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1 A New Dimension: Evolutionary Food Web Dynamics
2 in two Dimensional Trait Space

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6 **Abstract**

7 Species within a habitat are not uniformly distributed. However this
8 aspect of community structure, which is fundamental to many conservation
9 activities, is neglected in the majority of models of food web assembly. To ad-
10 dress this issue, we introduce a model which incorporates a second dimension,
11 which can be interpreted as space, into the trait space used in evolutionary
12 food web models. Our results show that the additional trait axis allows the
13 emergence of communities with a much greater range of network structures,
14 similar to the diversity observed in real ecological communities. Moreover,
15 the network properties of the food webs obtained are in good agreement with
16 those of empirical food webs. Community emergence follows a consistent pat-
17 tern with spread along the second trait axis occurring before the assembly of
18 higher trophic levels. Communities can reach either a static final structure,
19 or constantly evolve. We observe that the relative importance of competi-
20 tion and predation is a key determinant of the network structure and the
21 evolutionary dynamics. The latter are driven by the interaction – competi-
22 tion and predation – between small groups of species. The model remains
23 sufficiently simple that we are able to identify the factors, and mechanisms,
24 which determine the final community state.

25 *Keywords:* Spatial food webs, Higher dimensional trait space, Network
26 structure, Evolutionary dynamics, Large community-evolution models

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27 1. Introduction

28 Ecologists have long been interested in the complex structures exhibited
29 by empirical food webs, the first studies dating back at least to the seven-
30 teenth century (see [24, 23]). Food webs describe the structure of ‘who-eats-
31 whom’ in a community and constitute one of the most fundamental levels
32 of biological organization. This structural richness has inspired theoretical
33 approaches to capture food web topology and dynamics in terms of mathe-
34 matical models. Most theoretical food web studies can be separated into two
35 categories: generating food web structures or describing population dynam-
36 ics.

37 On the one hand, narrative statistical models have been put forward that
38 combine stochastic elements with simple link assignment rules and allow net-
39 works of trophic interactions between species that closely resemble empirical
40 food webs to be synthesised [23]. The most prominent examples are the cas-
41 cade model [19], the niche model [70] and the random model [34]. Models
42 of this type are able to provide a detailed understanding of the structural
43 complexity of food webs [60, 72, 61] and, with certain refinements, produce
44 ecologically reasonable food web structures [54, 3, 52]. However, the pop-
45 ulation dynamics of the resultant community are not addressed within this
46 framework and must be modelled separately.

47 Thus, a separate stream of research has focused on dynamical models,
48 describing the temporal change of populations within a food web structure.
49 These models have proven to be able to capture a huge range of dynamic
50 complexities, such as population cycles, multi-stability and chaotic dynam-
51 ics. However, they contain a large number of free parameters that have to be
52 carefully chosen to fit to empirical food webs, without over fitting the model
53 [29, 68]. This problem is elegantly solved in allometric food web models,
54 which were introduced by Yodzis and Innes [74] and extensively studied since
55 [14, 9]. These models automatically determine the model parametrization us-
56 ing allometric scaling to determine how species dynamics vary with bodysize.
57 Where the food web structure can be determined a priori such models can
58 accurately predict the dynamics of ecological communities [10, 28]. However,
59 just as statistical models cannot describe population dynamics, dynamical
60 models cannot be used to generate food web structure, since the food web
61 topology is required to initialize the model.

62 These two approaches are combined in population based, evolutionary
63 food web models [16, 22, 67, 56, 65, 66]. One prominent class of such models

64 are niche based evolutionary food web models, which were introduced by
65 Loeuille and Loreau [40]. In these models each species is characterised by a
66 position, related to its bodysize, on a continuous niche axis. The strengths
67 of interactions between species are then simply determined by their pairwise
68 distances along the niche axis and allometric scaling with bodysize. New
69 species can be added to the community simply by assigning them a trait
70 value, with the change in food web topology being determined automatically.
71 As such they provide a simple means to capture the combinatorial increase
72 in possible food web structures that occurs as community size increases.

73 Niche based coevolutionary food web models were examined in great de-
74 tail. Refinements of the original model [40] studied, for example: the in-
75 fluence of trade-offs in resource consumption on the network structure [37];
76 the emergence of diversification by incorporating gradual evolution [11]; and
77 evolvable shapes of the feeding interaction kernels to produce more realistic
78 food webs [5]. However these studies also revealed that niche based evolu-
79 tionary models do not generate the degree of variety in food web structure
80 [4] that is observed in empirical food webs. Additionally, whereas such mod-
81 els typically generate a single dynamic regime [40, 11, 5], it is assumed that
82 empirical food webs display a range of dynamical states [73, 50].

83 This limited variety could be related to the fact that these niche based
84 evolutionary models consider only a single evolutionary trait – bodysize. Sev-
85 eral studies have raised the question whether a larger number of traits may
86 be necessary to realistically describe species interactions or food web inter-
87 vality [3, 47, 62, 25]. In this case, trophic niche space would be spanned by
88 other factors or phenotypic traits, apart from bodysize. Subsequent studies
89 showed that the dimensionality of trophic niche space has strong implications
90 for food web structure and the adequate dimensionality of trophic niche space
91 remains an ongoing debate in the food web literature [18, 52, 55, 2, 44].

92 Thus, a higher dimensional trait space could resolve the aforementioned
93 limitations in the structural and dynamical variety of niche based evolution-
94 ary food web models. Zhang et al. [75] constructed one example of such a
95 model by incorporating a spatial dimension into the evolutionary food web
96 framework. In this model each species is characterized by two traits: body-
97 size and a spatial habitat preference, used to characterize a population’s
98 distribution in space. The strength of feeding interactions was modelled as
99 a function of the pairwise distance between predator and prey species in the
100 two-dimensional niche space. The analysis by Zhang et al. [75] showed that
101 the second trait dimension had significant influence on the emerging size

102 spectra and maximal trophic levels. However, this study did not investigate
103 how the interaction parameters in the two dimensional niche space influence
104 the variety of food web structures and dynamics which can emerge.

105 In this study, we propose a conceptual evolutionary food web model
106 that describes the population dynamics of a community of species in a two-
107 dimensional niche space, characterized by bodysize and a second abstract
108 trait. Our model is similar to that of Zhang et al. [75] although we fol-
109 low closely Loeuille and Loreau [40] when determining interactions along the
110 bodysize axis and introduce new species via an evolutionary algorithm. Most
111 notably, we model competitive interaction between species along the second
112 trait dimension. Thus, our model unifies the seminal MacArthur-Levin’s
113 model of competition on a niche axis with an evolutionary food web model
114 on a bodysize axis. In our model, species are described by their trait values
115 in a two dimensional space and their interactions – feeding and competition
116 – by the niche overlap in this space. The second trait can be interpreted
117 in a variety of ways, for example as a vertical position in a water column,
118 day time of activity, habitat preference, phylogeny, a hidden gradient (e.g.
119 temperature, salinity, rainfall, day length) or it may simply be regarded as a
120 spatial coordinate.

121 Our primary goal in this study is to investigate the diversity of food
122 web structure and dynamics that emerges when such a second trait axis
123 is introduced to the evolutionary food web framework. Note that using a
124 conceptual model that remains sufficiently simple, within the evolutionary
125 food web framework, it is possible to obtain insights into the factors and
126 mechanisms underlying particular phenomena. Thus a secondary aim of this
127 study will be to identify possible ecological processes that are responsible for
128 greater food web diversity. Using intensive numerical simulations we show
129 that the additional trait axis allows the emergence of communities with a
130 much greater range of network structures, similar to the diversity observed
131 in real ecological communities. Thereby, the combined interplay of evolution-
132 ary and population dynamics gives rise to a plethora of community structures
133 and dynamical outcomes, such as evolutionary outbursts where a top-layer of
134 morphs at high bodysize spontaneously emerges and collapses, or directed evo-
135 lutionary motion, where species are co-evolutionarily driven towards smaller
136 bodysizes. Community emergence follows a consistent pattern with spread
137 along the second trait axis occurring before the assembly of higher trophic
138 levels. Communities can reach either a static final structure, or constantly
139 evolve. We observe that the relative importance of competition and predation

140 is a key determinant of the network structure and the evolutionary dynamics.
141 Finally, we will show that the model produces ecologically reasonable results
142 by undertaking a limited comparison to empirical food webs.

143 **2. Model**

144 We develop an evolutionary food web model, describing the dynamics
145 of one resource and a variable number of evolving morphs ($i = 1, \dots, N$). We
146 use the term morph instead of species, since we neglect reproductive isolation
147 and the underlying isolation mechanism that leads to speciation. Each morph
148 is characterised by two evolutionary traits, logarithmic bodysize z_i , and an
149 abstract trait x_i , as well as a population biomass density B_i , which varies
150 due to interactions with other morphs. Following MacArthur and Levins [42],
151 the strength of morph interactions is determined by their pairwise distance
152 in the two dimensional trait space: competitive interactions decrease with
153 the distance between two morphs in either dimension; and so do feeding
154 interactions with regard to their abstract traits, but they are maximized
155 for a certain offset in the bodysize direction. This follows from empirical
156 observations that species typically consume prey that is a certain fraction
157 smaller than themselves [69, 12]. The resource of concentration R has a
158 bodysize $z_R = 0$ and is continuously distributed along the abstract trait
159 axis. The trait axis has a length of L , however we use periodic boundaries
160 to simulate an infinite range [59].

161 The model itself can be divided into two processes, the population dy-
162 namics of the community and an evolutionary algorithm, which occur on
163 separated time scales. The population dynamics determine the variation in
164 each morph's biomass B_i . The evolutionary algorithm operates on a slower
165 time scale, introducing new morphs after the population dynamics have ap-
166 proached a steady state. We now consider each component in more detail.

