 3 imply that we can ignore resource dynamics, i.e.,  $R = 0$ . We introduce a population density distribution function  $\mathcal{B}(w)$  defined such that  $\mathcal{B}(w)dw dx$  is the biomass of individuals in the size- and  $x$ -ranges  $[w, w + dw]$  and  $[x, x + dx]$ . When this definition is introduced in (5), we can derive an equation for  $\mathcal{B}(w)$ :

$$\frac{1}{\mathcal{B}} \frac{d\mathcal{B}}{d\tau} = \varepsilon w^{q-1} \int_0^\infty \mathcal{B}(w') \varphi(w/w') dw' - \int_0^\infty w'^{(q-1)} \mathcal{B}(w') \varphi(w'/w) dw' - k w^{n-1}. \quad (7)$$

We seek an equilibrium solution where  $d\mathcal{B}/d\tau = 0$  in the form of a power law  $\mathcal{B}(w) = \rho_0 w^{1-\lambda_1}$ , where  $\lambda_1$  is the size-spectrum exponent, and  $\rho_0$  is a constant. Inserting this ansatz into the right-hand side of (7) and integrating over the size preference function lead to

$$\varepsilon \beta^{\lambda_1-2} e^{(\lambda_1-2)^2 \sigma_m^2/2} - \beta^{1+q-\lambda_1} e^{(q-\lambda_1)^2 \sigma_m^2/2} = \frac{k}{\sqrt{2\pi} \rho_0 \sigma_m} w^{\lambda_1-(2+q-n)}. \quad (8)$$

As  $w$  enters into the last term in (8), Eq. (7) does not admit a pure power-law solution. By neglecting intrinsic losses,

i.e., setting  $k = 0$ , we obtain an approximate solution to  $\lambda_1$

$$\lambda_1 = \frac{1}{2} \left( 2 + q - \frac{\ln \varepsilon}{\ln \beta + \sigma_m^2 (q-1)/2} \right) \approx 2.05, \quad (9)$$

where the numerical values of the parameters are those in Table 1.

### Trophic chain solution

An alternative way to derive the size-spectrum exponent is by assuming that the food web is organized in a trophic chain where species are pooled into discrete trophic levels. Mathematically, it is equivalent to a set of species with a separation in weight equal to predator–prey mass ratio, i.e.,

$$w_i/w_{i-1} = \beta, \quad (10)$$

and the size-selection function  $\varphi(s) = 0$  for  $s \neq \beta$ . Thus, Eqs. (6) and (5) can be written as follows:

$$\begin{aligned} \frac{dB_0}{d\tau} \frac{1}{B_0} &= r(1 - B_0/K) - w_1^{q-1} B_1, \\ \frac{dB_i}{d\tau} \frac{1}{B_i} &= \varepsilon w_i^{q-1} B_{i-1} - k w_i^{n-1} - w_{i+1}^{q-1} B_{i+1}, \quad i = 1, 2, \dots \end{aligned}$$

where  $B_0 = \int_{-\infty}^\infty \psi(x) R dx = R$ . Let us assume that  $q = n$  and  $w_0 = 1$ . Then we have a linear recurrence relation for the equilibrium solution

$$\frac{B_{i+1}}{B_{i-1}} = \frac{\varepsilon}{\beta^{q-1}} - \frac{k}{\beta^{q-1} B_{i-1}}, \quad i = 2, 3, \dots \quad (11)$$

By using the ansatz  $B_i \propto w_i^{2-\lambda_2}$  and, as in Section “Size-spectrum solution”, neglecting intrinsic losses ( $k = 0$ ), we can find an approximate exponent explicitly

$$\lambda_1 = \frac{1}{2} \left( 3 + q - \frac{\ln \varepsilon}{\ln \beta} \right) \approx 2.05. \quad (12)$$

