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## Author's Accepted Manuscript

Emergence of evolutionary cycles in size-structured food webs

Daniel Ritterskamp, Daniel Bearup, Bernd Blasius



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1 Emergence of evolutionary cycles in size-structured food  
2 webs

3 Daniel Ritterskamp<sup>a,b,\*</sup>, Daniel Bearup<sup>b</sup>, Bernd Blasius<sup>b</sup>

4 <sup>a</sup>*University of Bristol, Faculty of Engineering, Merchant Venturers Building, BS8 1UB,*  
5 *United Kingdom*

6 <sup>b</sup>*CvO University Oldenburg, ICBM, Carl-von-Ossietzky-Strasse 9-11, 26111 Oldenburg,*  
7 *Germany*

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8 **Abstract**

9 The interplay of population dynamics and evolution within ecological com-  
10 munities has been of long-standing interest for ecologists and can give rise  
11 to evolutionary cycles, e.g. taxon cycles. Evolutionary cycling was intensely  
12 studied in small communities with asymmetric competition; the latter drives  
13 the evolutionary processes. Here we demonstrate that evolutionary cycling  
14 arises naturally in larger communities if trophic interactions are present, since  
15 these are intrinsically asymmetric. To investigate the evolutionary dynam-  
16 ics of a trophic community, we use an allometric food web model. We find  
17 that evolutionary cycles emerge naturally for a large parameter ranges. The  
18 origin of the evolutionary dynamics is an intrinsic asymmetry in the feeding  
19 kernel which creates an evolutionary ratchet, driving species towards larger  
20 bodysize. We reveal different kinds of cycles: single morph cycles, and coevo-  
21 lutionary and mixed cycling of complete food webs. The latter refers to the  
22 case where each trophic level can have different evolutionary dynamics. We  
23 discuss the generality of our findings and conclude that ongoing evolution in  
24 food webs may be more frequent than commonly believed.

25 *Keywords:* Community Cycling, Taxon Cycles, Coevolution, Red-Queen  
26 Dynamics, Evolutionary Limit Cycles

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\*Corresponding author

*Email addresses:* [daniel.ritterskamp@bristol.ac.uk](mailto:daniel.ritterskamp@bristol.ac.uk) (Daniel Ritterskamp ),  
[daniel.bearup@uni-oldenburg.de](mailto:daniel.bearup@uni-oldenburg.de) (Daniel Bearup), [blasius@icbm.de](mailto:blasius@icbm.de) (Bernd Blasius)

## 27 1. Introduction

28 One of the main goals of evolutionary ecology is to gain insights into the  
29 interplay of population dynamics and evolution, shaping the structure and  
30 dynamics of communities [13, 7]. The outcome of eco-evolutionary processes  
31 is not easy to understand from first principles, but much progress has been  
32 achieved by theoretical approaches. Of particular interest are the condi-  
33 tions under which eco-evolutionary processes within communities give rise to  
34 dynamic patterns. Early theoretical studies of evolutionary driven commu-  
35 nity dynamics were restricted to simple community-modules of two or three  
36 species with fixed species roles and primarily focused on temporal changes  
37 in the abundance and mean trait values of different species or populations.  
38 These works studied the influence of co-evolution on the stability of predator-  
39 prey systems [27, 3, 2], the occurrence of character displacement in models  
40 of competition mediated by a quantitative trait [38, 35, 36, 42, 41], as well as  
41 the dynamics of co-evolutionary arms races [43]. Further theoretical analysis  
42 showed that evolution can also induce temporal changes in the composition  
43 and diversity of a community and may either increase species richness, for  
44 example via speciation events [31, 11], but may also reduce species richness,  
45 for example via self-extinction through evolutionary suicide [24, 15, 25].

46 One major insight of these studies was that the interplay of ecological  
47 and evolutionary processes does not inevitably lead to an evolutionary equi-  
48 librium, but can lead to a situation of non-equilibrium states, characterized  
49 by sustained evolutionary change. One particularly intriguing case is that  
50 of evolutionary cycling, which is the emergence of ongoing periodic changes  
51 in species traits or community states [12, 19]. In one of the first studies  
52 of evolutionary cycling, Rummel and Roughgarden [35] suggested the ap-  
53 pearance of community cycles, i.e. the occurrence of evolutionary cycles in  
54 the community composition going together with sustained species turnover.  
55 Rummel and Roughgarden [35] simulated the buildup of island faunas based  
56 on a model of competitive interactions mediated by bodysize as the dominant  
57 phenotypic trait. Thereby, one key ingredient for the emergence of commu-  
58 nity cycles was attributed to the asymmetry of species interactions, The  
59 resulting community cycles, sometimes referred to as taxon cycles [45, 34],  
60 describe a scenario where an island (or local habitat), which is initially oc-  
61 cupied by a single resident, is colonised by a new invading species of larger  
62 bodysize. The invading species forces the smaller resident to evolve to smaller  
63 bodysize, while following this evolutionary movement. The resulting coevo-

64 lutionary arms-race towards smaller bodysizes weakens the viability of the  
65 resident which is eventually driven to extinction, leading again to a single  
66 species community. It was shown that this simple mechanism is able to de-  
67 scribe the empirical patterns in the build-up of island faunas in the case of  
68 *Anolis* lizards in the Lesser Antilles [34] and was subsequently investigated in  
69 a series of further studies (e.g. [36, 42, 41, 24]). In these studies, it was found  
70 that community cycles are a robust model outcome, but the details of the  
71 cycles depend on the specific model assumptions. In particular, it is possible  
72 that the bodysize change of the cycle operates in the reverse direction, so  
73 that species are driven towards larger bodysizes.

74 Despite this progress in describing generic mechanisms of evolutionary  
75 cycling, the studies mentioned above are limited in several respects. First,  
76 most demonstrations of evolutionary community cycles are restricted to small  
77 communities, consisting of very few species. Recently, there has been much  
78 interest in the evolutionary build-up of community structure in multi-species  
79 communities [17, 6, 20, 37, 32]. However, these studies typically observed  
80 static community structures, whereas not much is known about the condi-  
81 tions that favour the emergence of ongoing evolutionary change and commu-  
82 nity cycling in multi-species assemblages [40, 39]. A second related question  
83 is whether larger communities can exhibit different coevolutionary processes  
84 that occur independently from each other in different community modules,  
85 possibly at different frequencies. Finally, even though community cycles have  
86 been studied extensively for competitive interactions, not much is known  
87 about their relevance in trophically structured communities. This is quite  
88 astonishing, given the striking structural similarity of allometric evolutionary  
89 food web models [7] to competition models on a niche axis [35, 41].

