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Biodiversity and Ecosystem Functioning in Evolving Food Webs

K.T. Allhoff *, B. Drossel, †

February 9, 2016

Abstract

We use computer simulations in order to study the interplay between biodiversity and ecosystem functioning (BEF) both during the formation and during the ongoing evolution of large food webs. A species in our model is characterized by its own body mass, its preferred prey body mass, and the width of its potential prey body mass spectrum. On an ecological time scale, population dynamics determines which species are viable and which ones go extinct. On an evolutionary time scale, new species emerge as modifications of existing ones. The network structure thus emerges and evolves in a self-organized manner. We analyse the relation between the functional diversity and five community level measures of ecosystem functioning. These are the metabolic loss of the predator community, the total biomasses of the basal and the predator community and the consumption rates on the basal community and within the predator community. Clear BEF relations are observed during the initial build-up of the networks or when parameters are varied, causing bottom-up or top-down effects. However, ecosystem functioning measures fluctuate only very little during long-term evolution under constant environmental conditions, despite changes in the functional diversity. This result supports the hypothesis that trophic cascades are weaker in more complex food webs.

Keywords: Food web evolution models, Ecosystem services, Global change, Evolutionary emergence, Community assembly, Bioenergetics approach

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Introduction

During the last decades, the relation between biodiversity and ecosystem functioning (BEF) has been intensely investigated (for reviews see [1, 2, 3, 4, 5]). These BEF studies are motivated by the need to understand the mechanisms that mediate the functioning of diverse ecosystems and to predict the consequences of rapid changes in biodiversity due to current extinction events [6, 7]. Duffy et al. emphasized the importance of taking into account processes that occur both within and among trophic levels, because trophic processes between levels affect ecosystem functioning as much as facilitation and competition within trophic levels [2]. The authors point out that many earlier BEF studies focussed instead on rather simple systems, as for example on a single trophic level of randomly assembled species, but not on complex multi-trophic communities with a co-evolutionary history. While these studies provided first insights into BEF relations, they are far from providing a complete picture. An overview of new approaches dealing with multi-trophic and non-equilibrium biodiversity, with larger spatial or temporal scales and with different types of ecosystems can be found in the introductory chapter of this theme issue [8].

Here, we follow the suggestion of Loreau that evolutionary food web models provide an excellent tool to study BEF related questions [9]. Such models include evolutionary changes in species composition in addition to population dynamics [10, 11, 12]. The network structure is not static, but evolves in a co-evolutionary manner via the dynamical interplay between population dynamics and the introduction of new species or morphs. It is thus possible to investigate the time dependent behaviour of the functioning of large food webs, both during the initial build-up of a network and during the ongoing species turnover on larger time scales. Such a long-term perspective may lead to surprises that significantly differ from short-term experiments, as shown by Reich et al. [13].

Well-known examples of evolutionary food web models are the webworld model [14, 15] and the matching model [16, 17]. An individual-based approach was recently taken by Takahashi et al. [18], who found abrupt community transitions and cyclic evolutionary dynamics in complex food webs. These three models use abstract trait vectors to characterize the ecological niche of a species. By contrast, the model by Allhoff et al. [19] used here is based on body masses. It is related to the model by Loeuille and Loreau [20], and its later modifications [21, 22, 23]. The species in our model differ concerning their body masses (as in [20]), but also concerning their preferred prey body masses and the widths of their potential prey body mass spectrum. This reflects different possible feeding strategies and results in more realistic and less static food web structures [19].

We investigate the relationship between the functional diversity of the evolving networks and five

community level measures of ecosystem functioning. These are the metabolic loss of the predator community, the total biomasses of the basal and the predator community and the consumption rates on the basal community and within the predator community. Theoretical [24, 25, 26] and empirical [27] food webs studies suggest a large variety of different BEF relations, due to bottom-up or top-down effects. Other studies suggest a saturation of BEF relations due to the dampening of trophic cascades in complex and diverse communities [28, 29, 30, 31, 32, 33]. At the beginning of our simulations, when the networks are still relatively small, each species addition or extinction causes major changes in the network structure and hence in the ability of the consumer guild to exploit the resource. We therefore expect all measures of ecosystem functioning (except for resource biomass) to be positively correlated with biodiversity. However, we expect the ecosystem functioning to saturate during the ongoing fluctuations in the network structure long after this initial build-up, when a complex multi-trophic community has formed, where the function performed by a species that goes extinct can be retained by others.