### Maximum trophic level

In the previous solution, intrinsic losses were ignored. As  $w$  increases, specific intrinsic losses  $kw^{n-1}$  constitutes an increasing fraction of specific consumption  $\propto w^{1-\lambda+q}$ . At some size  $\propto k^{1/(2-\lambda+q-n)}$ , all consumption is used for intrinsic losses. This maximum trophic level can be determined accurately by solving the recursive Eq. (11):

$$\text{MTL} = \max \left\{ 1 + 2 \left\lfloor \frac{\ln \left( 1 + \frac{Kr(b-1)}{ar+aK\beta^{q-1}} \right)}{\ln b} \right\rfloor, 2 \left\lfloor \frac{\ln \left( 1 + \frac{Kr(b-1)}{ar+aK\beta^{q-1}/b} + \frac{(b-1)aK\beta^{q-1}}{arb+aK\beta^{q-1}} \right)}{\ln b} \right\rfloor \right\},$$

where  $a = k/\varepsilon$  and  $b = \beta^{q-1}/\varepsilon$ .  $\lfloor M \rfloor$  means the maximum integer smaller than  $M$ . Therefore, increasing  $K$  and  $r$  prolongs the trophic chain. The chosen parameter values (Table 1) yield five trophic levels above the resource.

### Resistance to invasions

A system where the per capita population growth rate of all resident species is zero and where no other species can invade is said to reside in an evolutionary stable state (ESS) (Maynard Smith and Price 1973). An ESS means that no species with trait values differing from those of the resident species can invade. The system is therefore completely resistant towards invasions of other species. In order to examine whether an ESS exists, we assume  $p$  coexisting species and a resource  $B_0$  at equilibrium of (5):

$$\begin{cases} 0 = r(1 - B_0/K) - \sum_{j=1}^p w_j^{q-1} B_j \varphi(w_j/w_0), \\ 0 = g(w_i) = \varepsilon w_i^{q-1} \sum_{j=0}^p B_j \varphi(w_i/w_j) - kw_i^{n-1} \\ \quad - \sum_{j=1}^p w_j^{q-1} B_j \varphi(w_j/w_i) \end{cases}$$

where  $w_i > w_{i-1}$ . There are three necessary conditions for the  $p$  resident species to form an ESS:

$$B_i > 0, \quad g(w_i) = 0 \quad \text{and} \quad g'(w_i) = 0. \quad (13)$$

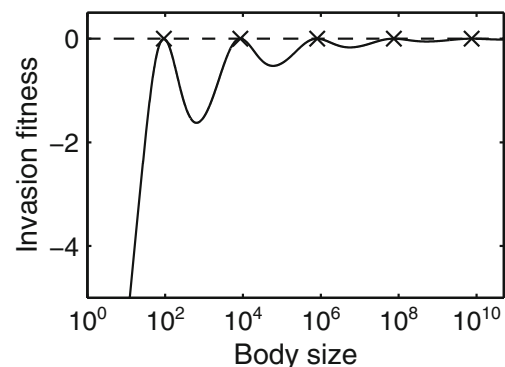
The first two conditions ensure that the  $p$  species can coexist at the equilibrium, while the last condition implies that the  $p$  species are at the local minimum or maximum on the fitness curve.

Solving (13) is mathematically challenging. Inspired by the simulated communities, we make the ansatz of  $p =$

5 coexisting species separated approximately by the preferred predator–prey mass ratio  $\beta$ . This separation means that effectively only neighboring resident species interact. Solving (13) numerically for  $w_i$  of the five species gave the solution  $(w_1^*, \dots, w_5^*) = (0.9167 \times 10^2, 0.7953 \times 10^4, 0.7424 \times 10^6, 0.6463 \times 10^8, \text{ and } 0.6463 \times 10^{10})$ , which indeed is an ESS as  $g(w) \leq 0$  for all  $w$  (Fig. 2). Further, numerical examinations (not shown) demonstrated that there is no other ESS for this set of parameters, suggesting that the ESS  $(w_1^*, \dots, w_5^*)$  is unique. Note that  $w_i^* \approx \beta^i$  which justifies the assumption (10). We expect that similar ESS states exist for parameters where the maximum trophic level is different from 5.