90 One of the first allometric evolutionary food web models was introduced  
91 by Loeuille and Loreau [20] and several variants were studied in great detail  
92 [21, 20, 4, 8, 5]. In this model class, similar to (Rummel and Roughgarden  
93 [35, 36]), each species is characterized by its bodysize as a major phenotypic  
94 trait, the interactions between species are determined by their differences  
95 in bodysize, and allometric relations are considered explicitly. The essential  
96 new ingredient of allometric food web models is that they not only con-  
97 sider competition between species of similar bodysize, but also incorporate  
98 trophic interactions between species, so that a large species is able to prey  
99 upon smaller species. Given the strong similarity between these two model  
100 classes and the fact that predator-prey interactions are naturally asymmet-  
101 ric, one would expect that evolutionary community cycles, similar to taxon

102 cycles in models of competition, are a typical outcome in evolutionary food  
103 web models. However, while several other studies have reported evolution-  
104 ary dynamics in such models, e.g. irregular extinction cascades [5], trophic  
105 outbursts [30] and Red Queen dynamics in two species communities [46], to  
106 date there has been no rigorous investigation of evolutionary cycling in this  
107 framework.

108 In this study, we revisit the well-studied evolutionary allometric food web  
109 model by Loeuille and Loreau [20]. We show that this model can indeed pro-  
110 duce evolutionary cycles in a large parameter range and that the possibility  
111 of evolutionary cycles is related to the competition between species. When  
112 Loeuille and Loreau [20] introduced this model, they found food webs that  
113 are relatively invariant over time. While these results proved to be robust  
114 to a broad range of feeding ranges and competition strength, the rest of  
115 the parameter space was relatively unexplored. In particular, the parameter  
116 governing the bodysize distance over which morphs can compete, the com-  
117 petition range, was limited to rather small values. While some biological  
118 justification for this range was given, we argue here that this range may be  
119 too small. If competition between species arises from niche overlap (sensu  
120 MacArthur and Levins [22]), we should expect a competition range that is  
121 significantly broader and is of the same order as the feeding range of a species.  
122 This would allow inter-species competition to have a much stronger effect on  
123 the evolutionary dynamics.

124 Motivated by this observation, we numerically investigate the evolution-  
125 ary behaviour in the model [20], by systematically varying the strength and  
126 range of the competition between species. Our simulations show that evolu-  
127 tionary cycling, where species are driven towards larger bodysizes, is natu-  
128 rally present in the model considered – not only between single species but  
129 also in large trophic communities. Thereby, we observe a plethora of regimes  
130 with distinct dynamics. Besides static food webs, we observe evolutionary  
131 single morph cycles, complex community cycles where different trophic levels  
132 undergo separate coevolutionary cycles, as well as transient dynamics. Us-  
133 ing invasion analysis and Pairwise Invasibility Plots (PIPs) we are able to  
134 support the numerical observations, which allows us to explain the mecha-  
135 nism underlying the evolutionary cycles. Our findings imply that ongoing  
136 evolution in food webs may be more frequent than commonly believed.

137 **2. Model**

138 We follow the evolutionary food web model by Loeuille and Loreau [20].  
 139 The model considers one basal resource, such as an inorganic nutrient, ( $i =$   
 140  $0$ ) and a variable number of evolving morphs ( $i = 1, \dots, N$ ). We use the  
 141 term morph, rather than species, since we are not considering the speciation  
 142 process. Each morph is described by its population biomass density  $B_i$  and  
 143 bodysize  $z_i$ . The resource has a total density  $B_0$  and is associated with a non-  
 144 evolving ‘bodysize’, which is fixed to the value  $z_0 = 0$ . The model consists of  
 145 two components: population dynamics and evolutionary dynamics, each of  
 146 which operate on different time scales. The population dynamics describe the  
 147 trophic interactions among morphs and determine their respective growth,  
 148 survival or extinction. On a longer time-scale, usually after the population  
 149 dynamics have reached an attractor, new morphs are added to the community  
 150 by an evolutionary algorithm.

151 *2.1. Population dynamics*

The change of biomass  $B_i$  of morph  $i$  is given by the Lotka-Volterra equations, accounting for reproduction, intrinsic mortality, and losses due to predation and interference competition [20]

$$\frac{dB_i}{dt} = B_i \left( \underbrace{f(z_i) \sum_{j=0}^N \gamma(z_i - z_j) B_j}_{\text{Reproduction}} - \underbrace{m(z_i)}_{\text{Mortality}} - \underbrace{\sum_{j=0}^N \gamma(z_j - z_i) B_j}_{\text{Predation loss}} - \underbrace{\sum_{j=1}^N \alpha(|z_i - z_j|) B_j}_{\text{Competition}} \right). \quad (1)$$

Here, the intrinsic mortality  $m(z_i) = m_0 z_i^{-0.25}$  and the production efficiency  $f(z_i) = f_0 z_i^{-0.25}$  scale according to allometric relations with bodysize [26]. The function  $\gamma(z_i - z_j)$  describes the consumption rate exerted by predator  $i$  on prey  $j$ . The model assumes that the feeding efficiency decays with the bodysize difference as a one tailed Gaussian function

$$\gamma(z_i - z_j) = \begin{cases} \frac{\gamma_0}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(z_i - z_j - d)^2}{\sigma^2}\right), & z_i > z_j, \\ 0, & z_i \leq z_j, \end{cases} \quad (2)$$

152 where  $d$  is the optimal predator-prey bodysize distance,  $\gamma_0$  can be used to  
 153 scale the maximal consumption strength, and  $\sigma$  describes the feeding range

154 of a morph (i.e., the Gaussian function has standard deviation of  $\sigma/\sqrt{2}$ ). The  
 155 cut-off for  $z_i \leq z_j$  in the feeding kernel implies that a predator is only able  
 156 to consume prey with a strictly smaller bodysize. This causes an asymmetry  
 157 in trophic interactions, giving the larger of two similar sized morphs a small  
 158 advantage since it can consume, but cannot be consumed by, the smaller  
 159 one. Additionally, we also tested a smooth feeding kernel. Our numerical  
 160 simulations revealed that our main conclusions are valid also for a smooth,  
 161 but asymmetrical feeding kernel (see Fig A.7).

The function  $\alpha(|z_i - z_j|)$  describes interference competition between two  
 morphs  $i$  and  $j$ . It is modelled as a symmetric rectangular function (the  
 competition kernel) of bodysize differences

$$\alpha(|z_i - z_j|) = \begin{cases} \alpha_0, & |z_i - z_j| < \beta, \\ 0, & |z_i - z_j| \geq \beta, \end{cases} \quad (3)$$

162 where  $\alpha_0$  is the competition strength and  $\beta$  the competition range.