We also analyse the impact of two model parameters on the BEF relations, which are both well-known to respond to prominent drivers of global change: The respiration and mortality rate increases due to an increased temperature in a climate change scenario [34, 35] and the carrying capacity may either increase due to nutrient enrichment or decrease with an increasing temperature [36]. Both parameters are assumed to have a significant impact on the resulting network structures. We expect that an increased carrying capacity leads to bottom-up effects that enable the emergence of a more diverse consumer community, whereas an increased respiration and mortality rate leads to biomass loss in the consumer guild and hence to a release of the resource due to a decreased top-down control.

Model

The model includes fast ecological processes (population dynamics) which determine for a given species composition the population sizes, the biomass flows, and whether a species is viable in the environment created by the other species. Additionally, slow evolutionary processes (speciation or invasion events) add new species to the system that are similar to existing ones, leading to an ever changing network structure. A species i is characterised by its body mass, m_i, the centre of its feeding range, f_i, and the width of its feeding range, s_i. These traits determine the feeding interactions in the community and thereby the population dynamics, as illustrated in Fig. 1.

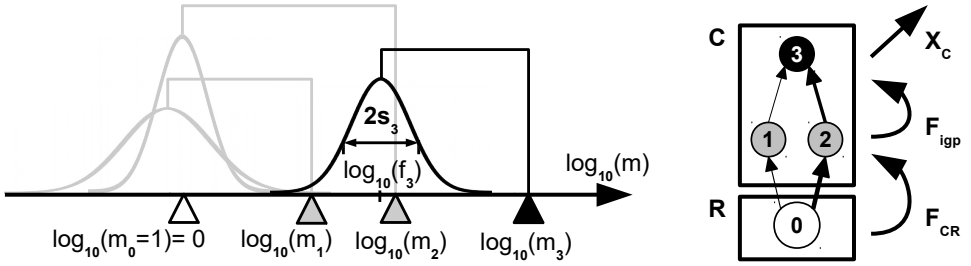


Figure 1: Model illustration using 4 species. Species 3 (black triangle) is characterised by its body mass m_3, the centre of its feeding range f_3, and the width of its feeding range s_3. The Gaussian function (black curve) describes its attack rate kernel N_{3j} on potential prey species. Here, species 3 feeds on species 2 and 1 (grey triangles) with a high resp. low attack rate. Species 1 and 2 are consumers of the external resource, represented as species 0 with a body mass $m_0 = 1$ (white triangle). Also illustrated is the corresponding network graph with the 5 measures of ecosystem functioning. After [19].

Population dynamics

The population dynamics follows the multi-species generalisation of the bioenergetics approach by Yodzis and Innes [37, 38]. The rates of change of the biomass densities B_i of the populations are given by

$$\dot{B}_0 = G_0 B_0 - \sum_{j=\text{consumers}} g_{j0} B_j \tag{1}$$

for the external resource (species 0 with body mass $m_0 = 1$) and by

$$\dot{B}_i = \sum_{j=\text{resources}} e_j g_{ij} B_i - \sum_{j=\text{consumers}} g_{ji} B_j \; - \; x_i B_i \tag{2}$$

for consumer species. The coefficient $G_0 = r(1 - B_0/K)$ describes the logistic growth of the external resource, with a growth rate r and a carrying capacity K. The time scale of the system is defined by setting $r = 1$. The efficiency e_j is prey dependent and equals either 0.45 for feeding on the resource or 0.85 for preying on other consumer species. g_{ij} is the mass-specific rate with which species i consumes species j, and $x_i = x_0 \cdot m_i^{-0.25}$ is a combined, mass-specific rate that describes i's losses due to respiration and mortality. The carrying capacity K (in the same units as biomass density) and the constant of the respiration and mortality rate x_0 (in units of $\frac{kg^{0.25}}{yr}$) are model parameters that are varied in this study.

The mass-specific consumption rate is described via a Beddington-deAngelis functional response [39],

$$g_{ij} = \frac{1}{m_i} \frac{a_{ij} B_j}{1 + \sum_{k=\text{res.}} h_i a_{ik} B_k + \sum_{l=\text{comp.}} c_{il} B_l} \,. \tag{3}$$

The per capita rate of successful attacks of predator i on prey j, a_{ij}, is based on a Gaussian feeding kernel N_{ij},

$$a_{ij} = m_i^{0.75} \cdot N_{ij} \tag{4}$$

$$= m_i^{0.75} \cdot \frac{1}{s_i\sqrt{2\pi}} \cdot \exp\left[-\frac{(\log_{10} f_i - \log_{10} m_j)^2}{2s_i^2}\right] . \tag{5}$$

The parameter $h_i = 0.398 \cdot m_i^{-0.75}$ in eq. (3) is the handling time of species i for one unit of prey biomass, and c_{il} quantifies interference competition among predators i and l. It depends on their similarity, as measured by the overlap $I_{il} = \int N_{ij} \cdot N_{lj} d(\log_{10} m_j)$ of their feeding kernels, via

$$c_{il} = c_{\text{food}} \cdot \frac{I_{il}}{I_{ii}} \quad \text{for} \quad i \neq l \, . \tag{6}$$

We assume that interference competition is higher within a species than between different species, e.g. due to territorial or mating behaviour. We therefore introduce an intra-specific competition parameter c_{intra} and set $c_{ii} = c_{\text{food}} + c_{\text{intra}}$. The influence of these competition parameters has been discussed in a previous article [19]. Here we use fixed values: $c_{\text{food}} = 0.8$ and $c_{\text{intra}} = 0.6$.