### Community assembly

Numerical analysis of model (6)–(5) is performed using sequential community assembly (Post and Pimm 1983; Taylor 1988; Drake 1990). This approach constructs a community by introducing species with low density one by one from an external pool of species. Two types of species pools are employed: discrete and continuous. The discrete pool contains a finite number of species with trait values randomly selected from a two-dimensional trait space  $(x, w) \in \Omega = [-25, 25] \times [1, 10^{11}]$ . Four sizes of finite species pools are constructed with 25, 50, 100, and 200 species. For each pool size, 50 pool replicates are generated, and from each species pool, 20 communities are assembled yielding 4,000 communities in total, 1,000 for each pool size. In the continuous species pool, trait values  $(x, w)$  are drawn at random from  $\Omega$ . In both discrete and continuous cases,  $x$  is chosen uniformly, while  $w$  is chosen log-uniformly. Details of the assembly algorithm are provided in the Appendix.



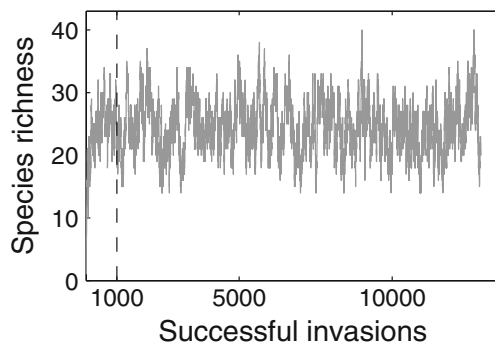
**Fig. 2** Fitness landscape of the ESS when only mass trait is considered and five trophic levels are assumed. The ESS is unique and contains five species (crosses) sitting separately on the peaks of the fitness curve with a body size separation that roughly equals the predator–prey mass ratio  $\beta$



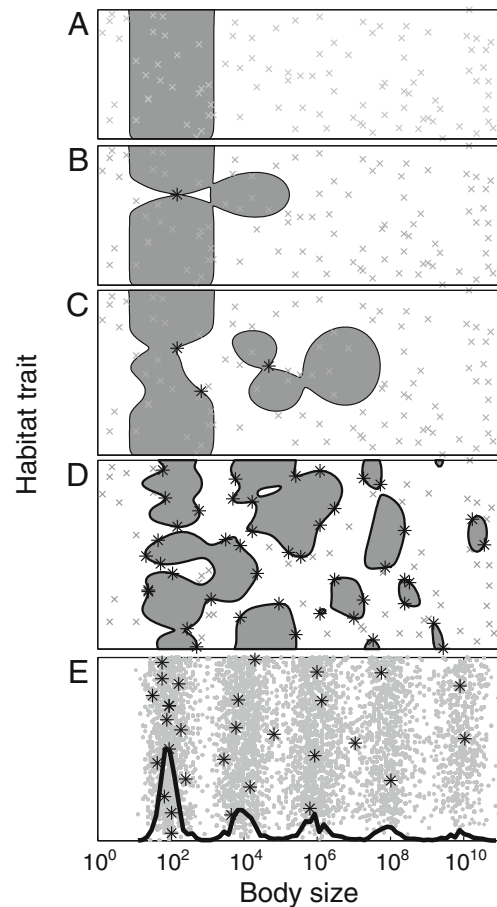
To analyze community-level properties of the size-spectrum exponent, maximum trophic level, and resistance to alien invaders, we collected the final communities emerging from the four discrete species pools, usually reached within 800 successful invasion attempts. In the cases where the assembly ends on a cyclic endstate (Morton and Law 1997), which occurs occasionally for species pools of size 200, but always for the continuous species pool (Fig. 3), we collect all realized communities after 1,000 successful invasions and use their averaged community-level properties. Results from numerical simulations are compared to the results from the analytic predictions.