The change in the density of the resource  $i = 0$  follows a chemostat  
 equation

$$\begin{aligned} \frac{dB_0}{dt} = & I - eB_0 - \sum_{j=1}^N \gamma(z_j) B_j B_0 + \nu \sum_{j=1}^N \sum_{i=1}^N \alpha(|z_j - z_i|) B_j B_i \\ & + \nu \sum_{j=1}^N m(z_j) B_j + \nu \sum_{j=1}^N \sum_{i=1}^N (1 - f(z_j)) \gamma(z_j - z_i) B_j B_i, \end{aligned} \quad (4)$$

163 consisting of a constant resource inflow  $I$ , a relative outflow of rate  $e$ , losses  
 164 due to consumption by morphs, and three terms describing the recycling of a  
 165 fraction  $\nu$  of dead biomass from interference competition, intrinsic mortality,  
 166 and consumption.

167 In this model, the interaction kernels for feeding and competition are both  
 168 discontinuous. This discontinuity could influence the population dynamics  
 169 and thus the evolutionary behaviour. However, we find that our results are  
 170 qualitatively unchanged when these discontinuous functions are replaced with  
 171 continuous functions (see Fig A.7).

## 172 2.2. Evolutionary dynamics

173 The system is initialized with the resource (trait value  $z_0 = 0$  and ini-  
 174 tial biomass  $B_0 = I/e$ ) and a single evolving morph of bodysize  $z_1 = d$ ,

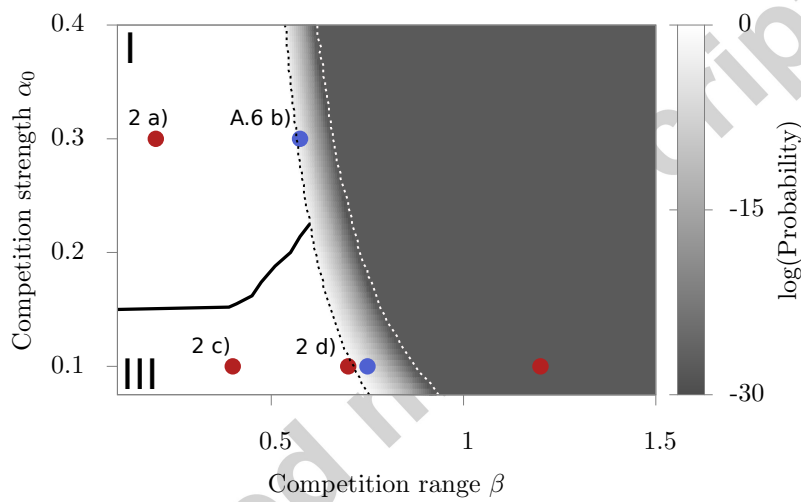


175 corresponding to a maximal consumption rate on the resource. Each morph  
 176 mutates at a constant rate of  $\omega_0$  per unit biomass and unit time. At each mu-  
 177 tation event of a morph  $k$ , a new morph is added to the system with bodysize  
 178  $z_M$  that is randomly chosen from the mutation interval  $[0.8 z_k, 1.2 z_k]$ . This  
 179 interval is centred around, and increases linearly with, the bodysize of the  
 180 mutating morph  $z_k$ . The new morph is introduced with an initial biomass of  
 181  $\theta$ , which is also the extinction threshold. If due to the population dynamics  
 182 the biomass  $B_k$  of any morph falls below this threshold  $\theta$ , it is considered  
 183 extinct and removed from the system.

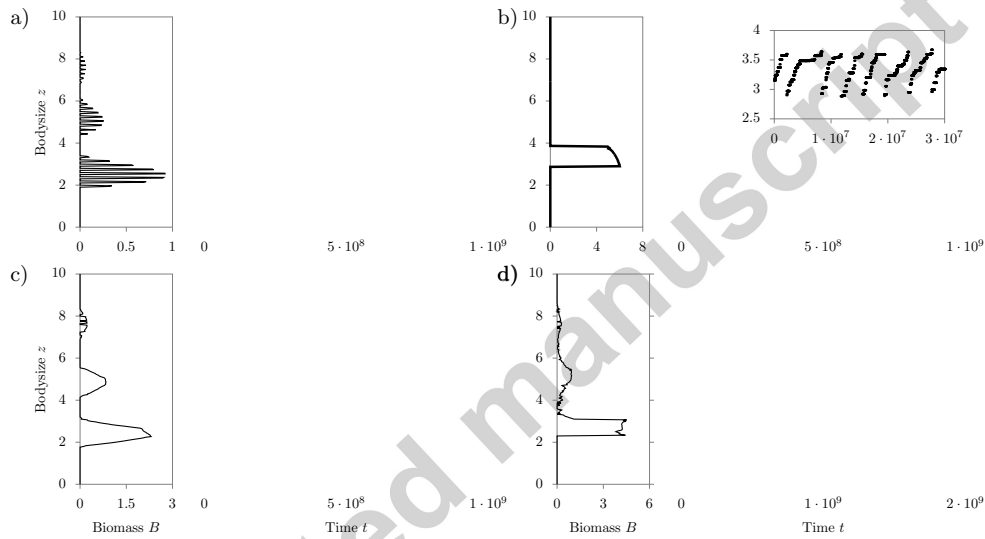
### 184 *2.3. Parameter values, implementation, and cycle detection*

185 We varied the range  $\beta$  and the strength  $\alpha_0$  of the competition kernel  
 186 as our main control parameters. The other model parameters are fixed to:  
 187  $f_0 = 0.3$ ,  $m_0 = 0.1$ ,  $\gamma_0 = 1/\sqrt{2}$ ,  $d = 2$ ,  $I = 10$ ,  $e = 0.1$ ,  $\nu = 0.5$ , and  
 188  $\sigma = \sqrt{2}$ . In contrast to Loeuille and Loreau [20] we increased the extinction  
 189 threshold from  $\Theta = 10^{-20}$  to  $\Theta = 10^{-10}$  (see also Allhoff and Drossel [4])  
 190 and the mutation rate from  $\omega_0 = 10^{-6}$  to  $\omega_0 = 10^{-5}$ . Our robustness tests  
 191 showed that these deviations from the original model formulation have no  
 192 effect on the model outcome, but they allowed us to substantially increase  
 193 the evolutionary time considered over our simulation runs. If not stated  
 194 elsewhere, the simulations were carried out over  $10^9$  time-units. Numerical  
 195 simulations were performed using a Runge-Kutta-Fehlberg method 4/5 [28]  
 196 which was implemented in C++.