Speciation events

Each simulation starts with a single ancestor species with body mass $m_1 = 100$ and optimal feeding parameters $f_1 = 1$ and $s_1 = 1$. The initial biomass densities are $B_0 = K = 100$ for the resource and $B_1 = m_1 \cdot \epsilon = 2 \cdot 10^{-2}$ for the ancestor species. The parameter $\epsilon = 2 \cdot 10^{-4}$ is the extinction threshold, i.e., the minimum population density required to survive.

A speciation event occurs every 10^4 time units. Then, each species with a population size below the extinction threshold is removed from the system and one of the remaining species (but not the external resource) is chosen randomly as parent species i for a "mutant" species j. The logarithm of the mutant's body mass, $\log_{10}(m_j)$, is chosen randomly from the interval $[\log_{10}(0.5m_i), \log_{10}(2m_i)]$, meaning that the body masses of parent and mutant species differ at most by a factor of 2. The mutant's initial biomass density is set to $B_j = m_j \cdot \epsilon$ and is taken from the parent species. The logarithm of the mutant's feeding centre, $\log_{10} f_j$, is drawn randomly from the interval $[(\log_{10}(m_j) - 3.5), (\log_{10}(m_j) - 0.5)]$, meaning that the preferred prey body mass is 3 to 1000 times smaller than the consumer's body mass, consistent with the results from Brose et al. [40]. The width of the feeding range, s_j, is drawn randomly from the interval $[0.5, 1.5]$. Several variations of these rules, most of them with only minor impacts on the resulting networks structures,

were discussed in a previous article [19].

Methods

Two species with similar feeding traits (e.g. species 1 and 2 in Fig. 1) have a similar function in the food web and are potentially redundant: One of them can retain their function when the other one goes extinct. Large extinction events may thus change the system's diversity (measured as the number of species S) with little impact on its functioning. To account for this, we use the following measure of functional diversity (taken from the work of Schneider et al. [41]):

$$FD = \int_{-\infty}^{+\infty} \max\left(N_{1j}, N_{2j}, ..., N_{Sj},\right)\ d\left(log_{10}(m_j)\right). \tag{7}$$

It represents the area below the envelope of all Gaussian feeding kernels N_{ij}, with $1 \leq i \leq S$. Note that the area below each feeding kernel is normalized to 1, so that two species with little (much) overlap in their feeding kernels have a functional diversity close to 2 (1). Consequently, the little network illustrated in Fig. 1 has a functional diversity slightly above 2. FD is thus a measure of complementarity in the feeding preferences and roughly corresponds to the number of trophic levels. Alternative definitions of functional diversities can be found in [42]. A measure of link overlap that additionally includes the overlap in predator links and that is applicable to discrete trophic layers was introduced by Poisot et al. [26].

We analyse the relationship between FD and 5 measures of ecosystem functioning:

1. The total biomass density of all consumer species $C = \sum_{i=1}^{S} B_i$
2. The total biomass density of the resource species $R = B_0$
3. The total energetic loss of the system due to the respiration and mortality of the consumers $X_C = \sum_{i=1}^{S} x_i \cdot B_i$
4. The total consumption rate on the resource $F_{CR} = \sum_{i=1}^{S} 0.45\ g_{i0} B_i$
5. The intra-guild consumption rate $F_{igp} = \sum_{i=1}^{S} \left(\sum_{j=1}^{S} 0.85\ g_{ij} B_i \right)$

We analyse the development of these measures during the initial build-up of the networks and during the ongoing species turnover later on. For each value of the respiration and mortality rate, $x_0 = 0.3, 0.5, 0.7, 0.9$, we performed 60 simulations (with a fixed value of the carrying capacity $K = 100$). Simulations with identical parameter values differ concerning the set of random numbers

and concerning their runtime ($T_{end} = 5 \cdot 10^8, 1 \cdot 10^8, 2.5 \cdot 10^7, 1 \cdot 10^7, 5 \cdot 10^6, 1 \cdot 1 \cdot 10^6$). For comparison, the generation time of the initial ancestor species with body size $m_1 = 100$ is of the order of $\frac{1}{x_1} = \frac{100^{0.25}}{0.314} \approx 10$ time units. The measures of ecosystem functioning are evaluated after every single, 10th or 50th mutation event, dependent on the runtime. In addition to these 240 simulations, we performed another 40 simulations with a runtime of $T_{end} = 5 \cdot 10^8$ and a fixed value of $x_0 = 0.3$, but with different values of the carrying capacity, $K = 50, 100, 150, 200$. K and x_0 both respond to prominent drivers of global change, as highlighted in the introduction. Their variation thus reflects different environmental conditions.