The size-spectrum exponent is estimated using the generalized cumulative distribution function (CDF) (Reuman et al. 2008). In ecological networks where species richness is low and/or total population abundance is dominated by few species, the generalized CDF method is more appropriate than other methods such as the bin-based approach, the CDF method, and the maximum likelihood estimation (Reuman et al. 2008). When assembling communities from the continuous species pool, we found that the bin approach produces much less bias than the general CDF method. This is because species are usually aggregated at different trophic levels (Fig. 4e), which naturally partitions species into several nonempty bins with roughly equal logarithmic bin width in the size direction. For the simulations with the continuous species pool, we therefore employ the bin approach to estimate the size-spectrum exponent.

The maximum trophic level is defined as the  $\beta$ -based logarithmic value of the size of the largest species in the system, i.e., maximum trophic level ( $MTL = \log_{\beta}(\max\{w_i\})$ ). The resistance of the community to invasions by alien species that do not belong to the species pool is calculated as the size of the area with positive invasion fitness once the community is assembled (Fig. 4d).



**Fig. 3** Number of species in assembled communities as a function of successful invasions from the continuous species pool. Communities are collected after 1,000 successful invasions (dashed line) for calculating community-level metrics



**Fig. 4** Assembly of a model community from a finite pool of 100 species (light gray crosses) (a–d) and from the continuous species pool (light gray dots represent previously successful invaders) (e). a Fitness landscape of the pristine environment showing areas where the invasion fitness is positive (gray). After each successful invasion (black stars), the fitness landscapes changes such that successful invaders sit on the boundaries of the gray islands where fitness is zero (b–d). d shows the final un-invadable endstate where no species in the species pool have trait values in the gray areas. In the final assembled community, 45 species coexist. Panel e shows the final state from the community assembly based on the continuous species pool. The distribution of previous successful invaders (gray dots and solid line) shows how species are grouped along the body size axis in integer multiples of the predator–prey mass ratio from the resource. The habitat trait ranges from –25 to 25 in each panel

## Results

The characterization of species by traits makes it possible to visualize the process of the food web assembly using the concept of invasion fitness (Fig. 4). In the pristine environment, the basal resource creates a positive fitness landscape where species with a size of  $w \sim \beta$  are able to colonize (Fig. 4a). After the first successful invasion, the fitness landscape is reshaped, and a new area of positive fitness values is opened that can be invaded by larger predators (Fig. 4b). This process continues (Fig. 4c) until none of the species in

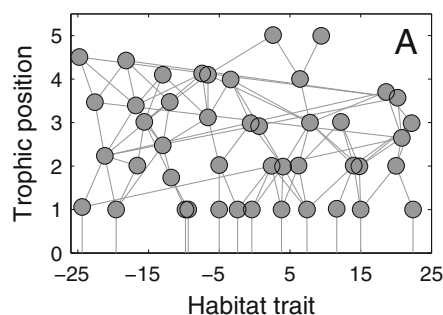
the species pool are able to invade the community, leading to an un-invadable endstate (Fig. 4d). The fitness landscape shows that there are still possibilities for species that are not part of the species pool (alien species) to invade, as there are islands with positive invasion fitness.

When assembly is performed from the continuous species pool, a closed endstate is unreachable because of frequent intermittent extinction avalanches (Fig. 3). However, a pattern of organization of the species in distinct trophic levels emerges (Fig. 4e). The emergence of this pattern may also be glimpsed from the pool with 100 species (Fig. 4d). It is this pattern that inspired to the ansatz (10) used in Sections “Trophic chain solution” and “Resistance to invasions” for the trophic chain solution and to find an ESS for the body size trait.