197 We say that we observe an evolutionary cycle if a simulated time series  
 198 contains at least one whole period of a cycle after an initial build up phase of  
 199  $10^8$  time-units. Therefore, the maximal observable period length is limited  
 200 by the remaining  $9 \cdot 10^8$  time-units. If the period length of a cycle is close  
 201 to this limit, cycling is difficult to detect and can depend on the build-up  
 202 phase. To aid detection, we consider 5 realisations per parameter set with  
 203 different seeds for the random numbers in the evolutionary algorithm. If  
 204 any of these runs displays cycling we classify the parameter set as producing  
 205 cycling behaviour. Thus, the distinction between static and cycling food  
 206 webs depends on the time interval and the threshold condition (one period)  
 207 used, especially in the transition regions.



**Figure 1:** Map of the evolutionary behaviour in dependence of the competition parameters. The map splits into four regions of distinct dynamic behaviour: Static food webs (region I), single morph cycles (region II), complex community dynamics (region III), and a transition regime in which single morph cycles occur but the system eventually becomes polymorphic (region IV). The black solid line separates the regions of static (region I) and cyclic (region III) polymorphic food webs and is obtained from numerical simulations. The grey scale indicates the probability  $P$  for a monomorphic system to become dimorphic during one cycle period and is calculated by analysis of the invasion fitness in a monomorphic system (see section 3.2). The black dotted line shows the isocline of  $P = 1$ . To the right of this line single morph cycles can occur. The white dotted line indicates the isocline of  $\log P = -30$  and separates regions II and IV. The red dots correspond to the examples shown in Fig. 2 and the blue dots to the transition states shown in Fig. Appendix A.6.



**Figure 2:** Evolutionary food web dynamics for different competition parameters  $\beta$  and  $\alpha_0$ . Each subplot (**a-d**) corresponds to the parameter combination of a red point in Fig. 1 and shows the time evolution of bodysizes of all morphs after the initial build-up phase (right) and the corresponding biomass-bodysize histograms (left). **a)** Static food web, as in [20], for  $\alpha_0 = 0.3$  and  $\beta = 0.2$ . **b)** Single morph cycles ( $\alpha_0 = 0.1$  and  $\beta = 1.2$ ). The inset shows a close-up of the simulated cycle in bodysize for a shorter time range. **c)** Complex community dynamics, showing different coevolutionary cycles in each trophic level ( $\alpha_0 = 0.1$  and  $\beta = 0.4$ ). The vertical lines mark time-points at which the two largest morphs in the lowest trophic level are within competition range. **d)** Mixed evolutionary cycle, showing the coexistence of a single morph cycle in the lowest trophic level and coevolutionary cycles in the higher trophic levels ( $\alpha_0 = 0.1$  and  $\beta = 0.7$ ).

### 208 3. Results

#### 209 3.1. Numerical simulations, revealing four dynamics regions

210 We used numerical simulations to study the dependence of the evolution-  
 211 ary dynamics of the food web model on inter-species competition. Exploring  
 212 the parameter space  $(\beta, \alpha_0)$  of the competition kernel, we identified four  
 213 distinct behavioural regimes (regions I - IV). The regions in which each of  
 214 these behaviours occur are presented in Fig. 1 and exemplary time series for  
 215 all regimes are shown in Figs. 2 and A.6. Region I is characterized by the  
 216 build-up of evolutionary and convergence stable food webs, as introduced by  
 217 Loeuille and Loreau [20]. Region II exhibits single morph cycles. In this  
 218 region the community is composed of the resource and a monomorphic con-  
 219 sumer with a bodysize that is not constant but undergoes evolutionary cycles  
 220 within a narrow range. Region III features complex community dynamics.  
 221 This region is characterized by co-occurring single morph and polymorphic  
 222 coevolutionary cycles that cover several trophic layers. Region IV is a tran-  
 223 sition area in which an initial period of single morph cycles eventually gives  
 224 way to a polymorphic community. The resulting food webs can be evolu-  
 225 tionarily static or dynamic. Our numerical simulations showed that the map  
 226 of evolutionary outcomes in Fig. 1 is generic towards parameter variation  
 227 (e.g.  $\sigma, \gamma_0$ ). That is, while the size of the regions may change, as long as the  
 228 parameters chosen allow trophic structure each of these types of behaviour  
 229 can be found. We consider each state, and the transition between states, in  
 230 more detail below.

231 *Static food webs: region I.* For small competition ranges  $\beta$  and high com-  
 232 petition strengths  $\alpha_0$  (region I) we obtain food webs that are close to an  
 233 evolutionarily and convergence stable state. This is exactly the behaviour  
 234 observed by Loeuille and Loreau [20]. Fig. 2a shows an example time series  
 235 for a static food web and its distribution of biomass relative to bodysize.  
 236 After an initial build-up (not shown), the network structure and morph com-  
 237 position of the food web is practically static. It consists of several distinct  
 238 bodysize clusters, each centred at a bodysize which is a multiple of the op-  
 239 timal feeding distance  $d$ . These clusters are analogous to trophic levels. In  
 240 particular, a morph in a given cluster predominantly consumes morphs in the  
 241 cluster immediately below it and, similarly, is mainly consumed by morphs  
 242 in the cluster immediately above it. Trophic levels are further separated into  
 243 sharp bodysize layers. That is, morphs in the same trophic level are sepa-  
 244 rated by a bodysize distance of  $\beta$ , which allows them to avoid interference

245 competition (note that here  $\beta$  is much smaller than the optimal feeding dis-  
 246 tance  $d$ ). In the left panel of Fig. 2a, we plot the average biomass of morphs  
 247 of a given bodysize throughout the simulation. This distribution is com-  
 248 posed of single peaks indicating that the morph composition is static after  
 249 the initial build up of the network. The envelope of all peaks within a trophic  
 250 level is bell shaped. This arises due to differences in growth rate within the  
 251 trophic level; morphs close to the centre of a trophic level are at the optimal  
 252 feeding distance to the centre of the trophic level below and thus are able to  
 253 grow faster. The total biomass of a trophic level decreases with increasing  
 254 bodysize, due to efficiency losses.

255 In the example given, the trophic levels are distinct. Increasing the feed-  
 256 ing range  $\sigma$ , or competition strength  $\alpha_0$  causes the trophic levels to widen  
 257 until the trophic levels merge. As the competition range  $\beta$  increases, the  
 258 bodysize distance between morphs within a trophic level increases and fewer  
 259 morphs can coexist in each level. For sufficiently large  $\beta$  only a single morph  
 260 can exist in the system and we enter region II.