Results

Time series

Examples of the initial build-up (columns 2 and 4) and of the long-term behaviour (columns 1 and 3) of the evolving networks are shown in Fig. 2. After a short period of strong diversification, we observe a fairly layer-like structure. With a low respiration and mortality rate, $x_0 = 0.3$, we obtain networks with approximately three body mass clusters around 1, 2.5, and 4. Note that the species in one body mass cluster can differ in their feeding preferences and hence belong to different trophic levels. Higher respiration and mortality rates represent an increased biomass loss so that the emergence of higher level species is hampered. With $x_0 = 0.9$, only two body mass clusters can emerge. The ongoing species turnover is due to newly emerging mutants that are better adapted to available prey species or experience less predation pressure, and therefore displace other species with similar feeding preferences.

Comparing the two long-term simulations, we find that both parameter sets lead to food webs with a similar number of species. Their network structure and the measures of ecosystem functioning however differ significantly. This confirms the expectation that functional diversity is a better predictor of ecosystem functioning than the pure number of species. For comparison, the same analysis as in the following, but with the species number instead of the functional diversity, is presented in the supplementary material.

The functional diversity (Fig. 2, line 4) increases at the beginning of the simulations. Later, it fluctuates around a constant value in case of $x_0 = 0.3$ or it shows a step-like behaviour in case of $x_0 = 0.9$. This step-like behaviour represents a changing number of trophic levels: The species with body masses around 3 occurring in the middle of the simulation run feed on the external resource,