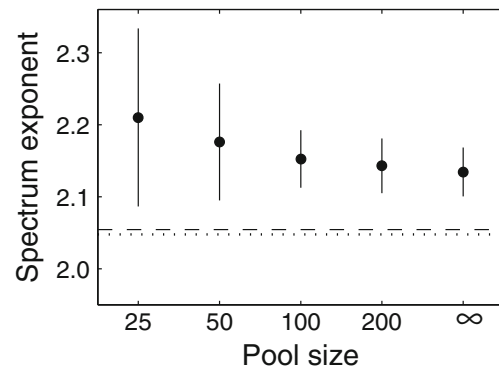
An example of the trophic structure and biomass size spectrum as a function of body size is presented in Fig. 5. The trophic pattern shows that up to five trophic levels were developed in the endstate. The distribution of individual abundance over size reveals that the size-spectrum pattern is well approximated by a power law with an exponent  $\lambda = 2.14$ . This exponent is slightly larger than the predicted values from the size-spectrum solution (9) and the trophic chain solution (12), where intrinsic losses and habitat trait are ignored.

As the pool size increases, both the average slope and the variance of the slope decrease (Fig. 6), and the size-spectrum exponent converges towards a value of 2.13 that is greater than that estimated from the size-spectrum and trophic chain solutions. The large variation in small pools is due to many small webs with a sparse species distribution in the mass-habitat trait space.

The maximum trophic level that an assembled community can reach varies markedly within small species pools (less than 50 species) but insignificantly within large species



**Fig. 5** Trophic structure (a) and biomass size-spectrum (b) of the assembled community in Fig. 4d (pool size, 100). Trophic level is fractional and calculated as the average trophic level of the prey of the focal species plus 1 (Odum and Heald 1975; Levine 1980). Two species (nodes) are connected from prey (low) to predator (high) if the prey makes a contribution greater than 5 % to the total diet of the consumer. In panel b, the solid line indicates fitted individual biomass size spectrum with a slope of  $-0.14$ , which corresponds to a density



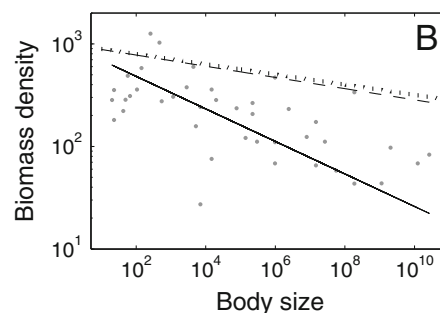
**Fig. 6** Mean values (solid circles) and standard deviations (vertical lines) of the size-spectrum exponent as a function of the species pool size. Analytic solution from the size-spectrum and trophic chain solutions are shown with dashed and dotted lines. The result from the continuous species pool is denoted by an infinity sign

pools (Fig. 7a). The general pattern is that the larger the pool size, the higher the probability of a high MTL. The resource productivity plays a role by setting the maximum possible MTL (Fig. 7b) in agreement with the analytic prediction (12).

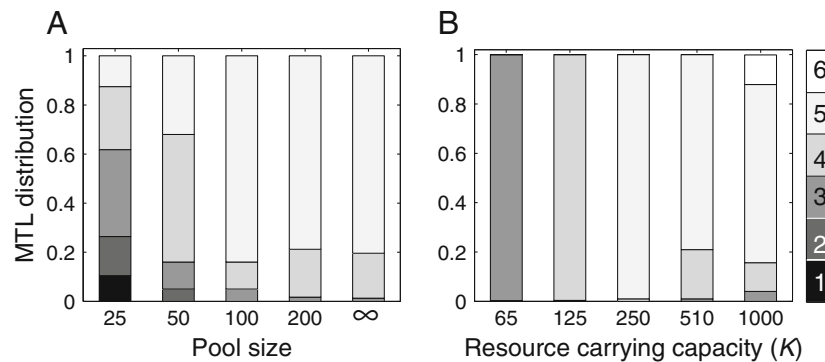
The invasion resistance to alien species that do not belong to the species pool displays remarkably small variation across species pool size (Fig. 8).