167 *2.1. Population Dynamics*

The change of biomass B_i of morph i is given by Lotka-Volterra equations,
accounting for reproduction by consuming other morphs and the resource,

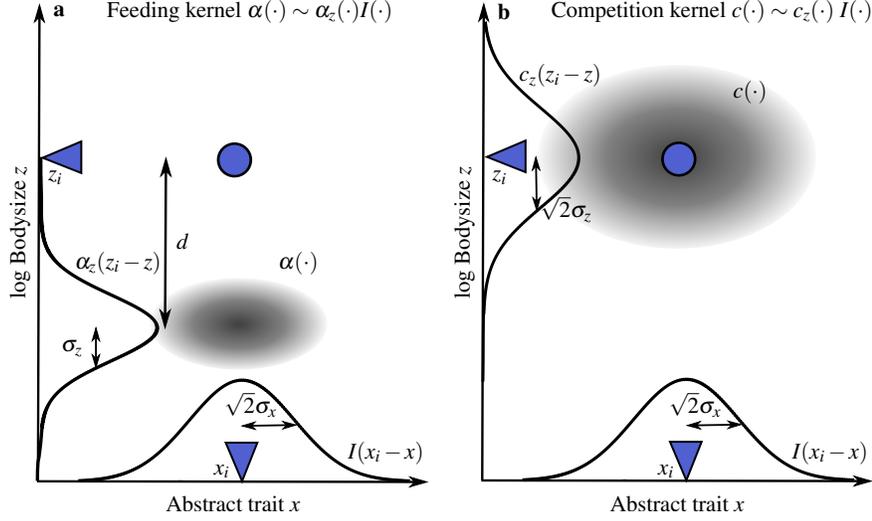


Figure 1: Interaction kernels of the two dimensional food web model. The plots show the interaction strength described by two-dimensional Gaussian functions (ellipses) of a species with trait value x_i and bodysize z_i (indicated by blue circle and triangles). **a:** The feeding kernel $\alpha(\cdot)$ is modelled as the product of the bodysize feeding kernel $\alpha_z(z_i - z)$, with a maximum at $z = z_i - \log(d)$ and a width of σ_z , and the dependency on the abstract trait $I(x_i - x)$, centred around $x = x_i$ with a width of $\sqrt{2}\sigma_x$. **b:** The competition kernel $c(\cdot)$ is modelled as the product of $I(x_i - x)$ and the competition kernel in bodysize $c_z(z_i - z)$ with a width of $\sqrt{2}\sigma_z$, given by the overlap of the bodysize feeding kernels of the competing morphs. Since the competition kernel is determined by niche overlap the competition ranges are not independent parameters (see Fig. A.8).

and losses due to mortality and respiration, predation and competition

$$\begin{aligned}
 \frac{dB_i}{dt} = & B_i \left(\underbrace{f_0 a(z_i) \sum_{j=1, i \neq j}^N \alpha(z_i, z_j, x_i, x_j) B_j + f_0 a(z_i) \int_0^L dx \alpha(z_i, z_R, x_i, x) R(x)}_{\text{Reproduction}} \right. \\
 & \left. - \underbrace{m_0 a(z_i)}_{\text{Mortality}} - \underbrace{\sum_{j=1, i \neq j}^N a(z_j) \alpha(z_j, z_i, x_j, x_i) B_j}_{\text{Predation loss}} - \underbrace{\sum_{j=1}^N c(z_i, z_j, x_i, x_j) B_j}_{\text{Competition}} \right), \tag{1}
 \end{aligned}$$

168 where f_0 is the conversion efficiency and m_0 is the basic mortality rate. Feed-
 169 ing interactions and biomass loss rates scale according to allometric relations
 170 with bodysize [48], which is expressed by $a(z_i) = 10^{-0.25z_i}$.

171 The feeding kernel $\alpha(\cdot)$ describes the ability of predator i to consume prey
 172 j . We assume that it is the product of two functions (Fig. 1a), describing
 173 the bodysize and abstract trait dependency,

$$\alpha(z_i, z_j, x_i, x_j) = \alpha_0 \alpha_z(z_i, z_j) I(x_i, x_j), \quad (2)$$

174 with α_0 being the attack strength.

Empirical studies suggest that feeding interactions depend on the loga-
 rithmic bodysize distances between morphs and are hump shaped [69, 12].
 To represent this, we express the bodysize dependency of the feeding kernel
 by a Gaussian function,

$$\alpha_z(z_i, z_j) = \frac{1}{\sigma_z \sqrt{2\pi}} \exp\left(-\frac{(z_i - z_j - \log(d))^2}{2\sigma_z^2}\right), \quad (3)$$

175 where d is the optimal predator-prey bodysize distance and σ_z corresponds
 176 to the feeding range of a morph.

177 Even though cannibalism is not uncommon in some cases [27], we ex-
 178 plicitly exclude cannibalistic feeding interactions ($\alpha(z_i, z_i, x_i, x_i) = 0$). The
 179 alternative, in this model, is to require that every morph be a cannibal which
 180 also seems unrealistic. Nonetheless, we expect our results to be relatively gen-
 181 eral, since cannibalism can be described by an additional contribution to the
 182 intra-specific competition strength; this would slightly decrease the biomass
 183 of the cannibalistic morph [5], but the general evolutionary outcome would
 184 not be affected. This is confirmed by numerical investigations which showed
 185 that the qualitative model outcomes are independent of this choice.

The dependency of the feeding kernel on the abstract trait is given by

$$I(x_i, x_j) = \frac{1}{\sigma_x \sqrt{4\pi}} \exp\left(-\frac{(|x_i - x_j|)^2}{4\sigma_x^2}\right), \quad (4)$$

186 which is of Gaussian shape with a width of $\sqrt{2}\sigma_x$ and states the interaction
 187 strength of two morphs along the abstract trait axis, see Fig A.8 for its
 188 derivation.

Motivated by the model of MacArthur and Levins [42], the competition

kernel $c(\cdot)$ is determined by the niche overlap between two morphs in the two dimensional trait space (Fig 1b), as the overlap in abstract space $I(\cdot)$ and the prey they have in common $c_z(\cdot)$,

$$c(z_i, z_j, x_i, x_j) = c_0 c_z(z_i - z_j) I(x_i, x_j), \quad (5)$$

where c_0 is the competition strength and

$$c_z(z_i - z_j) = \frac{1}{\sigma_z 2\sqrt{\pi}} \exp\left(-\frac{(z_i - z_j)^2}{4\sigma_z^2}\right). \quad (6)$$

189 The latter is calculated by the overlap of the bodysize feeding kernels $\alpha_z(\cdot)$
 190 of both morphs, see Fig. A.8 for more details. The width of the feeding
 191 and competition kernels in both dimensions are determined by the same
 192 parameters, with competition range being by a factor of $\sqrt{2}$ larger than the
 193 feeding range.

Unlike the evolving morphs, the resource has a constant bodysize and is continuously distributed along the abstract trait axis. The dynamics of the resource are given by the following chemostat equation

$$\frac{dR(x)}{dt} = I - eR(x) - \sum_{j=1}^N \alpha(z_j, z_R, x_j, x) B_j R(x). \quad (7)$$

194 Here, the first and second terms represent a constant input and an outflow
 195 relative to the resource biomass and the final term describes losses due to
 196 consumption by the morphs in the system.

197 Following the original formulation of these models by MacArthur and
 198 Levins [42] and Loeuille and Loreau [40], we intentionally keep our model as
 199 simple as possible. In particular, we describe predation rates using linear,
 200 rather than more realistic [35] functional responses. This allows us to truly
 201 unify both models. If all species have the same bodysize, our model reduces
 202 to the MacArthur and Levins model of competition along a niche axis [42].
 203 In contrast, if all species have the same value of their abstract trait our model
 204 reduces to an evolutionary food web model, similar to Loeuille and Loreau
 205 [40].

206 *2.2. Evolutionary Dynamics*

207 Every t_m time units a randomly chosen morph k mutates, and a mutant
208 m is added to the system, with a new abstract trait $x_m \in [x_k - \Delta_x, x_k + \Delta_x]$,
209 and logarithmic bodysize $z_m \in [z_k - \Delta_z, z_k + \Delta_z]$. In our model, the mutant
210 is then introduced with an initial biomass of θ , which is also the extinction
211 threshold. If the biomass B_k of any morph falls below this threshold, as
212 a result of the population dynamics, it is considered to be extinct and is
213 removed from the system.

214 *2.3. Initialization and Parameter Values*

215 Simulations are performed using the Sundials CVODE solver [20] in C++
216 with absolute and relative errors per time step set to 10^{-12} . The abstract trait
217 axis is discretised by one hundred grid points per unit length and periodic
218 boundaries are applied. All simulations are initialized with the resource
219 (logarithmic bodysize $z_R = 0$ and a concentration of $R(x) = I/e$) and a
220 single evolving morph with an abstract trait of $x_1 = \frac{L}{2}$ and logarithmic
221 bodysize $z_1 = \log(d)$.

222 The parameters regarding the population dynamics were set to $f_0 = 0.3$,
223 $m_0 = 0.1$, and $\log(d) = 2$, following [40]. For the evolutionary parameters
224 we set $\theta = 10^{-10}$ ([4]) and $\Delta_z = \log(2)$, as in [5]. The mutation time
225 t_m is set to 10^5 , which is sufficiently high for the population dynamics to
226 reach an equilibrium before the next mutation event. Parameters describing
227 interactions along the abstract trait dimension were fixed as follows: $I =$
228 1000 , $e = 0.1$, $\sigma_x = 0.05$, and $L = 1$. Tests of alternative values of these
229 parameters found that they had no qualitative effect on our results (see
230 Results). As discussed in Section 3 these parameters mainly influence the
231 effective length of the abstract trait axis. Furthermore, we choose a relatively
232 narrow mutation range in this direction, $\Delta_x = 0.08$, to ensure that mutants
233 are similar to their parents. Finally, to reduce the number of free parameters,
234 we set the attack strength, $\alpha_0 = 1.0$, and in the simulations presented in this
235 work we vary the competition strength c_0 and feeding range σ_z as our main
236 control parameters.

237 *2.4. Data Evaluation*

238 Since the evolutionary outcome depends on the sequence of random num-
239 bers, we perform one hundred simulation runs for each parameter set, with
240 different seeds. Each simulation runs for 10^{10} time units, if not stated oth-
241 erwise. To calculate the network characteristics we collect 20 networks from

242 each simulation run, each $5 \cdot 10^8$ time units, starting at a time of $5 \cdot 10^8$ to
243 omit the initial assembly phase. This produces a total of 2000 networks for
244 each parameter set. To calculate the network structure we follow [5] and
245 remove all links that supply less than 75% of the biomass contributed by
246 the average link. This cut-off criterion depends on the feeding kernel and
247 the prey's biomass density and therefore mimics sampling limits in empirical
248 data.