261 *Single morph cycles: region II.* For large competition ranges  $\beta$  (region II) we  
 262 observe a new dynamic regime for this model, which we term single morph  
 263 cycles. This regime is characterized by a dynamic monomorphic community  
 264 that consists of the basal resource (of bodysize  $z_0 = 0$ ) and a single consumer  
 265 morph with a bodysize that is not constant but undergoes an evolutionary  
 266 cycle, see Fig. 2b. The inset shows a close-up of the time series which displays  
 267 the bodysize cycle more clearly. In addition, a close-up of the temporal  
 268 evolution of the bodysize and biomass over four complete periods of the cycle  
 269 is shown in the Appendix (Fig. A.5). At the beginning of a cycle, starting  
 270 with a small initial bodysize, the resident is repeatedly replaced by a slightly  
 271 larger morph. As the resident's bodysize increases, its biomass decreases,  
 272 as seen in the trapezoidal structure of the biomass-bodysize distribution in  
 273 the left panel of Fig. 2b and in Fig. A.5b in the Appendix. At the end of a  
 274 cycle, the now large resident is invaded and outcompeted by a small mutant  
 275 and the single morph cycle resets. The mechanism underlying this behaviour  
 276 is discussed in Section 3.2. In contrast to region I, the biomass-bodysize  
 277 distribution is continuous and not composed of single peaks, because morphs  
 278 occur across the whole bodysize range of a cycle.

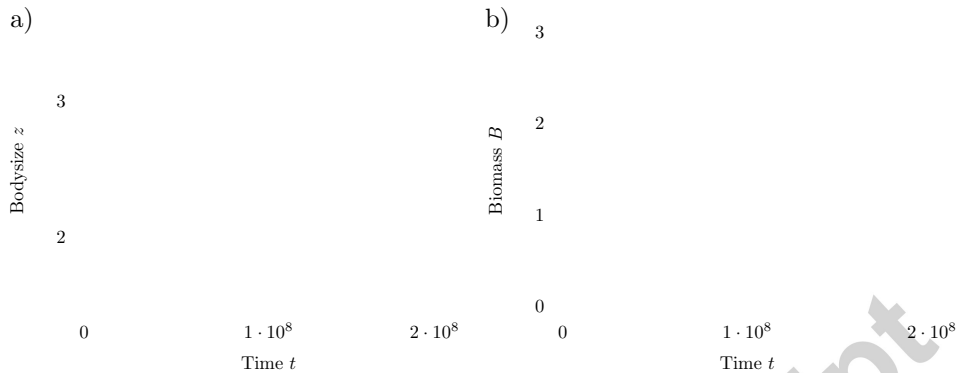
279 With increasing competition strength  $\alpha_0$  the frequency and amplitude of  
 280 the cycle decrease (not shown). The amplitude also decreases with decreasing  
 281 feeding range  $\sigma$ , but cycles are still present for  $\sigma < 0.5$ . We note that the

282 competition range  $\beta$  always encompasses the entirety of the bodysize range of  
 283 a single morph cycle. As  $\beta$  decreases we eventually reach a threshold where  
 284 the system can support a polymorphic food web and enter either region I or  
 285 region III.

286 *Complex community dynamics and coevolutionary cycles: regions III and*  
 287 *IV.* For low competition strength  $\alpha_0$  and small to intermediate competition  
 288 range  $\beta$  we obtain a regime of complex community dynamics (region III),  
 289 characterized by polymorphic food webs which are evolutionarily dynamic.  
 290 Example time series for this region are plotted in Figs. 2c and d. In this  
 291 regime, each trophic level within the food web undergoes an evolutionary  
 292 cycle. This can be a single morph cycle, as described in the previous section  
 293 (e.g., the lowest trophic level in Fig. 2d), or a coevolutionary cycle, in which  
 294 the trophic level consists of multiple coevolving morphs (e.g., the lowest  
 295 trophic level in Fig. 2c).

296 A close-up of the temporal dynamics of bodysizes and biomasses during  
 297 a coevolutionary cycle is shown in Fig. 3. At the beginning of the cycle,  
 298 the bodysizes of all morphs within the trophic level increase gradually in  
 299 successive interdependent mutational steps, while maintaining a constant  
 300 bodysize distance equal to the competition range. Initially this increase is  
 301 gradual until, eventually, the largest morph goes extinct. The remaining  
 302 morphs then rapidly increase their bodysize to fill this vacated niche. This  
 303 effect cascades down to each of the smaller morphs allowing them to increase  
 304 their bodysizes at a similar rate. This upwards movement also leaves a niche  
 305 at small bodysize which a new morph can invade, which functionally resets  
 306 the cycle to its initial state. The biomasses of the larger two morphs decrease  
 307 as their bodysize increases (e.g. red curve in Fig. 3). This is because as their  
 308 bodysize increases they move away from the optimal distance at which to  
 309 feed on the next lowest trophic level. In contrast, the biomass of the smallest  
 310 morph increases (e.g. blue or yellow curves), as it approaches the optimal  
 311 feeding distance. The biomass of the intermediate morph (e.g. black or blue  
 312 curves) stays relatively constant, as its bodysize moves from one side of the  
 313 optimal feeding distance to the other.

314 While this describes the coevolutionary cycle within a trophic layer, dif-  
 315 ferent trophic levels within a food web undergo independent cycles. Fig. 2c,  
 316 for example, shows a food web in which only coevolutionary cycles occur.  
 317 The network has basically the same structure as in the static case, consisting  
 318 of three trophic levels (Fig. 2a), but it is evolutionarily dynamic. Within a



**Figure 3:** Evolutionary dynamics during a coevolution cycle. **a)** Close-up of the time evolution of morph bodysizes  $z_i(t)$  within one trophic layer, here shown for the first trophic level of Fig. 2c. **b)** Corresponding time evolution of morph biomasses  $B_i(t)$ . Identical colours denote evolutionary akin morphs. The vertical lines mark time instances at which the two largest morphs in this trophic layer have a bodysize distance smaller than  $\beta$ . At these points the largest morph goes extinct and a new morph with smaller bodysize can invade the system.

319 trophic level, morphs coevolve, increasing their bodysize together, but these  
 320 coevolutionary dynamics seem to be independent of the cycling within other  
 321 trophic levels. In particular, the frequency of these cycles decreases with  
 322 trophic level; about two or three cycles of the lowest trophic level occur for  
 323 every single cycle of intermediate trophic level, while the highest trophic level  
 324 is nearly static. This decrease reflects the fact that the overall mutation rate  
 325 decreases with trophic level since, as observed in the static case (region I),  
 326 the biomass of each successive trophic level is less than that of the previous  
 327 one. In contrast to the static case, the cycling causes the biomass-bodysize  
 328 distribution to become continuous as for single morph cycles (region II). This  
 329 biomass distribution does not vary through a cycle, and, as a consequence  
 330 the cycling of lower trophic levels does not influence higher trophic levels.