## Discussion

We have developed a trait-based food web model where interactions between species are characterized solely by the traits of the involved species: body size and habitat trait. Analytic and semi-analytic solutions of the model have been developed by reducing the model to a purely size-based



size-spectrum exponent of 2.14. The theoretical predictions (that ignore intrinsic losses and the habitat trait) from the size-spectrum solution (9) and the trophic chain solution (11) are shown with dashed and dotted lines. Gray dots denote species biomass. Note that the individual biomass spectrum almost, but not quite, follows the species biomass distribution (gray dots). There is a slight deviation between the two due to the decrease in species diversity with size



**Fig. 7** The impacts of species pool size (a) and the resource productivity (b) on the maximum trophic level. In both panels, the proportion of communities with the various MTL is shown in the vertical direction, and each bin represents the fractional trophic value in the range

between two integer values. In panel a, the continuous species pool is indicated by an *infinity sign*. In panel b, communities were assembled from the continuous species pool with resource carrying capacity ( $K$ ). The predicted MTL is shown on the *color bar*

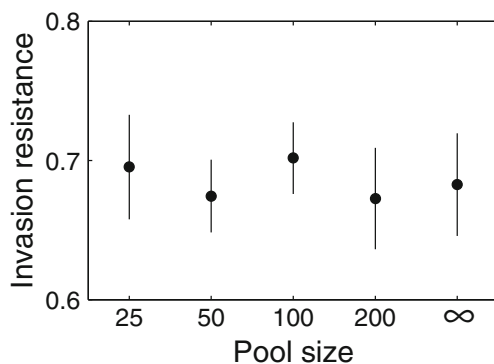
model. Simulations of the full food web models were compared to the analytic predictions. The general conclusions are that the analytic solutions to the size-based models are good predictors of the size-spectrum exponent and the maximum trophic level, provided that the species diversity in the food web is sufficiently high. The size-based model was predicted to be un-invadable because there existed an ESS solution. This prediction was proven not to hold in the food web model.

#### Size-spectrum exponent

We derived two almost identical analytic solutions to the size-spectrum exponent. The difference between the solutions stems from the difference in approximation: one solution assumed a continuous and infinite size spectrum, while the other assumed a binning in trophic levels. Our food web model ignores ontogenetic growth, but theoretic arguments that takes ontogenetic growth into consideration

lead to very similar predictions of size-spectrum exponent (Benoît and Rochet 2004; Datta et al. 2011). A common characteristic of these explanations is that they are derived by considering the balance between growth of predators and the mortality they inflict on their prey. There exists another class of theoretical explanations for the size-spectrum exponent derived by employing the “metabolic” assumption that the consumption rate is  $\propto m^{3/4}$  (see review by Borgmann (1987)). The metabolic assumption leads to two predictions: Kerr (1974) and Sheldon et al. (1977) described a community divided into discrete trophic levels, as in our trophic chain solution, and found a scaling exponent  $\lambda \approx n + 1 - \ln(\epsilon_T)/\ln(\beta)$ , where  $\epsilon_T$  is the trophic efficiency. In contrast, Andersen and Beyer (2006) considered a continuous spectrum and found an exponent  $2 + n - q$ . Thus, the metabolic argument apparently leads to conflicting results. These two results can be united by relating the trophic efficiency  $\epsilon_T$  to  $q$ ,  $\beta$  and the metabolic exponent  $3/4$  (Borgmann 1987; Andersen et al. 2009). The two classes of theoretical explanations (growth–mortality balance and metabolic) can be combined by requiring that the predicted consumption from the growth–mortality type of explanations corresponds to the metabolic assumption. In our explanation, that would require  $q = 1$ , which is in correspondence with observations (Andersen and Beyer 2006). Rossberg (2012) created a general theory that yielded both the “growth–mortality” and the “metabolic” solutions, termed the “oligotrophic” and “eutrophic” regimes. The important conclusion is that even though there are apparently conflicting explanations for the exponent of the size spectrum, their numeric predictions are very similar and they can be united theoretically.