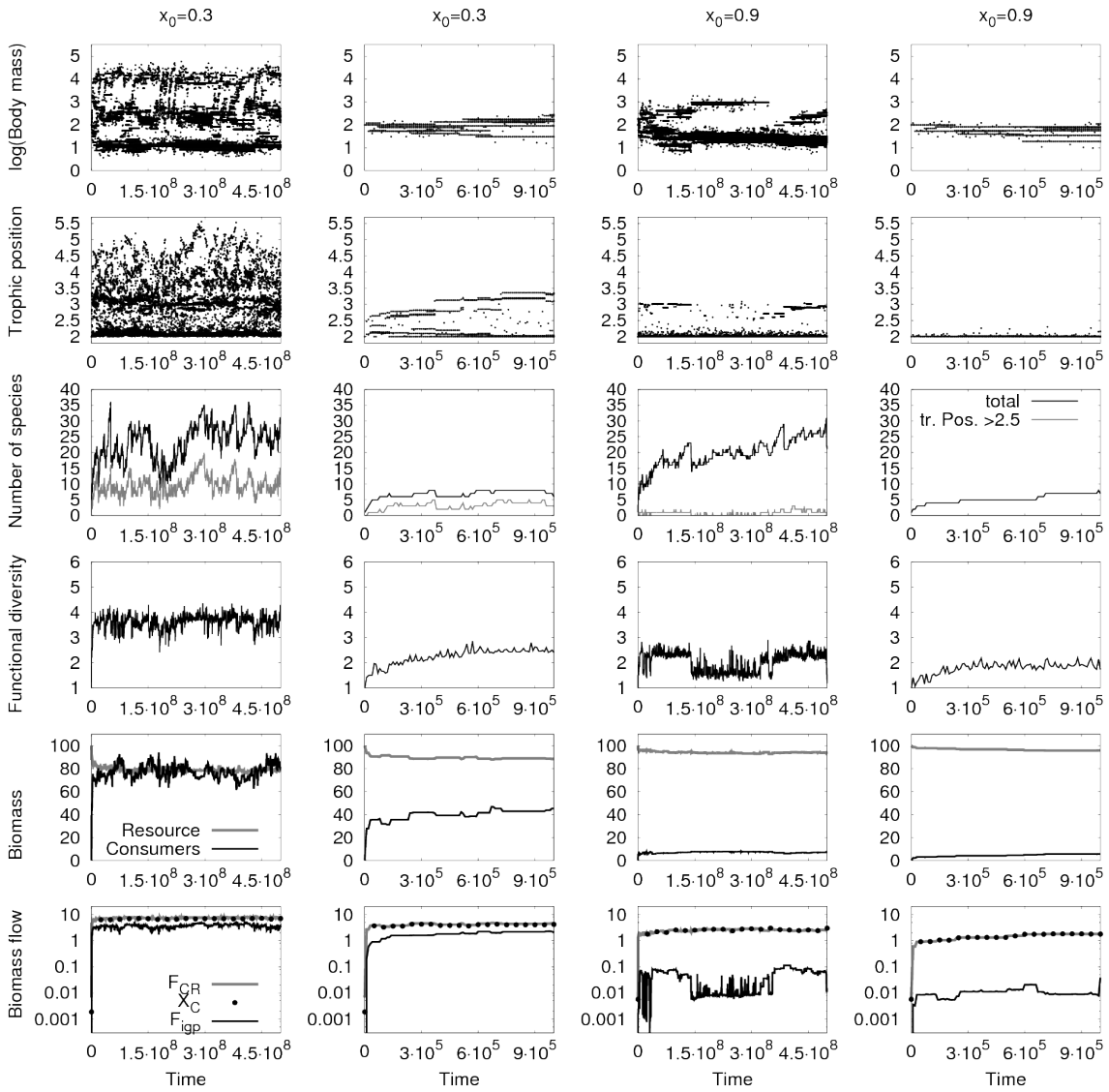


Figure 2: Four exemplary simulation runs with different run times and different values of the respiration and mortality rate x_0. Shown is the evolution of body masses and flow-based trophic positions and the time series of the measures that are defined in the Methods section. A detailed analysis of various network properties can be found in [19].

so that both body mass clusters form a single trophic level. The two body mass clusters that emerge at the end of the simulation represent two distinct trophic layers, as also reflected in the increased values of functional diversity and intra-guild predation.

In general, the measures of ecosystem functioning (lines 5 and 6) remain surprisingly stable after the initial build-up, despite the ongoing changes in the trophic structure. Note that at population equilibria we find

$$0 = \sum \dot{B}_i = F_{CR} - X_C - \frac{1 - e_j}{e_j} F_{igp}. \tag{8}$$

The last term (describing efficiency losses due to intra-guild-predation) is by far the smallest, so

that the predation on the resource F_{CR} and the total metabolic loss X_C are of the same order of magnitude.