331 Coevolution cycles arise in food webs when the competition strength  $\alpha_0$   
 332 and the competition range  $\beta$  are low (see Fig.1). They also occur if  $\alpha_0$   
 333 is zero. As for single morph cycles, when  $\alpha_0$  increases the frequency and  
 334 amplitude of a coevolution cycle decreases, until at sufficient large values of  
 335  $\alpha_0$  the different trophic layers of the food web become evolutionarily static  
 336 in a series of successive infinite period bifurcations. Finally, when a critical  
 337 threshold is passed the system enters region I. On the other hand, starting  
 338 again in region III, with increasing  $\beta$  fewer morphs can exist in a trophic level  
 339 (in an analogous way to that described in Section 3.1). As a consequence, the

340 frequency of these cycles slightly increases with  $\beta$  because with decreasing  
 341 number of morphs but constant nutrient input, each morph can acquire a  
 342 higher biomass, which increases the mutation rates and the evolutionary  
 343 speed. Finally, for sufficiently large  $\beta$  we observe the collapse of the whole  
 344 polymorphic system into a single morph cycle (region II).

345 For intermediate values of  $\beta$ , it is also possible for the lowest trophic level  
 346 to transition to single morph cycles, while the other trophic levels are un-  
 347 affected, see Fig. 2d. We call such cases mixed evolutionary cycles. Food  
 348 webs undergoing mixed evolutionary cycling have clear similarities to those  
 349 displaying purely coevolutionary cycling. In Fig. 2d we still see three distinct  
 350 trophic levels with continuous biomass-bodysize distributions. However, the  
 351 upper two trophic levels are much closer together than in the purely coevolu-  
 352 tionary case. In addition, while the biomass-bodysize distributions of these  
 353 levels remain bell shaped the distribution for the lower trophic level is ap-  
 354 proximately rectangular, a clear precursor to the trapezoidal form obtained  
 355 for single morph cycles, see Fig. 2b. Note that the lower trophic level can  
 356 occasionally support a second resident, see Fig. 2d at time  $t = 5 \cdot 10^8$ . The  
 357 single morph cycle stops and both residents increase in bodysize. Eventu-  
 358 ally the bigger morph goes extinct, as in a coevolution cycle, and the single  
 359 morph cycle starts again. The origin of mixed evolutionary cycles can be ex-  
 360 plained by the observation that the lowest trophic level is subject to especially  
 361 strong predation pressure because its residents can be consumed by morphs  
 362 in all higher trophic levels. Predation and competition strength,  $\alpha_0$ , have  
 363 the same structure, so the effect of higher predation is similar to imposing a  
 364 higher value of  $\alpha_0$  on the lowest trophic level. As a consequence, by compar-  
 365 ison with Fig. 1, this trophic level can collapse into a single morph cycle for  
 366 a value of  $\beta$  at which the higher trophic levels still perform coevolutionary  
 367 cycles.

368 The transition into region II, by further increase of  $\beta$ , is characterized  
 369 by a region of transient single morph cycles (region IV). In this regime,  
 370 we can observe single morph cycles that persist only for a finite time and  
 371 eventually become polymorphic. The resulting polymorphism can be either  
 372 evolutionarily static or dynamic, depending on the competition strength  $\alpha_0$ .  
 373 If decreasing  $\beta$  returns the system to region III, as above, we obtain a mixed  
 374 evolutionary cycle (see example time series in Fig. A.6a). Alternatively, if  
 375 decreasing  $\beta$  returns the system to region I then we will obtain a static food  
 376 web (see Fig. A.6b). As  $\beta$  increases, the probability that a polymorphic state  
 377 emerges from these single morph cycles declines, eventually reaching zero as



378 the system enters region II.

379 *3.2. Invasion analysis*

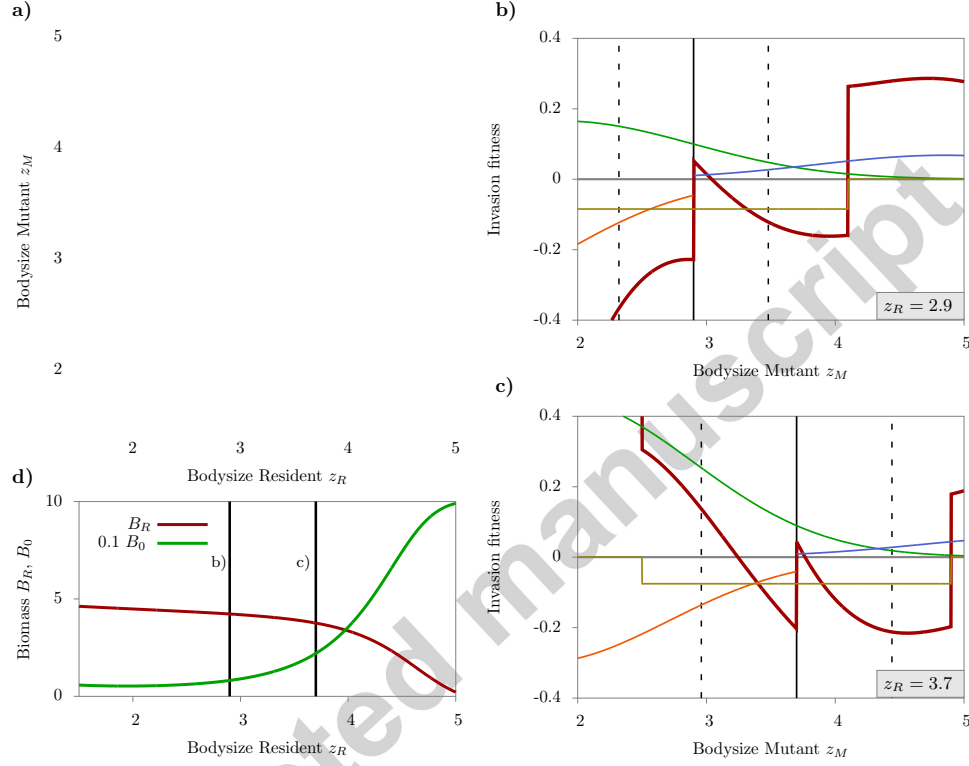
*Anatomy of a Single Morph Cycle.* The existence of evolutionarily dynamic food webs has not previously been observed in this model. In this section we seek to develop an understanding of these dynamic states. We start by considering single morph cycles, which are characterized by a monomorphic system that undergoes a sequence of replacements of a resident,  $z_R$ , by a slightly larger mutant,  $z_M$ . Eventually this gradual increase in resident bodysize ends when a small morph is able to invade and the cycle resets (Fig. 2b). To gain insight into this process, we consider the invasion fitness  $s(z_M, z_R)$  of a mutant  $z_M$  in a monomorphic system of bodysize  $z_R$  [14]. The invasion fitness  $s(z_M, z_R)$  can be derived from Eq. (1) and is given by:

$$\begin{aligned} s(z_M, z_R) = & f(z_M) \gamma(z_M) B_0 + f(z_M) \gamma(z_M - z_R) B_R - m(z_M) \\ & - \gamma(z_R - z_M) B_R - \alpha(|z_M - z_R|) B_R. \end{aligned} \quad (5)$$