249 The emerging networks are compared to empirical data, in particular the
250 50 aquatic food webs in the Adirondack lake data set [64] (see Havens [32]
251 for details concerning the construction of these food webs). Since the model
252 can only produce networks with one resource, we treat all species in the first
253 trophic level of the empirical food webs as a single species, as proposed by
254 [54]. The trophic level is calculated using the prey-averaged trophic level, for
255 the empirical data, and the flow-based trophic level, for networks obtained
256 from simulations [71].

257 **3. Results**

258 We now investigate how morph interactions influence the emergence of
259 the network structure and evolutionary behaviour. A systematic screening
260 of the parameter subspace, composed of competition strength c_0 and feeding
261 range σ_z , reveals regions that are dominated by three distinct community
262 types (Fig. 2). (We say that a community type is dominant when 80% of
263 simulated outcomes are of that type.) The first community type is charac-
264 terised by a complete absence of trophic structure. A single trophic level
265 builds up, consisting of morphs that consume the resource, but no further
266 trophic levels emerge. The areas of parameter space where such communities
267 dominate are denoted Region I. The second type of community has trophic
268 structure and is evolutionarily static. That is, after an initial dynamic phase
269 of community assembly, the morphs, and the interactions between them,
270 become fixed. Such food webs dominate in Region II. The third type of com-
271 munity has trophic structure and is evolutionarily dynamic. The morphs in
272 such communities, and their interactions, change constantly over time and
273 leading to the temporary emergence of higher trophic levels (evolutionary
274 outbursts) and cases where a given morph progressively decreases its body-
275 size (evolutionary downwards movement). Region III is dominated by food
276 webs of this type. In addition, we observe an additional area that is not
277 dominated by a specific behaviour which we refer to as Region IV.

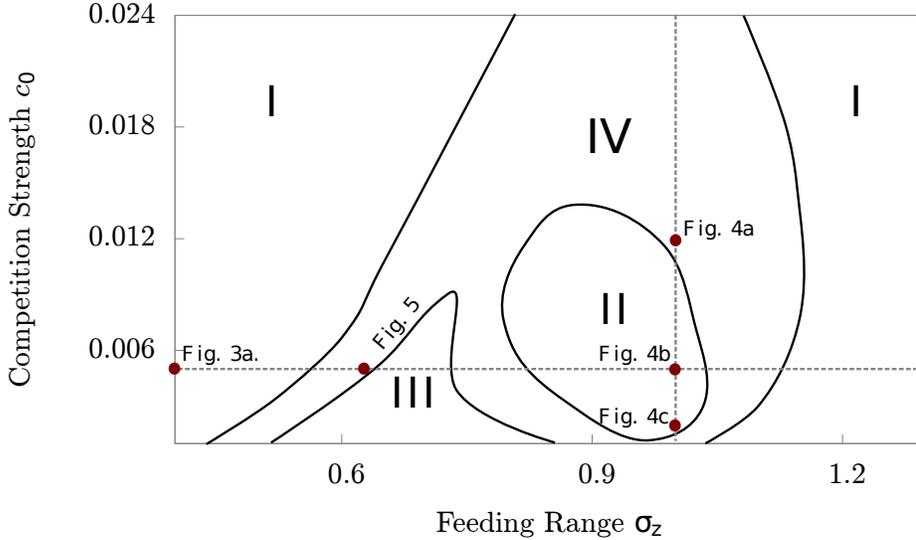


Figure 2: Effect of feeding range σ_z and competition strength c_0 on the model outcome. Four regions in parameter space occur, three of them are dominated by a particular type of community: Region I is dominated by communities with no trophic structure; Region II by evolutionarily static food webs; and Region III by evolutionarily dynamic food webs. In between these, an additional region occurs that is not dominated by a specific community type (i.e., less than 80% of simulated communities correspond to a single state, see also Fig. A.9 for the frequencies of each state), which is referred to as Region IV. Points denote examples further analysed in Figs. 3-5 and dotted lines represent the cross sections shown in Figs. 6 and 7.

278 These regions are robust with respect to variation of the parameters gov-
 279 erning interactions along the abstract trait dimension (see Section 2.3 for a
 280 specific list). Increasing the level of resources available, determined by I and
 281 e , (beyond the level necessary to support multiple bodysize layers) or the
 282 length of the abstract trait axis L , increases the number of morphs that can
 283 coexist, but does not change the food web type, whereas a larger value of σ_x
 284 is equivalent to a decrease in available resources or an increase in L .

285 3.1. Communities with no trophic structure (Region I)

286 Region I is dominated by evolutionarily static communities with a single
 287 trophic layer of primary consumers. This region is split into two sub-regions
 288 with distinct community characteristics, see Fig. 3. For small feeding ranges
 289 σ_z , the community contains many morphs with nearly identical bodysizes
 290 packed densely along the abstract trait axis. Consequently, the distribution
 291 of biomass along this axis is nearly uniform. In contrast, for large σ_z , there

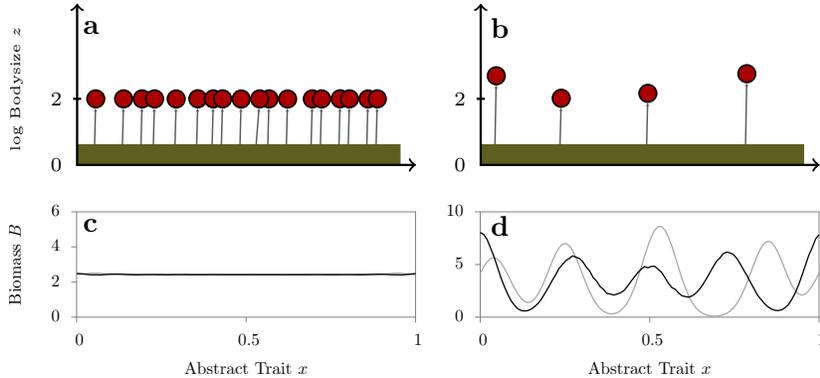


Figure 3: Two characteristic patterns of static communities without trophic structure (Region I), emerging for the case of a narrow feeding range ($\sigma_z = 0.4$, left column) and a large feeding range ($\sigma_z = 1.5$, right column). **a,b:** Positioning of morphs (represented by red circles) in two dimensional trait space. The green bar illustrates the resource. **c,d:** Biomass distribution along the abstract trait axis of the presented network (grey). It is assumed that a morph's biomass is distributed around the abstract trait, x_i , according to a Gaussian of width σ_x (see Fig. A.8). The black line denotes the average over 100 different simulated networks, whereby all biomass distributions are aligned by setting the maximum biomass value to an abstract trait value of zero. Therefore an artificial maximum and a subsequent minimum occur at the edges of the abstract trait axis. **Left column** ($\sigma_z = 0.4$): Dense morph packing along the abstract trait axis of morphs with similar bodysize. The biomass is continuously distributed along the trait axis, with the distributions of the single run and the average overlapping, since the interval between morphs is close to the distribution range along the abstract trait, σ_x . **Right column** ($\sigma_z = 1.5$): Food web wherein morphs keep a maximal characteristic distance to each other in trait space (see averaged distribution). Only four morphs are contained, which differ in bodysize, but are restricted to the same trophic level. In all simulations, the competition strength is fixed to $c_0 = 0.005$.

292 are relatively few morphs with a much greater diversity in bodysize spaced
 293 at relatively broad intervals along the abstract trait axis. In this case, the
 294 average biomass distribution displays a regular pattern of biomass peaks (see
 295 Section 3.3 for more details)

296 3.2. Communities with trophic structure

297 In our simulations, communities with trophic structure emerge with high
 298 frequency only for low to intermediate competition strengths c_0 and interme-
 299 diate feeding ranges σ_z . This was also observed and explained in detail by
 300 [41], who studied the emergence of trophic structures in niche based evolu-
 301 tionary food web models by evolutionary branching. However in our model,

302 after a branching event in bodysize, morphs of similar – though varying –
303 bodysize spread along this abstract trait dimension. Only after the bodysize
304 layer is established across a region of the abstract trait axis, does another
305 branching event become possible, allowing a new layer can emerge. The vari-
306 ation in the bodysizes of morphs along the abstract trait dimension induces
307 variation in the bodysize layer of larger morphs, as these morphs optimise
308 their bodysize to feed on local prey morphs.

309 As mentioned above, two types of food web emerge, characterised by
310 whether they are static or dynamic on evolutionary time scales. The lat-
311 ter case, evolutionarily dynamic food webs, occurs for small competition
312 strengths and lower feeding ranges. In this parameter range, morphs occupy
313 relatively small niches in the trait space, due to the sharpness of the feed-
314 ing and competition kernels. Consequently vacant niches are always present,
315 which allows new invasion events to occur frequently. We consider each of
316 these evolutionary behaviours below, beginning with the simpler case of evo-
317 lutionarily static food webs.

318 *3.2.1. Evolutionarily static food webs (Region II)*

319 Evolutionarily static food webs dominate in Region II (ellipsoid region,
320 Fig. 2). Three representative food webs with different competition strengths
321 c_0 are plotted in Fig. 4. In each case, after an initial assembly phase, the
322 bodysize distribution of the community becomes static (Fig.4a-c). We also
323 observe two patterns in the structure of these communities relative to com-
324 petition strength.

325 Firstly, as competition strength decreases the trophic structure of the food
326 webs becomes less regular (Fig. 4d-e). For high c_0 morphs with a similar
327 bodysize tend to have the same trophic level. With decreasing c_0 these
328 trophic level start to merge and for small c_0 a given bodysize range can
329 contain morphs of different trophic levels. Additionally, for high c_0 the food
330 web structure is relatively consistent along the abstract trait axis, while for
331 smaller c_0 values this structure becomes more variable.

332 This observation is reinforced by the plots of trophic level against log
333 bodysize (Fig. 4j-l). For high c_0 there is a strict hierarchical ordering of
334 morphs by bodysize. As c_0 decreases a concave shoulder emerges, indicating
335 that a morph's role in the food web is less strongly determined by its bodysize.
336 The flat section of these plots, at a trophic level of two, arises from the small
337 number of communities with no trophic structure, which occur in this region
338 (see Section 3.1 and Fig. A.13).