BEF during the initial build-up of the networks

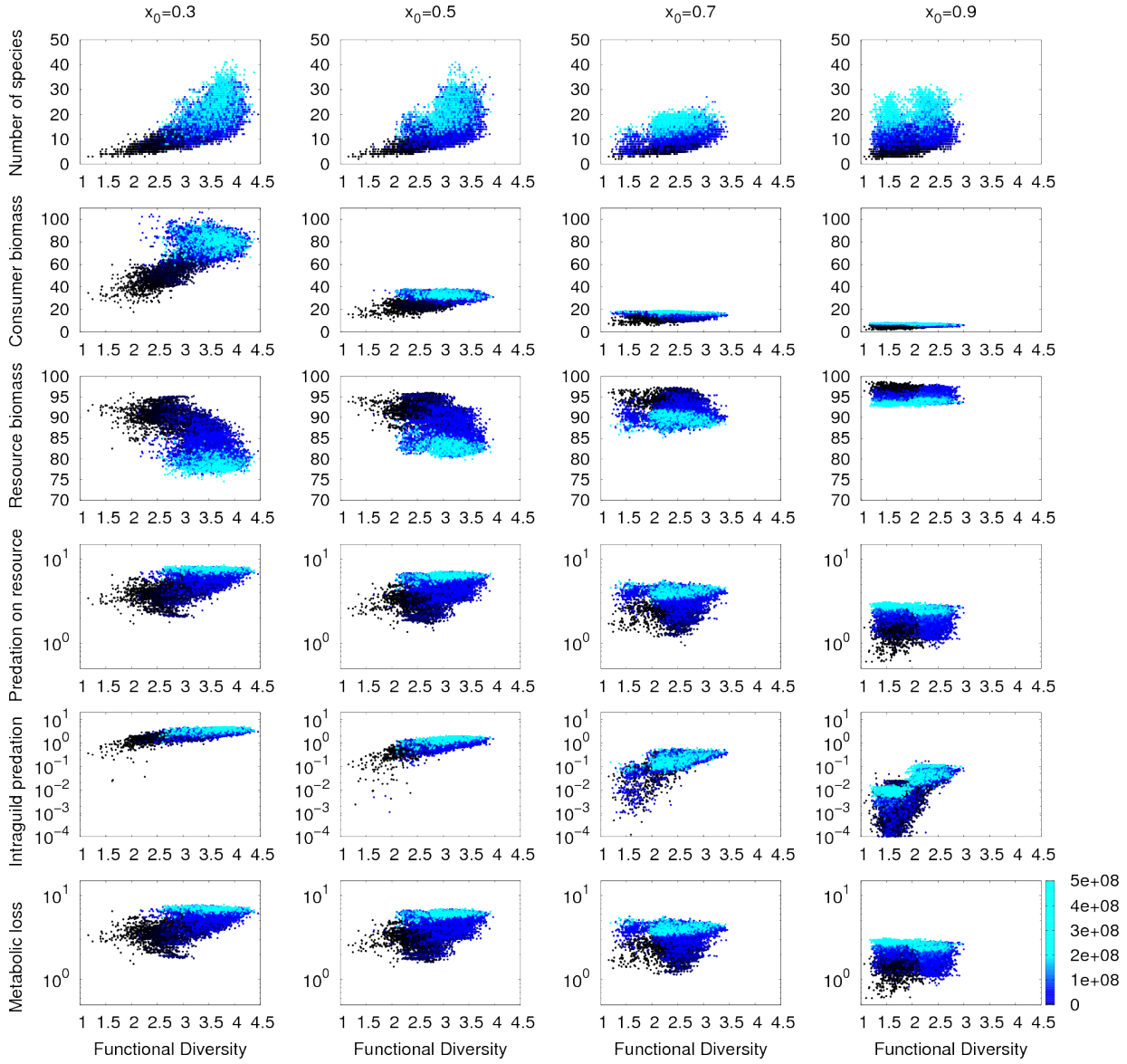


Figure 3: The relationship between biodiversity and ecosystem functioning during the evolutionary history of the food webs with different values of the respiration and mortality rate x_0. The carrying capacity is set to $K = 100$. Different colours indicate different times: Black (in the background) represents data from networks shortly after the simulation start, whereas light blue (in the foreground) represents data from fully developed networks after $1.5 \cdot 10^8$ time units.

Fig. 3 shows BEF relations during the evolutionary history of the networks, with early and later stages coded in black or light blue. For a low respiration and mortality rate, ($x_0 = 0.3$, column 1), the number of species and the functional diversity increase during the initial period

of diversification. The more diverse the consumer guild gets, the more biomass is accumulated, which can be observed as an increasing value of the total consumer biomass C. This leads to a decreasing resource biomass R, due to an increased predation pressure F_{CR} on the resource. We also observe an increasing intra-guild predation F_{igp}, due to the emergence of higher trophic levels, and an increasing total metabolic loss X_C. If we focus on the data points long after the initial build-up (in light blue), we find that the measures of ecosystem functioning remain surprisingly stable, even though the functional diversity fluctuates between 2.5 and 4.5, representing networks with different numbers of trophic levels.

The comparison of the different columns reveals the strong impact of the respiration and mortality rate x_0. The data clouds shift to the left with increasing values of x_0, reflecting flatter network structures with fewer trophic levels and hence lower values of the functional diversity. However, all data sets result in networks of similar species numbers, again highlighting the importance of the functional diversity. In the last column, we observe two clusters of data points that reflect the existence or absence of a second trophic level above the resource, as explained in the previous subsection.

The influence of environmental conditions on BEF relations

The different colors in Fig. 4 represent different values of the respiration and mortality rate x_0. In the first panel, we observe again that the resulting networks differ strongly in their functional diversity, but not so much in species number. Looking at the other panels, we observe the same qualitative trends as in Fig. 3 with data from the initial build-up. This is due to a top-down effect: Increasing values of x_0 lead to less biomass flow into higher trophic levels and hence to flatter network structures with lower functional diversities and smaller amounts of consumer biomass and therefore to a reduced predation pressure on the resource.

However, this is not a universal pattern. Fig. 5 shows data that was generated with different values of the carrying capacity K. Here, we observe a bottom-up effect: Higher values of the carrying capacity correspond to more resource biomass and therefore to a larger amount of available energy for the system. This enables the emergence of larger networks (both in terms of number of species and in terms of functional diversity) and explains the increase in the consumer biomass and in the rates of biomass flow. A similar (but weaker) effect can be obtained by increasing the growth rate r of the resource, as shown in the supplementary material.