380

381 Here,  $B_0$  and  $B_R$  denote the equilibrium biomasses of the resource and the  
382 resident in the monomorphic system and are given by Eqs. (1) and (4). To  
383 gain analytically tractable expressions for the invasion fitness, we neglect the  
384 nutrient recycling terms in Eq. (4), that is we take  $\nu$  equal to zero.

385 A positive invasion fitness  $s(z_M, z_R) > 0$  indicates that the mutant is able  
386 to invade and establish itself. Assuming that the population stays monomor-  
387 phic, we can use Eq. (5) to construct the bodysize ranges which characterize  
388 a viable mutant for a given resident bodysize. These ranges can be summa-  
389 rized graphically using Pairwise Invasibility Plots (PIP) [14]. In Fig. 4a we  
390 plot a PIP for the parameter set used to obtain Fig. 2b. Using this PIP  
391 we find that the evolutionary cycle can be split into two phases as follows.  
392 Phase 1: For small resident bodysizes ( $z_R < 3.54$ ) only mutants with larger  
393 bodysizes have positive fitness. Thus, the resident's bodysize increases over  
394 evolutionary time via a series of replacements by a larger mutant (blue arrow  
395 in Fig. 4a). Phase 2: When the resident's bodysize reaches a critical value  
396 ( $z_R \geq z_J = 3.54$ ), a second positive fitness region emerges corresponding  
397 to mutants which are smaller than the resident. At this point a jump to a  
398 smaller bodysize becomes possible (green arrows in Fig. 4a). Such a jump  
399 can produce a resident morph small enough to return the cycle to its initial



**Figure 4:** Invasion analysis of a single morph cycle. **a)** Pairwise Invasibility Plot (PIP) in dependence of the bodysize of the resident  $z_R$  and of the mutant  $z_M$ . Regions with negative invasion fitness,  $s(z_M, z_R) < 0$ , are marked in white and regions with  $s(z_M, z_R) > 0$  in grey. The bold line designates the points at which mutant and resident have identical bodysizes ( $z_M = z_R$ ), dashed lines enclose the mutation interval ( $0.8z_R$  and  $1.2z_R$ ), and dashed-dotted lines the competition range ( $z_R \pm \beta$ ). The arrows outline trajectories during a single morph cycle. The shaded areas delineate the variance of bodysizes during a cycle, where a resident may exceed the jump point (blue shaded area) or have varying initial bodysize (green shaded area). **b, c)** Fitness landscape as a function of the mutant's bodysize  $z_M$ , at the beginning of a cycle for  $z_R = 2.9$  (**b**) and close to the end for  $z_R = 3.7$  (**c**). The plot shows the invasion fitness (red) and its composition by growth due to resource consumption (green) and predation (blue) and by losses due to predation (orange), and interference competition (yellow), according to Eq. (5). For visualization all growth terms are rescaled by a factor of 0.2. The vertical solid line marks the bodysize  $z_R$  of the resident and the two dashed lines border the mutation interval. **d)** Equilibrium biomass of the resident,  $B_R$ , and of the resource,  $B_0$ , as a function of  $z_R$ . The vertical lines mark the values of  $z_R$  corresponding to panels **b**) and **c**). Parameter values are  $\beta = 1.2$ ,  $\alpha = 0.1$ , corresponding to Point 2b in Fig. 1.

400 state. Having outlined the cycle we now consider its two phases in more  
 401 detail.

402 In Fig. 4b we plot the invasion fitness (i.e., a cross-section of the PIP)  
 403 for a typical point ( $z_R = 2.9$ ) in Phase 1 of the cycle. The dependence of  
 404 the invasion fitness  $s(z_M, z_R)$  on the bodysize of the mutant  $z_M$  (red curve)  
 405 shows a non-monotonic behaviour, which can be explained by the way in  
 406 which  $s(z_M, z_R)$  is composed by different gain and loss terms in Eq. (5). We  
 407 see that the effects of intrinsic mortality (purple) and competition (grey)  
 408 are relatively constant with respect to mutant bodysize, at least within the  
 409 mutation interval. Note though, that the competition loss disappears for  
 410  $z_M > z_R + \beta$ , giving rise to the upward jump of the invasion fitness at  
 411  $z_M = 4.1$ . Here, this region of increased invasion fitness is outside of the  
 412 mutation interval and does not interfere with the single morph cycle. Growth  
 413 due to resource consumption (green) declines gradually with mutant size,  
 414 as larger morphs have lower resource feeding efficiency (the size difference  
 415 becomes larger than the optimal feeding distance  $z_M - z_0 > d$ ). The most  
 416 significant factor is the effect of asymmetry in the predation interactions. In  
 417 particular, mutants that are larger than the resident are able to increase their  
 418 growth by feeding on it (blue), while mutants smaller than the resident suffer  
 419 from predation by the resident (orange). This results in an upward jump of  
 420 the invasion fitness at  $z_M = z_R$ , which is sufficient to off-set the moderated  
 421 decay in feeding efficiency creating a region of positive invasion fitness for  
 422 increased bodysizes  $z_M > z_R$ . Consequently, the only viable evolutionary  
 423 path in Phase 1 is increasing bodysize (blue arrow).