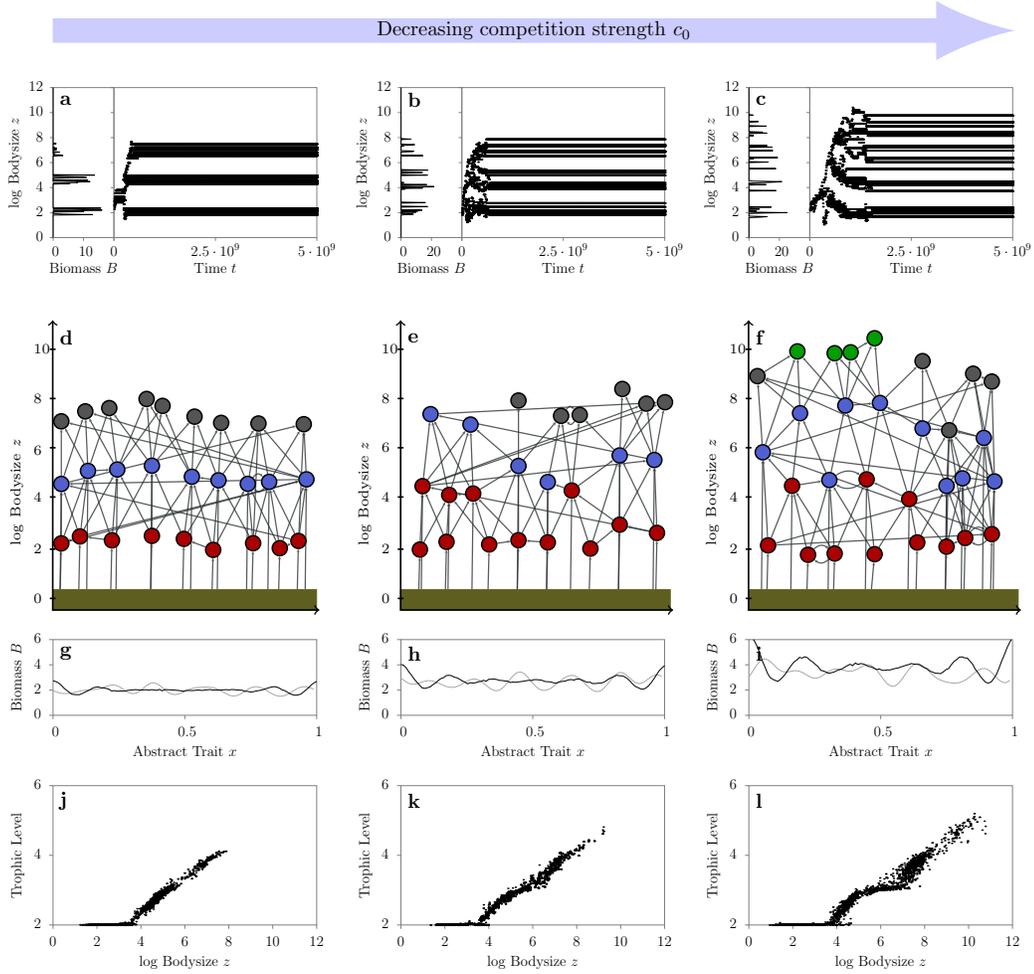


Figure 4: Structure of evolutionarily static food webs (Region II). Each column presents a different competition strength c_0 , decreasing from left to right (see Fig. 2 for position in parameter space). **Left column** ($c_0 = 0.012$): Static network with distinct bodysize layers. **Middle column** ($c_0 = 0.005$): Static network with slightly merged bodysize layers. **Right column** ($c_0 = 0.002$): Static network with intertwined bodysize layers. **a,b,c:** Temporal evolution of bodysizes (right panels) and bodysize-biomass histograms (left panels) of specific networks over the last $2.5 \cdot 10^9$ time units. **d,e,f:** Positioning of morphs in two dimensional trait space and interaction network. **g,h,i:** Biomass distribution of all morphs along the abstract axis of the network shown (grey) and the average over 100 aligned biomass distributions (see caption of Fig. 3 for more details). **j,k,l:** Morphs' trophic level against logarithmic bodysize for 100 simulated communities. In all simulations, the feeding range was fixed to $\sigma_z = 1$.

339 Secondly, structure emerges in the distribution of community biomass
340 along the abstract trait axis as competition strength decreases (Fig. 4g-f).
341 For high c_0 the average biomass distribution along this axis is nearly uniform
342 indicating that fluctuations in biomass occur randomly. As c_0 decreases,
343 regularly spaced peaks emerge in the biomass distribution, suggesting an
344 underlying pattern in the distribution of morphs along this axis. This phe-
345 nomenon is similar to that observed for communities without trophic struc-
346 ture (Fig. 3c-d), although the differences are less pronounced.

347 These two patterns, and the underlying mechanism producing them, will
348 be discussed in more detail in Section 3.3.

349 *3.2.2. Evolutionarily dynamic food webs (Region III)*

350 Evolutionarily dynamic food webs dominate in Region III (triangular re-
351 gion, Fig. 2), which is positioned at the lower end of feeding ranges and
352 competition strengths of parameter space for that communities with trophic
353 structure are likely. A characteristic example is shown in Fig. 5. Three dis-
354 tinct bodysize layers are present at all times, but the morph composition
355 changes continuously. Occasionally an additional unstable bodysize layer
356 emerges – the trophic structure of the community changes and the number of
357 morphs temporarily increase – before the bodysize layer collapses again (see
358 Figs. 5a,b,d,e). We refer to this phenomenon as an evolutionary outburst.
359 The waiting times between outbursts and durations of outburst are best de-
360 scribed by exponential distributions (Fig. A.10). In addition to evolutionary
361 outbursts, we also observe cases where morphs decrease their bodysize pro-
362 gressively, a phenomenon we refer to as evolutionary downwards movement.
363 This movement can traverse several bodysize layers (Fig. 5c). The biomass
364 distributions for individual networks exhibit small fluctuations, however the
365 average distribution is nearly constant indicating that these fluctuations do
366 not reflect an underlying structure along the abstract trait axis (Fig. 5f).

367 To gain more insight into the two evolutionary phenomena, outbursts and
368 downward movements, we set up a simple community which can only con-
369 tain two morphs, a predator and a prey (see Appendix A.1 for details). In
370 this simplified system, the two species co-evolve, with the predator following
371 the prey along abstract trait axis, a phenomenon called red-queen dynamics
372 [1, 53, 21]. In larger systems with several morphs, this process can result in
373 local compaction of morphs with similar bodysizes along the abstract trait
374 axis. Morphs in the same layer generally optimize their pairwise distance
375 along the abstract trait axis to avoid competition. However, if the losses

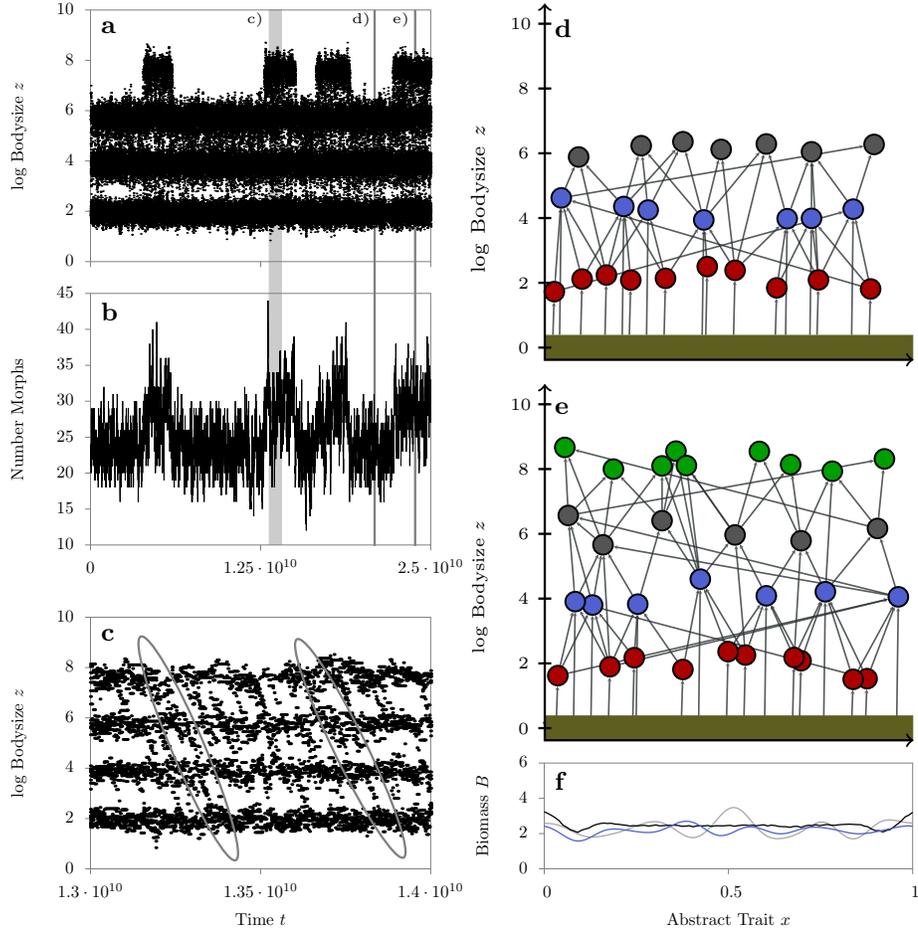


Figure 5: Characteristics of an evolutionarily dynamic food web (Region III). **a:** Temporal behaviour of bodysizes, showing four evolutionary outbursts. **b:** Corresponding total number of morphs as a function of time. **c:** Close up of the temporal development of the bodysizes shown in (a), demonstrating the evolutionary downwards movement in bodysize (marked as grey ellipses). The corresponding time window is indicated as grey shaded area in (a) and (b). **d,e:** Positioning of morphs in trait space and interaction networks, before (d) and during (e) an evolutionary outburst. Time instances are marked by vertical lines in (a) and (b). **f:** Biomass distribution along the abstract trait axis of the networks shown in (d) (grey) and (e) (blue), and averaged over 100 simulation runs (black). Parameter values $c_0 = 0.005$ and $\sigma_z = 0.625$ (see also Fig. 2).