The food web simulations yielded communities where the size distribution roughly followed a power law in accordance with theory, and the exponent of the power law converged to a constant value with increased pool size. The



**Fig. 8** Mean values (black dots) and standard deviations (vertical lines) of invasion resistance as a function of the species pool size. Invasion resistance is measured as the ratio of the areas with negative fitness (white areas in Fig. 4) to the total area of the trait space  $\Omega$



size-spectrum exponent has been shown to be robust also to changes in other food web parameters than species pool size (Gomez-Canchong et al. 2012). The exponents from the simulated food webs were slightly, but significantly, larger (steeper spectrum) than the predicted exponents. We propose two candidate mechanisms for this discrepancy. One is the ignored intrinsic losses. Intrinsic losses are most strongly felt in the highest trophic levels, which lead to slightly smaller biomasses than predicted by the theory, which again would lead to a slightly higher fitted exponent than predicted. A second mechanism is the decrease in diversity with size and trophic level (see Fig. 5b). A smaller diversity makes it harder to construct the last trophic level which again leads to the fitted exponent being slightly larger than predicted.

### Maximum trophic level

When intrinsic losses are taken into account in the size-spectrum and trophic chain solutions, the scaling solution disappears, and the spectrum diverges towards zero at a maximally possible trophic level. The maximum trophic level from the food web simulations is never higher than the predicted upper limit, but often smaller. This result can be used to qualify the debate on whether the maximum trophic level is limited by energetic or structural constraints (Post 2002). The analytic prediction of an upper limit to the maximum trophic level is in agreement with the general energy limitation hypothesis (Lindeman 1942) which posits that the maximum trophic level is constrained by energy flow through the trophic levels determined by the resource availability and individual losses through efficiency and metabolic costs (Oksanen et al. 1981; Yodzis 1984). The limit set by the energetic constraint is an upper maximum trophic level that may not be realizable due to structural constraints: a species-poor food web might be unable to construct a food chain long enough to realize the energetically possible maximum trophic level, as intermediate species required by large trophic level species may be absent. The topology of the food web thus introduces a structural constraint: the smaller the pool size, the more heterogeneous the pool structure, and the harder it is to construct a long food chain within the energetic limits (Fig. 7). As pool size increases, the distribution of species in trait space becomes more homogeneous, and the effects of structural constraints are gradually lost. Taken together, the model illustrates that maximum trophic level is not determined solely by energetic or structural constraints. Both constraints act in concert with one of them taking a dominant role depending on diversity and dimensionality of the trait space which determines predator–prey interactions. In this manner, the maximum trophic level in a particular system will appear to be limited by just one constraint.

### Community stability

The ultimate stable community is one that has reached a global ESS. If this state exists, no mutants of existing species or species from outside the community will be able to invade. We found an ESS for the size-based model where species are organized in a trophic chain with a body size spacing approximately equal to the preferred predator–prey mass ratio. Assembled communities from the full food web model, however, did not reach an ESS since they can always be invaded by alien species that do not belong to the species pool due to the existence of islands of positive invasion fitness in trait space (gray areas in Fig. 4). It should be noted that the resistance to alien species is different from the resistance of invasion from nonalien species, i.e., species which do come from the species pool. For that case, Post and Pimm (1983) determined invasion probability, and Law and Morton (1996) found the invasion resistance to be an increasing function of pool size, meaning that species-rich systems are less vulnerable to species invasions from the species pool (i.e., surrounding communities). In contrast, the resistance to alien invasions (i.e., species from outside the community) turned out to be independent of species pool size (Fig. 8). The differences between the analytic results (invasion impossible) and the simulation results (invasion is always possible) suggest that increasing the dimensionality of trait space might alter the nature of the attractor contained in low-dimensional trait space: a low-dimensional trait space (in this case, just size) leads to a community with an ESS, while the addition of an extra trait dimension removes the ESS. In other words, increasing trait diversity decreases the stability of the community towards invasions.