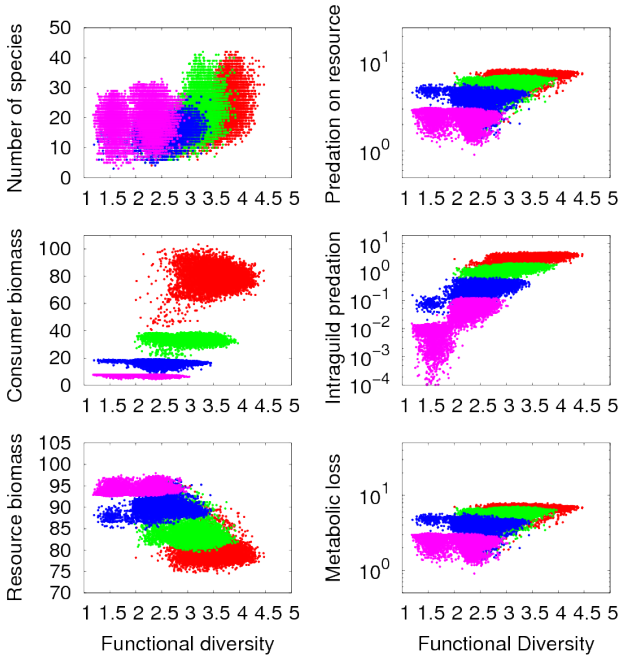


Figure 4: The relationship between biodiversity and ecosystem functioning during the ongoing species turnover after the initial build-up of the emerging food webs. Only those data points that emerged from the simulations with the longest runtime, $t_{\text{end}} = 5 \cdot 10^8$, are shown so that the initial build-up plays only a minor role. The colors represent four different values of the respiration and mortality rate: red (in the background) $x_0 = 0.3$, green $x_0 = 0.5$, blue $x_0 = 0.7$, pink (in the foreground) $x_0 = 0.9$. The carrying capacity is set to $K = 100$.

Discussion

As Loreau highlighted, evolutionary food web models can provide major contributions to the BEF debate [9]. Communities generated with such models emerge from individual-level processes and share a co-evolutionary history, instead of being randomly put together or suffering from random, artificial extinction events. In our study, we analyse BEF relations 1) during the initial build-up of our networks and 2) during ongoing changes in the species composition after that. The former reveals that an increasing functional diversity (which corresponds to an increasing trophic complexity in the consumer guild) correlates with an increasing total consumer biomass, a decreasing resource biomass, and increasing biomass flows into, within and out of the consumer guild (Fig. 3). This can be explained with a top-down argument: The larger the network, the more biomass can be accumulated and the higher is the predation pressure on the resource. A similar pattern has been found in a meta-analysis of experimental studies [43]. The authors show that the average effect of a decreasing species richness is to decrease the abundance or biomass of the focal trophic group, leading to less complete depletion of resources used by that group.

Our results are also consistent with a study by Schneider et al.[41], who investigated the same

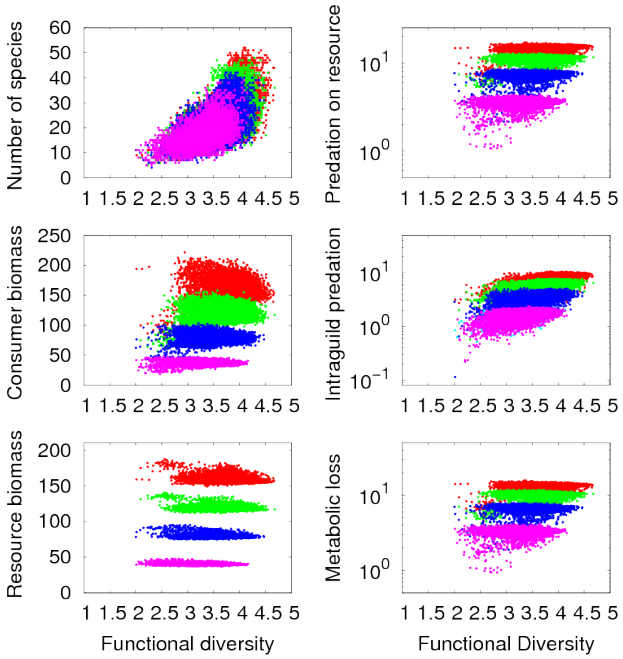


Figure 5: As in Fig 4, but with different values of the carrying capacity: red (in the background) $K = 200$, green $K = 150$, blue $K = 100$, pink (in the foreground) $K = 50$. The respiration and mortality rate is set to $x_0 = 0.3$.

measures of ecosystem functioning in a non-evolving food web model. The authors reject a long-established hypothesis, which suggests the release of the basal community from feeding pressure with growing functional diversity, due to an increased intraguild predation within the consumer community [2, 3, 44, 30]. Schneider et al. showed that such an increase of the functional diversity indeed leads to an increased intraguild predation in the consumer community, but not to an increase of the total biomass of the basal community. A diverse predator community might simultaneously be more exploitative but less efficient than a species-poor community.