376 of prey morphs due to predation exceed the losses from increased competi-
377 tion, a coherent evolutionary motion of prey morphs along the abstract trait
378 axis can be induced. As described above, predators will tend to follow this
379 evolutionary movement, causing complex co-evolutionary dynamics [21] and
380 giving rise to transient localised regions of unusually high biomass across all
381 bodysize layers. These regions are able to support larger morphs, producing
382 evolutionary outbursts. This co-evolutionary process also contributes to the
383 termination of outbursts. Over time the top predators repulse their prey
384 morphs, decreasing the biomass density in the bodysize layer immediately
385 below them. As the support for the top predators decreases, they either go
386 extinct or reduce their bodysize by an evolutionary downwards movement.
387 Eventually this happens to all top predators and the evolutionary outburst
388 terminates (see Fig. A.12).

389 The phenomenon of evolutionary downwards movement can be explained
390 in a similar way. As an alternative to following its prey along the abstract
391 trait axis, a predator can instead evolve downwards in bodysize to feed on
392 lower bodysize layers. When this occurs in a region of lower biomass (due
393 to compaction), the downwards drift may persist over a large number of
394 evolutionary steps and traverse several trophic levels. If no other prey are
395 found, the downward movement will terminate when the morph is able to
396 feed optimally on the resource.

397 *3.3. Community patterns and structural influence of interactions*

398 The competition strength c_0 and feeding range σ_z of morphs determine
399 the type of community that emerges from our model (Fig. 2). In addition
400 we observe that the structural features of particular communities vary with
401 these parameters (Sections 3.1 and 3.2.1). To determine the full extent of
402 these patterns we plot bodysize and average biomass distributions (over 100
403 realisations for each parameter set) along two cross-sections of the parameter
404 space (Fig. 6). Competition strength varies along Cross-section I, feeding
405 range varies along Cross-section II, in each case the other parameter is held
406 constant.

407 Figs. 6a & d show how the proportions of community types vary along
408 each cross-section for reference. The average biomass distributions (Figs. 6b
409 & e) show that the patterns previously observed extend across the entire
410 parameter space. In particular as competition strength decreases, or feed-
411 ing range increases, a regular pattern of biomass peaks emerges along the
412 abstract trait axis. The biomass distribution is almost completely uniform

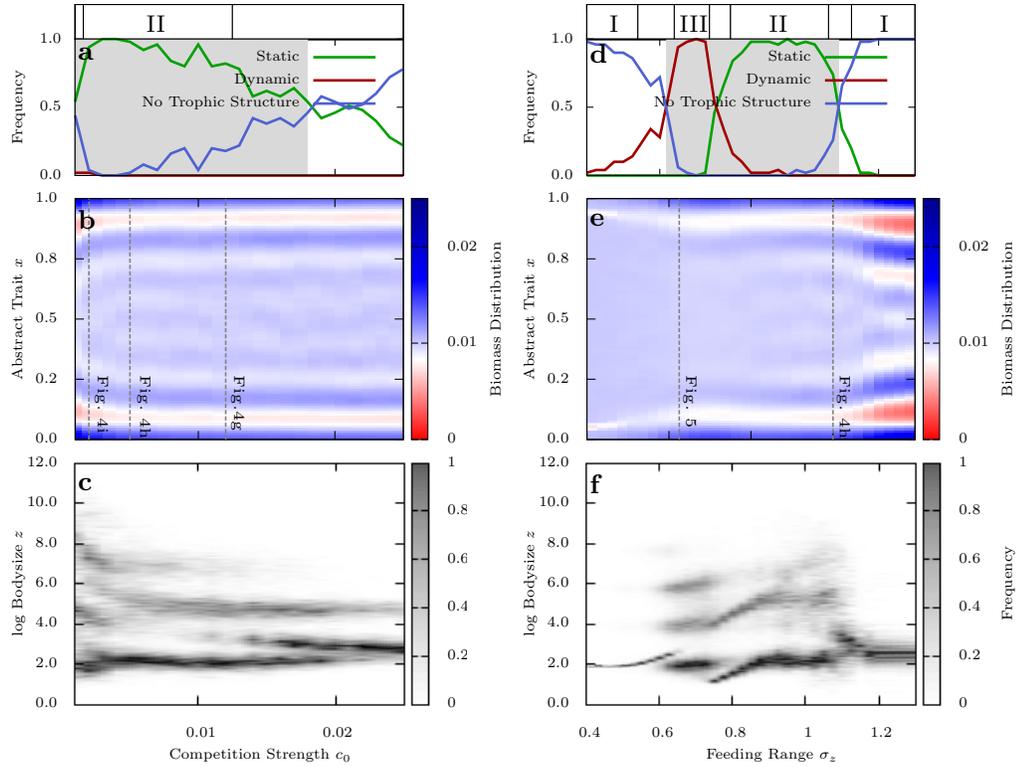


Figure 6: Model outcome along the cross sections through parameter space, shown in Fig. 2. **Left column:** different values of competition strength c_0 for fixed $\sigma_z = 1$ (cross section I). **Right column:** different values of feeding range σ_z for fixed $c_0 = 0.005$ (cross section II). **a,d:** Frequencies of the different community types (indicated by colours) in repeated simulation runs. The grey area marks the regime in which at least 50% of all networks have a trophic structure (i.e., a maximum trophic level greater than 2.5). The bar above this plot indicates the region of parameter space (Roman numeral) in which the parameter combination lies. **b,e:** Average biomass distribution along the abstract trait axis, normalized by the total biomass, as described in Fig. 3. Vertical lines indicate parameter values for which biomass distributions have been shown in Figs. 4-5. **c,f:** Probability density function of log bodysize. The same distributions are shown in Fig. A.13 for the different community structures. For each parameter we averaged over 100 simulation runs.

413 for small feeding ranges and becomes strongly structured for large feeding
414 ranges. By contrast, the biomass distribution varies relatively little along
415 the competition strength cross-section; a weak structure is present across the
416 majority of the range and strengthens slightly for small c_0 . High bodysize
417 diversity, and thus food web complexity, occurs for low c_0 and intermediate
418 σ_z (Figs. 6c & f). Additionally, we observe that bodysize layers become more
419 distinct as c_0 increases, corresponding to more regular food web structure.
420 By contrast, bodysize layers are relatively distinct across the entire feed rang-
421 ing cross-section, although individual layers do become broader, indicating
422 greater bodysize diversity within layers, as feeding range increases.

423 These patterns are explained by a trade-off between competition and
424 feeding input. On the one hand, a morph tries to optimise its feeding input
425 by maintaining an optimal logarithmic bodysize separation of $\log(d)$ and a
426 minimal distance in the abstract trait from its prey. On the other hand, it
427 maximizes the distance in trait space to other morphs that feed on the same
428 prey range to minimise competition.

429 If the competition strength c_0 is high, competition losses exceed the feed-
430 ing input, and morphs in the same layer increase their separation along the
431 abstract trait. At the same time optimization of the feeding input is impor-
432 tant to compensate competition losses. These two constraints combine to
433 create locally optimal niches in trait space, which results in a regular food
434 web structure (e.g. Fig.4d). For lower c_0 , these constraints become weaker
435 and consequently the optimal niches are less strictly defined. As a result, the
436 first morph introduced into a niche is often able to fill it, and the network
437 structure becomes irregular (e.g. Fig.4f).

438 Increasing feeding range σ_z has a similar effect. For small σ_z , predators
439 are highly specialised and thus only a narrow range of mutant bodysizes are
440 viable, resulting in a distinct bodysize network structure. As σ_z increases
441 predators become less specialised and the fitness landscape becomes flatter,
442 allowing greater bodysize diversity and a more irregular network structure.
443 However, this also reduces the feeding input from any given source. Conse-
444 quently in communities with no trophic structure, where morphs feed only
445 on the resource, even low levels of competition are sufficient to prevent co-
446 existence of morphs in close proximity (e.g. Figs. 3 b & d). This results in
447 a structured biomass distribution, with large biomass maxima separated by
448 a characteristic interval. By contrast, for small feeding ranges, morphs feed
449 efficiently on the resource, and thus the spacing of morphs along the abstract
450 trait axis can be more random (e.g. Figs. 3a & c).

451 Similar patterns emerge in communities with trophic structure. In food
452 webs with an irregular trophic structure, the morph composition of local
453 regions varies, and consequently so too does the local biomass (e.g. Figs. 4f
454 & i). Regions of high biomass impose a high level of competition on the
455 surrounding area reducing the number of morphs, and hence biomass, that
456 can be sustained, producing a regular biomass pattern. Food webs with more
457 regular trophic structure (e.g. Figs 4d & g) produce a relatively uniform
458 biomass distribution, since the morph composition of any local region is
459 relatively consistent.

460 *3.4. Empirical data: finding model parameters that reproduce natural food* 461 *webs*

462 In order to show that our model produces ecologically reasonable food
463 webs, and to estimate a ecological parametrisation, we compare the resulting
464 food webs to empirical data, collected from 50 lakes in the Adirondack region
465 [64]. We want to stress that our intention is not provide a comparison between
466 our model and reality (which would require a different model to begin with,
467 including e.g. saturating functional responses). Instead our goal is to find
468 model parameters, which produce a food web with characteristics that are
469 similar to empirical ones.

470 To compare food web topologies directly, we choose three common com-
471 munity characteristics for comparison: number of morphs, maximal trophic
472 level, and food web connectance. In addition, we consider the fraction of
473 unconsumed potential prey per morph (Fig. 7), which is a measure of inter-
474 vality, a phenomenon that is not possible if we restrict our model to a one
475 dimensional deterministic trait space (but see [55]). The fraction of uncon-
476 sumed potential prey per morph is based on the measure for diet contiguity
477 [60, 17] (number of species belonging to gaps in a consumer diet), which is
478 normalised by the total number of species that fall into the bodysize feeding
479 range of a consumer.