### Model architecture

The construction of the interaction matrix through a specification of traits makes it possible to (1) create food webs that naturally respect the trade-offs between the traits in the model; (2) to use the concept of fitness from evolutionary ecology to visualize the assembly process and characterize the endstate; (3) to construct a measure of density of species within the trait space; and (4) to determine the stability of the assembled food web to invasions from alien species, i.e., species not belonging to the species pool. The traits chosen here are body size and a habitat trait. The habitat trait is inspired by the classic niche model for species competition (MacArthur and Levins 1967), which was also used in a simpler form to examine the relation between predation and competition by Chesson and Kuang (2008). The home range of the habitat trait,  $\sigma_x$ , is increasing with size, since larger individuals may roam over a larger area than smaller individuals. If the home range did not increase with body size, the assembled communities would be weakly

coupled parallel food chains. The increase of  $\sigma_x$  couples the food web across the habitat trait in a similar manner to how large species combine different basal energy pathways in an ecosystem (Rooney et al. 2006). Therefore, even though we have made the  $x$ -trait inspired by the spatial extent of a habitat, it may also represent more abstract notions of food selection choice.

The most important aspect of the trait-based formulation of the food web model is that it lends itself to generalization to other traits where appropriate trade-offs can be constructed. In this study, we ignore ontogenetic growth. This is a strong assumption for marine ecosystems, but the methodology can be extended to include this (Andersen and Beyer 2006; Giacomini et al. 2009; Hartvig et al. 2011; Rossberg 2012; Maury and Poggiale 2013). Reduction of the trait space can be achieved formally (Rossberg et al. 2010). Traits can be roughly divided into three categories: (1) trophic traits that determine the interaction matrix. Examples are the way size and habitat are used here, or investments into defense or attack traits (Rossberg et al. 2010); (2) physiological traits, like activity which has a trade-off between the benefit of higher attack rate  $\gamma$  at a cost of higher metabolic losses  $k$ ; and (3) environmental traits which specify the specialization to an external environment, like the optimal temperature.

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## Appendix: Assembly algorithm

The assembly algorithm is a replicate of that by Hartvig (2011), but presented below for completeness.

Model communities are formed using sequential assembly by introducing one new species at a time in low density ( $10^{-10}$  g/vol) (Post and Pimm 1983; Drake 1990; Law 1999) from a species pool. If invasion fitness is positive, then the system is stimulated till it reaches steady state which can be a fixed point, periodic, or even chaotic, detected using heuristic algorithm. Fitness is measured using the per capita population growth rate (i.e., the evaluation of the right-hand side of Eq. (5)). A species is assumed to be in steady state if its absolute fitness is smaller than  $1/1,000$  year $^{-1}$ . During simulation, species are removed if they are going to extinction, defined as (1) population biomass falls below the extinction threshold  $10^{-20}$  g/vol; (2) fitness is smaller than  $-1/250$  year $^{-1}$ , while the biomass is below  $10^{-5}$  g/vol; or (3) fitness is smaller than  $-1/1,000$  year $^{-1}$ , while the biomass is below  $10^{-10}$  g/vol. The assembly proceeds to a

new invader if the introduced invader has negative invasion fitness, or if the augmented community (resident community plus invader) has reached equilibrium state.

In addition, the continuous species pool is discretized evenly in the  $x$  direction with a step size  $\delta x = 0.2$  and logarithmically evenly in the  $w$  direction with a step size  $\delta \log w = 0.1$ . Results appear independent of the choice of discretization.

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