However, the described BEF relations are not valid over the whole simulation time. Our measures of ecosystem functioning become almost constant after the initial build-up of the networks, although the functional diversity continues to vary significantly, reflecting ongoing changes in the trophic structure (Fig. 3). A saturation of ecosystem functioning is known from leaf breakdown by stream fungi [45] and from other single trophic layer systems. Saturation was also predicted by the early hypothesis of the redundancy model [46]. It is nevertheless surprising in our model context, since there is theoretical evidence that ecosystem properties greatly depend on the functional biodiversity and in particular on the trophic structure [24, 25, 26]. Also empirical studies suggest diverse BEF relations based on bottom-up or top-down effects in multi-trophic communities. For example, Gamfeldt et al. studied a controlled marine microbial system and found that increasing consumer richness leads to reduced prey and increased consumer biomass, whereas an increased prey richness

leads to enhanced energy transfer into higher trophic levels and thus to increased biomasses of consumers and prey [27].

One possible explanation for the discrepancy between these diverse results and our observed saturation might be the usage of different approaches to generate communities with different biodiversities. Random extinction events, as commonly used, might be too simple: Fung et al. analysed a marine food-web under harvesting and showed that the relation between total biomass production and the proportion of remaining fish species strongly depends on the algorithm of species deletion [47]. The need to study more realistic scenarios of extinction was also highlighted in the reviews by Duffy et al. [2] and Cardinale et al. [3]. But no matter what algorithm is used, most studies assume that the species loss is irreversible, without taking into account that empty niches might be refilled via evolution or immigration. In our model, many extinction events take place, because one existing species is replaced by a similar, but slightly better adapted new species. In this particular case intact functioning is indeed no surprise.

However, we observe intact functioning even if occasionally a whole trophic level disappears, supporting the hypothesis that trophic cascades are weaker in more complex food webs [28, 29, 30]. Duffy predicted that the addition of a new top predator to a diverse, multi-trophic system influences species abundances in the trophic level directly below, but this influence does not necessarily cascade down to even lower levels (see fig. 4 in [31]), because formerly rare predator-resistant species might be released from competition so that their feeding compensates for loss of formerly dominant species that are know eaten by the new predator. This hypothesis was supported in a meta-analysis by Schmitz et al. [32]. Finke and Denno analysed a coastal marsh community and found that adding more and more predators can further dampen trophic cascades due to increased intraguild predation [33]. These processes can only occur in communities that are sufficiently complex and diverse. We assume that this is given after, but not during the initial build-up of our networks.

Another reason why we do not find such strong and diverse BEF relations as observed in previous studies could be the fact that ecosystems in different study sites experience and adapt to different environmental conditions [48]. This is equivalent to combining in our model simulations performed with different respiration and mortality rates or carrying capacities. Both parameters are well-known to respond to environmental conditions [34, 35, 36].

By varying the respiration and mortality rate x_0 we found the same BEF relations as during the initial build-up of the networks (Fig. 4). Again, this can be explained with a top-down argument: Higher values of the respiration rate increase the biomass loss of the system, which directly leads to

a decreased total amount of consumer biomass, which then leads to an decreased predation pressure on the resource. Moreover, the decreased consumer biomass hampers the emergence of higher level species, which goes hand in hand with lower values of the functional diversity. These trends become more obvious when considering the functional diversity instead of the number of species, as has been observed already by many other researchers (see [49] and references therein).

In contrast, varying the carrying capacity leads to positive BEF relations both for the resource biomass and for the consumer biomass (Fig. 5). This can be explained with a bottom-up argument: An increased value of the carrying capacity K directly corresponds to an increased resource biomass and therefore to a larger amount of energy that is available to the consumer guild. Thus, larger networks with a higher functional diversity and with a larger amount of consumer biomass can emerge. A similar bottom-up effect was found in a data set from the Cedar Creek Ecosystem Science Reserve (see [5] for more information about this study system): Haddad et al. showed that the species richness and abundance in higher trophic levels (predatory and parasitoid anthropods) is strongly and positively related to the species richness in lower trophic levels (plants) [50]. Also Scherber et al. reported that plant diversity has strong bottom-up effects in multi-trophic networks [51].

To conclude, within a single food web model we found instances of positive, negative or no correlations between functional diversity and ecosystem functioning measures. The diversity of our results highlights the fact that there is no global answer to the question of how biodiversity interacts with ecosystem functioning, because different mechanism are involved and each of them affects BEF relations in different ways.

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Author contribution statement

Both authors designed the study and analysed the results. K.T.A. performed the simulations and wrote the manuscript draft. Both authors reviewed the manuscript.

Additional information

The authors declare no competing financial interests.

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