480 Since the model only considers a single resource, following [54], we treated
481 all species of trophic level one in the empirical data as a single species. For
482 each parameter pair along the two cross sections described above (see Section
483 2.4) we collected 2000 simulated food webs. This ensemble includes commu-
484 nities with a trophic structure (trophic level larger than 2.5, Region II and
485 III) and without (Region I). Therefore changes in the community charac-
486 teristics could be due to either changes in the ratio of occurrences of these
487 types or due to a transition in the food web structure itself. To separate

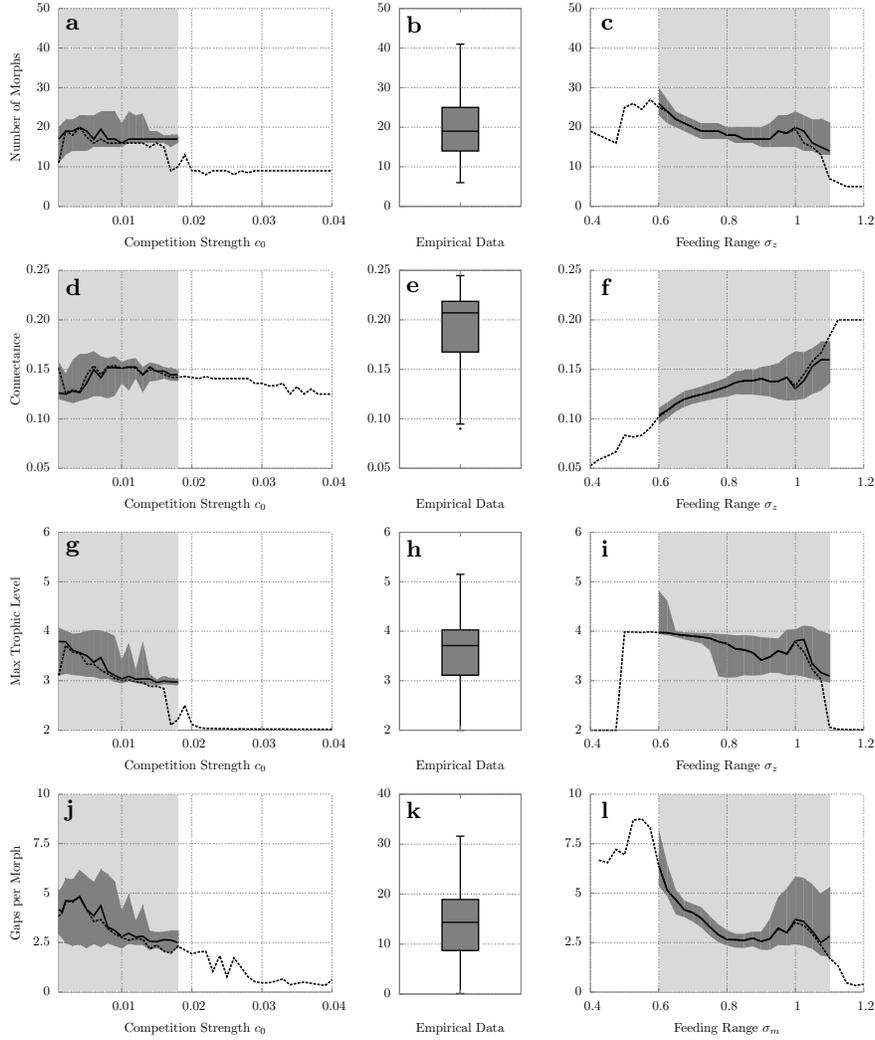


Figure 7: Comparison of characteristics of empirical food webs with simulated networks along the two cross sections. **Left column:** different values of competition strength c_0 for fixed $\sigma_z = 1$ (cross section I). **Middle column:** empirical data, collected from the Adirondack lakes [64] using boxplots (whiskers extend to 1.5 times the interquartile range above and below the upper and lower quartiles.) **Right column:** different values of feeding range σ_z for fixed $c_0 = 0.005$ (cross section II). Along the cross sections the dashed lines represent the median over the complete ensemble of all 100 runs per parameter set. The grey area denotes the parameter regime in which at least 50% of all networks have a trophic structure (trophic level larger than 2.5). Within this area we considered the trophic ensemble, all networks with a trophic structure, and calculated the median (black curve) and the first and third quartile (represented by the dark grey area). **a,b,c:** Total number of morphs, **d,e,f:** connectance, **g,h,i:** maximal trophic level and **j,k,l:** number of unconsumed potential prey per morph. See text for further details.

488 these effects, we consider a sub-ensemble, consisting only of communities
489 with trophic structure, in the parameter range where at least 50% of all
490 communities have such a structure (light grey area, Fig. 7). The median
491 values of the community characteristics chosen are plotted against the varied
492 parameter values for the complete and trophic ensembles (dashed and solid
493 lines in Fig. 7). The interquartile range for the trophic ensemble is plotted
494 in dark grey and is directly comparable to the interquartile range (grey area)
495 in the empirical values of these characteristics.

496 The empirical food webs contain a median of 19.1 species, with an inter-
497 quartile range between 14 and 25. For both cross sections the trophic
498 ensemble is in good agreement with these values, as is the complete ensemble
499 for small feeding ranges (Fig. 7a-c). The median maximal trophic level
500 for the empirical food webs is 3.7 with an interquartile range between 3.1
501 up to 4.0. The trophic ensembles along each cross section are also in good
502 agreement with these values (Fig. 7g-i).

503 The median connectance of the empirical food webs is 0.20, with an inter-
504 quartile range between 0.17 and 0.21. Along the parameter ranges shown
505 here, our simulated communities have lower median connectance (Fig. 7d-f).
506 Only communities with two trophic levels and a small number of morphs
507 (see Fig. 3a) are in good agreement with the empirical values. However
508 by combining the maxima of both cross sections (larger feeding ranges, low
509 competition strength) one can gain networks with a higher connectance.

510 The median number of unconsumed potential prey per morph of the em-
511 pirical food webs is 9.9, with an interquartile range between 8.8 and 18.7. In
512 comparison, all simulated food webs underestimate these values and there-
513 fore produce lower levels of intervality (Fig. 7j-l). However, higher levels of
514 intervality can be obtained by increasing the length of the abstract trait axis
515 L or decreasing the feeding range σ_z .

516 Finally, we note that the lower end of extreme values for each charac-
517 teristic, except the fraction of unconsumed potential prey per morph, (the
518 lower whisker) tends to be in good agreement with the complete ensemble at
519 the upper end of competition strengths and feeding ranges. Empirical food
520 webs with these features typically come from lakes which are relatively poor
521 habitats which, as such, are unable to support a large number of species and
522 high trophic levels. This situation would be most naturally represented by
523 taking a lower value of the resource input I . However the resource limitation
524 could also be expressed by high competition or a low feeding input (which
525 results from relatively unspecialised feeding interactions), so this similarity

526 is reasonable.

527 4. Discussion

528 We have proposed a framework for evolutionary food webs that extends
529 previous models [40, 11, 5, 31] by considering a second niche-space dimension.
530 A similar model was introduced by Zhang et al. [75], but it differs from our
531 model in two notable properties:

532 First, in contrast to our study Zhang et al., did not incorporate direct
533 competition, but only indirect competition via a shared prey. Thus, our
534 model constitutes a true synthesis of the MacArthur-Levins model of com-
535 petition on a niche axis with an evolutionary food web model on a bodysize
536 axis. Second, in [75] invaders are drawn from an external (predefined or
537 continuous) species pool, whereas we consider an evolutionary algorithm and
538 therefore reduce the range of invading morphs in dependency of their ancestor
539 trait values. Thus, our species assembly algorithm considers the evolutionary
540 history of a species. When [75] draw invaders from the complete trait space,
541 they observe an ongoing evolutionary change of the food web. In contrast,
542 our extended model produces both types of behaviour, dependent on the
543 characteristics of morph interactions. Furthermore, even for food webs of a
544 given evolutionary type, change in these interactions affects the structural
545 properties of the emergent food webs (e.g. the degree of hierarchy, or distri-
546 bution along the second niche axis), a phenomenon which has not been seen
547 in many evolutionary food web models.

548 Our model framework allows us to describe a great variety of communities.
549 This is important, because ecological food webs also display a significant
550 degree of structural, and to a lesser degree dynamical, variety. Freshwater
551 ecosystems have very distinct, hierarchical structures [63, 46], while soil and
552 marine ecosystems are often more amorphous [49]. In addition, a variety
553 of relationships between bodysize and trophic-level – or even the lack of a
554 significant correlation – is reported in empirical studies [51, 38]. While most
555 empirical studies consider food webs to be constant over time, taxon cycles
556 have been observed in small trophic communities [57]. Thus, it is assumed
557 that larger communities can also be dynamic [50].

558 Since all of these behaviours are reproducible within our relatively sim-
559 ple model, it is possible to identify the model properties, and mechanisms,
560 responsible for these differences. For example, our finding that the rela-
561 tive importance of predation and competition is a key determinant of food

562 web regularity is supported by empirical observations [36, 33]. Our model
563 suggests that, in highly competitive environments, the pressure to achieve
564 optimal feeding relationships forces the formation of a very rigid food web
565 structure. In contrast, when competition is weaker, the food web structure
566 is looser as the niches within the community are less strictly defined. The
567 degree of specialisation on a given prey type has a similar effect, for the
568 same reasons; we are not aware of a study which has previously made this
569 connection.

570 The primary technical difference between our model and its predecessors
571 is the extension of the trait space into a second dimension. As such it fol-
572 lows that this second dimension is responsible for the increase in community
573 diversity that we observe. We explain this as follows. In a one dimensional
574 trait space, for instance in the model of Loeuille and Loreau [40], morphs
575 feed on all morphs in the lower trophic level [4] and consequently the whole
576 community is linked, directly or indirectly, by feeding interactions. In a two
577 dimensional trait space this is no longer the case; if morphs are sufficiently
578 far apart in the second dimension, then they have only negligible influence
579 on each other. This allows the emergence of local variation in the food web
580 structure. Additionally the expanded trait space provides morphs with a sec-
581 ond evolutionary strategy; in addition to maximising feeding input they can
582 now attempt to avoid predation (or equivalently search for higher densities
583 of prey).

584 Previous work using evolutionary food web models has focused on the ef-
585 fects of trophic interactions on community structure. However, recent empir-
586 ical studies have highlighted the influence of spatial factors on the structure
587 of ecological communities [6, 13, 23]. While we have not explicitly included
588 space in our model, it would not be uncommon that the position on the ab-
589 stract trait axis is associated to a spatial coordinate. This might describe
590 situations where the trait value corresponds to habitat choice or preference
591 for certain environmental characteristics, such as temperature, humidity, or
592 altitude. In such cases, the abstract trait axis can be naturally interpreted as
593 a spatial dimension (e.g. geographic latitude), with the abstract trait value
594 corresponding to the spatial centre of a morph, around which the latter is
595 distributed with a width of σ_x . Consequently, the effects attributed to the
596 second trait dimension, localisation and avoidance, obtain a straightforward
597 spatial interpretation.

598 On this basis, we can draw two conclusions about the dynamics of spatial
599 community emergence, in particular considering large spatial scales. Firstly,

600 the spatial assembly (horizontal) of food webs is faster than the trophic
601 (vertical). This occurs because a persistent predator can only emerge after
602 a contiguous region of space has been occupied by their potential prey. Prey
603 in the centre of this region can not avoid the predator evolutionarily, since it
604 is confined by competition with other prey populations. For an unconfined
605 prey, an arms race emerges between predator and prey (Fig. A.11) and the
606 predator eventually focuses on the resource. Secondly, for evolutionary static
607 food webs, propagation of similar morphs across space follows the principle of
608 “First come, first served” [43, 15]. That is, the first viable morph introduced
609 in a spatial region establishes and determines the local food web. This is
610 supported by the observation that the lowest bodysize layer of our simulated
611 food webs is irregular, even when morph feeding is specialised (low feeding
612 range). Thus, the theoretically optimal morph, with bodysize d , does not
613 become established universally. This is a potential explanation for spatial
614 species turnover, that is the empirical observation that the species filling a
615 given ecological niche vary across a landscape [30].

616 While the dynamics of community emergence are consistent for all food
617 webs generated by our model, the structure of these communities is more
618 variable. As noted above the food web structure is determined by the char-
619 acteristics of morph interactions. However, we also observe variation in the
620 distribution of biomass across the habitat which appears to be related to
621 variations in the trophic structure of the food web. In particular regular
622 trophic structure induces a uniform biomass distribution, while irregular
623 trophic structure results in regular biomass peaks, see Section 3.3. Spatial
624 variation in food web structure and biomass distribution in homogeneous
625 space have been observed in empirical studies [8, 26, 58, 39], but the two
626 phenomena have not previously been connected.

627 The dynamics of large communities are difficult to observe experimentally
628 due to the time scales and sampling effort involved [45]. Consequently stud-
629 ies of such phenomena are largely theoretical. However, our results suggest
630 that such dynamics arise from the cumulative effect of interactions between
631 small groups of species which can be more easily studied. In particular, the
632 primary driver of community dynamics in our model, is the coevolution of
633 predator and prey, red-queen dynamics [1, 53, 21]. In small communities this
634 produces characteristic spatio-temporal patterns: bodysize oscillations and
635 spatial chasing (Fig. A.11) which are also observed in experimental studies
636 [36]. In large communities these patterns combine to produce evolutionary
637 outbursts, that is the recurring emergence of higher trophic levels for a limited

638 period. These are similar to the cycling between high and low trophic com-
639 munity states, discovered by [65, 66]. The build-up of these higher trophic
640 states is due to a prey abundant community, which is similar to our observa-
641 tion. However, in our model, they are not terminated by evolutionary suicide.
642 Instead when the outburst collapses, top predators reduce their bodysize un-
643 til they are able to sustain themselves in an environment with lower prey
644 density.

645 The presence of evolutionary outbursts in a community indicates that
646 energy flows from the resource to the higher trophic levels are unstable. Note
647 that the resources supplied are constant, the instability lies in the community
648 structure itself. This is supported by the theoretical study of Zhang et al. [75],
649 which states that the maximal trophic level is constrained by energetic and
650 structural constraints. In our case, the temporary collapse of a population
651 of top predators is not necessarily an indication that a given community is
652 endangered. Nonetheless, we note that changes in resource availability or in
653 species interactions, say due to the introduction of an invasive species, can
654 have similar effects.

655 One obvious criticism of the spatial interpretation of the second trait axis,
656 is that species dispersal typically occurs on a different time scale to evolution-
657 ary adaptation. However, resolving these processes on separate time scales
658 had little effect on the results obtained. Other criticisms include the simpli-
659 fying assumptions, such as the use of linear functional responses instead of a
660 more realistic multi-species functional response [35], or the fact that competi-
661 tion leads to biomass losses instead of being described as a time consuming
662 factor in the functional response [7]. As explained in the Model section, one
663 major motivation for these simplifications was to preserve the elegance of
664 the model. By keeping the model close to the original formulation in [42]
665 and [40], our model naturally unifies the two seminal models that describe
666 species interactions, either competitive [42] or trophic [40], from species posi-
667 tions in niche space. Future investigations should consider these factors and
668 explore more realistic extensions, such as saturating functional responses
669 which could destabilise the population dynamics, e.g. “paradox of enrich-
670 ment”. Nevertheless, the food webs generated by this model are in relatively
671 good agreement with empirical data. Again, our intention was not to repro-
672 duce the fine-structure or empirical communities in detail, as has been done
673 for example in [10, 28]. Instead we explored the structural and dynamical
674 complexities that arise in this conceptual model. Further, we explicitly ex-
675 cluded cannibalism, even though cannibalism is not uncommon in empirical

676 food webs [27]. We have performed intensive numerical investigations, which
677 confirm that cannibalism does not change the evolutionary behaviour of the
678 model, since the ensemble of evolutionary behaviours stays unchanged. Can-
679 nibalism does appear to have an effect on community type for large feeding
680 ranges σ_z , with communities with no trophic structure dominating only for
681 large competition strengths c_0 while for low competition strengths no com-
682 munity type dominates. In addition, communities with no trophic structure
683 in this range display a more homogeneous biomass distribution along the
684 abstract trait axis than was observed without cannibalism (i.e. the regular
685 pattern of biomass peaks disappears in Fig. 3). This is explained by the fact
686 that cannibalism can allow nearly neutral coexistence of very similar morphs
687 and enables morphs of large population sizes to divide into smaller similar
688 populations. However, assuming all species are cannibalistic seems as unre-
689 alistic as excluding cannibalism entirely, and thus incorporating cannibalism
690 realistically in this model is a challenge for future work.

691 In summary, we have shown that, by adding a second trait dimension,
692 with spatial properties, to the evolutionary food web framework, much more
693 of the variety found in ecological communities can be described. Moreover,
694 the framework remains simple enough to allow the factors determining the
695 type of community obtained to be identified. As such this model represents
696 a step towards a more general theory of ecological community assembly,
697 structure and dynamics.

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Appendix A. Appendix

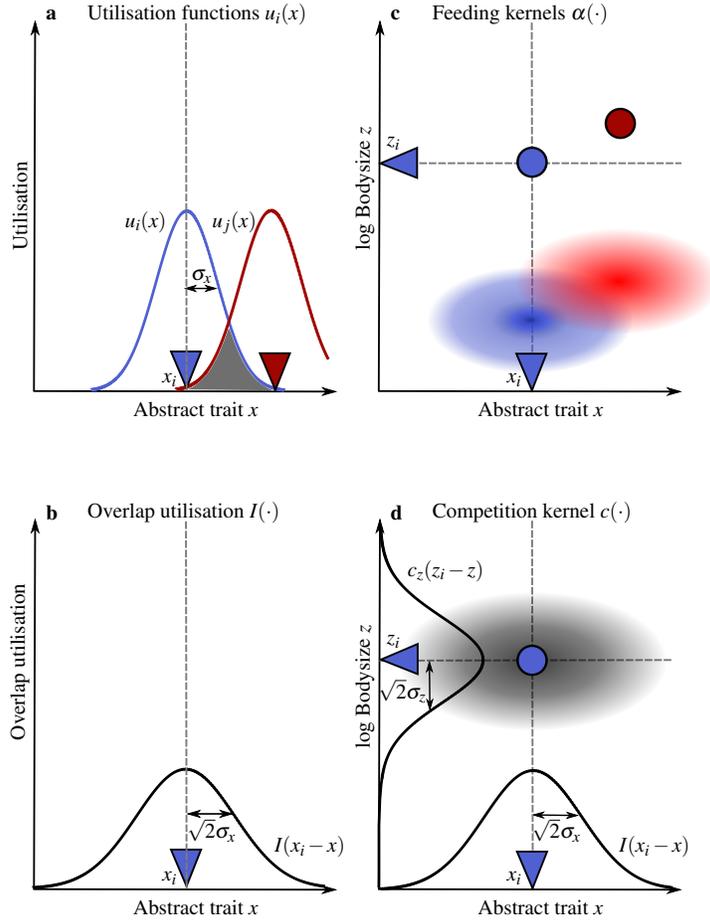


Figure A.8: Derivation of the interaction kernels. **Left Column:** Deduction of the utilisation overlap $I(\cdot)$, describing the interaction strength along the abstract trait dimension. **a:** Utilisation function $u_k(x)$, which can be interpreted as the distribution of morph k along the abstract trait axis. Following MacArthur and Levins [42], we assume that a morph k utilises a certain range around its abstract trait value x_k

$$u_k(x) = \frac{1}{\sigma_x \sqrt{2\pi}} \exp\left(-\frac{(|x_i - x|)^2}{2\sigma_x^2}\right),$$

which has a width of σ_x . **b:** The utilisation overlap $I(\cdot)$ between two morphs is given by the normalized overlap [59] of their utilisation functions:

$$I(x_i, x_j) = \frac{\int_{-\infty}^{\infty} dx u_i(x) u_j(x)}{\int_{-\infty}^{\infty} dx u_i^2(x)} = \frac{1}{\sigma_x \sqrt{4\pi}} \exp\left(-\frac{(|x_i - x_j|)^2}{4\sigma_x^2}\right),$$

resulting in a Gaussian function with a width of $\sqrt{2}\sigma_x$. **Right Column:** Derivation of the competition kernel $c(\cdot)$ in two dimensional trait space. **c:** Feeding kernels $\alpha(\cdot)$ of two morphs in two dimensional trait space. **d:** Competition kernel $c(\cdot)$, given by the normalised overlap of the bodysize feeding kernel $c_z(\cdot) \sim \int_{-\infty}^{\infty} dx \alpha(z_i - z) \alpha(z_j - z)$, multiplied with the overlap $I(\cdot)$ of their utilisation functions. This results in a two dimensional Gaussian. The competition ranges are proportional to the width of the kernels of a single morph and are therefore no independent parameters.

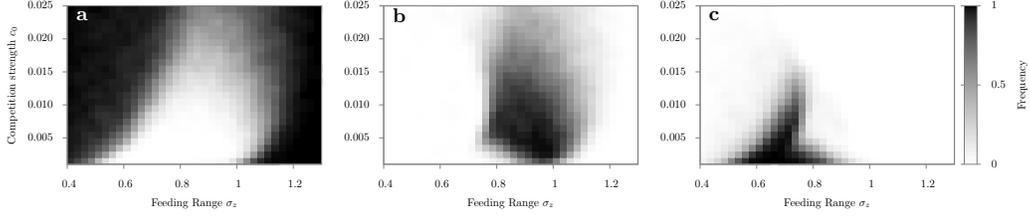


Figure A.9: Frequencies of occurrence (indicated in grey shading) of the different community types in repeated simulations, in dependency of the feeding range, σ_z , and competition strength, c_0 (compare to Fig. 2). **a:** Communities with no trophic structure, **b:** evolutionary static food webs, and **c:** evolutionary dynamic food webs. See Section 2.3 for more details.

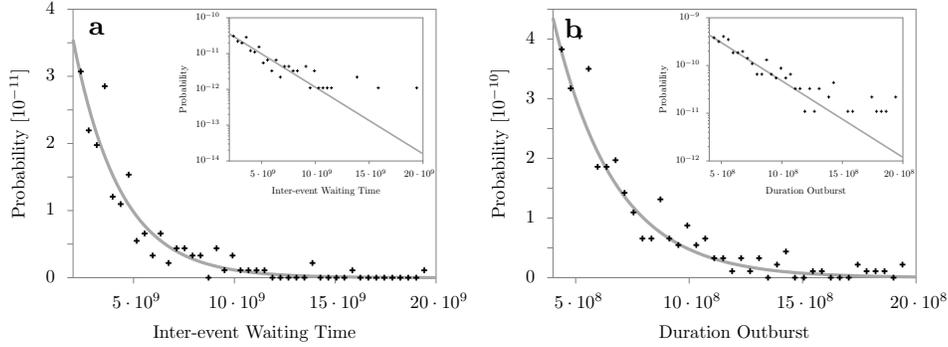


Figure A.10: Inter-event waiting time and duration of evolutionary outbursts. **a:** Probability density function of the inter-event waiting times between outbursts. **b:** Probability density function of the outburst duration. The insets in **a** and **b** show the same data in a semi-logarithmic plot. Solid lines show exponential functions fitted to the data, which yields typical time constants of $2.3 \pm 0.2 \cdot 10^9$ (inter-event waiting time) and $2.7 \pm 0.1 \cdot 10^8$ (outburst duration). Note, the different time scales between inter-event waiting times, the duration of single outbursts, the downward evolutionary motion and the breakdown of an evolutionary outburst (see also Fig. 5). The same parameters as in Fig. 5 were used. In total 2300 events were recorded.

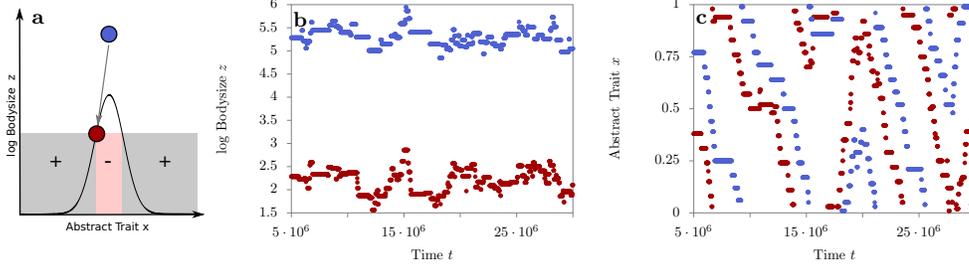


Figure A.11: Predator-prey arms race. The system was parametrised (by setting $I = 100, \sigma_x = 0.17, \sigma_z = 0.7, c_0 = 0.001$) so that it only contains a single predator (blue) and prey (red) morph. **a:** Positioning of predator and prey morphs (circles) in two-dimensional niche space and sketch of the feeding strength (solid line) and the prey’s fitness landscape in dependence of the value of the abstract trait. Coloured shading indicates regions of negative (red) and positive (grey) fitness. **b,c:** Evolution of bodysize and abstract trait of the predator and prey morph, demonstrating the emergence of bodysize oscillations (**b**) and arms races (**c**). The predator is chasing the prey along the abstract trait axis. It is even possible for this movement to change directions: If the predator’s and prey’s abstract traits are similar, the mutational range can exceed the area of negative fitness (red area in **a**) and a mutant can occur on the other side of the predator.

Appendix A.1. Red-queen dynamics in a small community

In a small community, which can contain only two morphs, one predator and one prey, it is possible to disentangle population dynamics and evolutionary processes (Fig A.11). Assume that the predator in this system has bodysize z_1 and abstract trait value x_1 . The prey’s fitness increases the further it is separated from the centre ($z_1 - d, x_1$) of the predator’s feeding range (see sketch in Fig. A.11a). As such, over evolutionary time, the prey will evolve away from this centre due to a sequence of invasions by more fit mutants. This, in turn, decreases the predator’s fitness, and consequently, the predator follows the prey by the same evolutionary process, Fig. A.11b,c. The result is an evolutionary arms race or red-queen dynamics [1, 53, 21] between predator and prey.

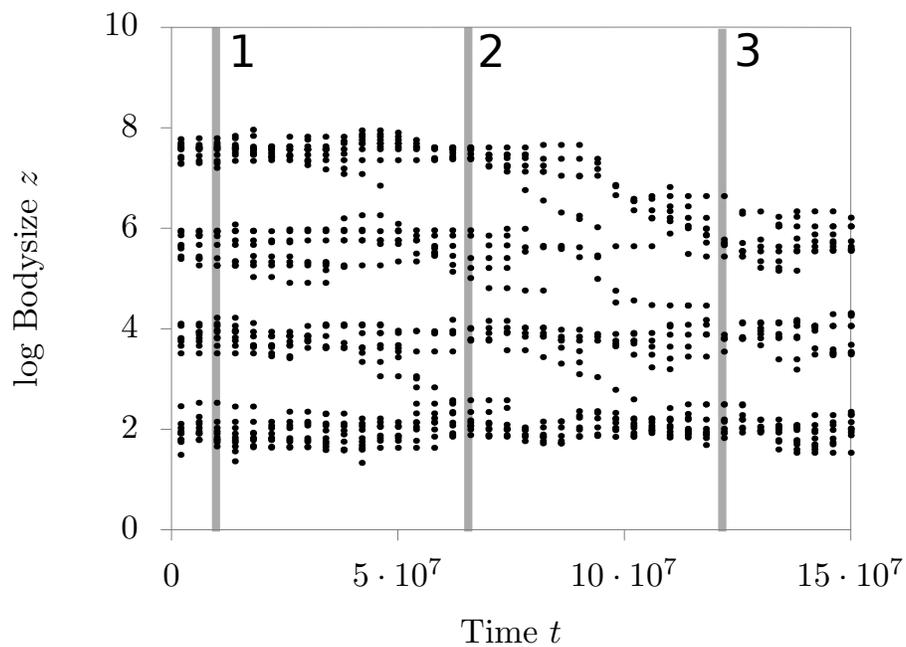


Figure A.12: Snapshot of the termination of an evolutionary outburst for the system shown in Fig. 5 (note that the time scale has been reduced to allow the dynamics of this process to be seen clearly). Evolutionary outbursts are characterised by the presence of an additional, unstable, layer of morphs at high bodysizes (1). The onset of termination occurs when there is insufficient resource flow to this layer, due to decreased morph density in the bodysize layer below it (2). The morphs in the upper bodysize layer slowly decrease their bodysize via numerous mutational steps, leaving this layer empty (3).

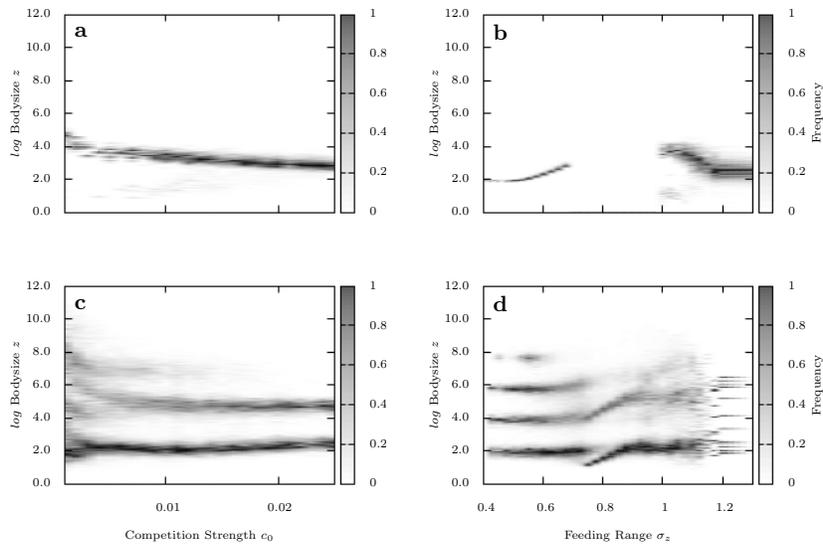


Figure A.13: Bodysize spectrum of communities with and without a trophic structure, along the cross sections of the parameter space, shown in Fig. 2. The first column shows cross section I (different values of competition strength c_0 , fixed $\sigma_z = 1$). The second column depicts cross section II (different values of feeding range σ_z , fixed $c_0 = 0.005$). For each parameter we averaged over 100 simulation runs. **a,b:** Bodysize probability density function of communities without a trophic structure. **c,d:** Bodysize probability density function of communities with a trophic structure.