424 With increasing bodysize of the resident  $z_R$ , the decline in the feeding  
 425 efficiency on the resource becomes more severe because the deviation from  
 426 the optimal feeding distance to the resource increases. As a consequence,  
 427 the invasion fitness is increasingly dominated by the relative contribution of  
 428 the feeding efficiency (green). In contrast, the jump in the invasion fitness  
 429 at  $z_M = z_R$  due to the asymmetry of predation remains largely independent  
 430 of  $z_R$ . As a consequence, the region of positive fitness for larger mutants  
 431 ( $z_M > z_R$ ) shrinks with increasing  $z_R$  (see Figs. 4a and c). Using analyti-  
 432 cal and numerical calculations (not shown) we found that this region finally  
 433 disappears for a resident bodysize of  $z_{max} = 5.09$  (independent of the com-  
 434 petition parameters  $\alpha_0$  and  $\beta$ ). As such  $z_{max}$  is the maximal achievable  
 435 bodysize of a morph in a monomorphic system for the given parameter val-  
 436 ues. Furthermore note that the probability of an evolutionary change, and  
 437 hence the speed of the evolutionary dynamics, is proportional to the ratio

438 of the positive fitness interval to the mutation interval. Thus, as the fitness  
 439 interval for larger morphs shrinks, the rate of increase in resident bodysize  
 440 decreases, going to zero as  $z_R$  approaches  $z_{max}$ .

441 These effects stem from the apparently paradoxical observation that,  
 442 while increasing bodysize is evolutionarily favoured, it results in a less fit  
 443 resident. The larger resident's lower feeding efficiency results in it being less  
 444 able to exploit the remaining resource at  $z_0$ . Consequently, as resident body-  
 445 size,  $z_R$ , increases, resident biomass and utilization of the resource decline.  
 446 This effect can be seen clearly by plotting resident and resource biomass  
 447 against resident bodysize, see Fig. 4d.

448 The increased availability of the resource is responsible for the emergence  
 449 of a second positive fitness interval found in Phase 2 of the cycle. A typical  
 450 invasion fitness profile is plotted in Fig. 4c. The contributions of most growth  
 451 factors are similar to those obtained in Phase 1 (Fig. 4b). However, now the  
 452 growth due to resource consumption depends more strongly on mutant size  
 453 and its maximum contribution is much higher. For sufficiently small mutants  
 454 the extra growth gained from greater feeding efficiency is able to off-set the  
 455 increased losses from predation, allowing a smaller mutant to displace the  
 456 resident (green arrows). We refer to the smallest resident bodysize for which  
 457 this is possible as the jump point  $z_J$  (for the chosen parameter values  $z_J =$   
 458 3.54). When a mutant with bodysize less than this threshold successfully  
 459 invades the system, the system resets to Phase 1.

460 Note that, since mutational steps are random, the range of bodysizes dur-  
 461 ing an evolutionary cycle varies. The resident's bodysize can exceed the jump  
 462 point before the smaller mutant invades (blue shaded area in Fig. 4a). Fur-  
 463 thermore, the smaller mutant can occur anywhere within the positive region  
 464 of the fitness cross-section obtained for a given resident. The combination  
 465 of these two effects allows the smaller mutant to emerge in a relatively wide  
 466 range (green shaded area in Fig. 4a).

467 We observed previously that the frequency of single morph cycles was  
 468 related to the competition strength  $\alpha_0$ . This can now be explained as fol-  
 469 lows. Note first that once the jump point is reached the cycle can be reset  
 470 in a single step. Furthermore, such a reset has a high probability, since the  
 471 positive fitness region for the smaller mutant is bigger than that for a larger  
 472 mutant. Thus, the system is unlikely to spend a significant amount of evo-  
 473 lutionary time in Phase 2. Consequently, the length of a cycle is primarily  
 474 determined by the number of evolutionary steps required to produce a resi-  
 475 dent with bodysize greater than  $z_J$ . The region of positive fitness larger than

476 the resident, which is responsible for the upwards movement (see Figs. 4a  
 477 and c), narrows with increasing competition strength  $\alpha_0$  (because the fitness  
 478 landscape is shifted downwards within the competition range). Therefore  
 479 increasing the competition strength reduces the evolutionary speed and thus  
 480 the frequency of the cycle.

481 In summary, the intrinsic asymmetry in the feeding kernel  $\gamma(\cdot)$  in Eq. (3)  
 482 creates an evolutionary ratchet, which results in an increase in the resident's  
 483 bodysize. However, the concomitant decrease in resident feeding efficiency  
 484 generates a nutrient environment which ultimately allows the invasion of a  
 485 small mutant. The interplay between these two processes results in a single  
 486 morph evolutionary cycle.

487 *Transition region to dimorphic states.* While in single morph cycles the mu-  
 488 tant always replaces the resident, we observed that in region IV single morph  
 489 cycles can become polymorphic. While the dynamics of such a polymor-  
 490 phic state are analytically intractable (at least using the techniques outlined  
 491 above), we are able to determine conditions under which a dimorphic state  
 492 can form. In particular, in this model two species are able to coexist only  
 493 if they do not compete directly; that is if the distance between their body-  
 494 sizes is greater than the competitive range,  $\beta$ . Thus a dimorphism becomes  
 495 possible when the mutation interval,  $[0.8z_R, 1.2z_R]$ , contains the competition  
 496 interval,  $[z_R - \beta, z_R + \beta]$ . We call the smallest resident bodysize where this  
 497 condition holds the dimorphic point,  $z_D$ , and note that it is related to the  
 498 competition range as follows,  $z_D = 5\beta$ . With this in mind the transitory sin-  
 499 gle morph cycles found in region IV can be explained by the random nature  
 500 of the mutational steps. In particular, when  $z_D > z_J$  the resident bodysize  
 501 must increase past  $z_J$  in order to reach the dimorphic point. Consequently  
 502 the system must enter Phase 2 and thus the possibility of the cycle reset-  
 503 ting before the system becomes polymorphic exists. The further above  $z_D$   
 504 from  $z_J$  the more likely it becomes that the cycle resets before it becomes  
 505 dimorphic. This intuition is justified formally below.

506 In Fig. 1, we plotted the probability of a single morph cycle becoming di-  
 507 morphic during a single cycle. This probability was estimated as follows: for  
 508 a fixed resident bodysize, the probability for a given mutational step attain-  
 509 ing a particular evolutionary outcome (dimorphism, upwards or downwards  
 510 movement in bodysize) is given by the range in the invasion fitness that leads  
 511 to the evolutionary event divided by the whole positive fitness area. The neg-  
 512 ative fitness area is not considered since an unsuccessful invasion does not

513 alter the system. We start with a resident of a bodysize of  $z_J$  and calculate  
 514 the probability of each evolutionary outcome (transition probability) for that  
 515 resident bodysize. In the next step, we increase the resident bodysize by the  
 516 expected mutational step-size of the upwards movement. (This is given by  
 517 the centre of the positive fitness responsible for upwards movement.) Thus  
 518 we calculate the transition probabilities at each of the expected bodysizes  
 519 between  $z_J$  and  $z_{max}$  and by doing this consecutively we consider all possible  
 520 evolutionary trajectories. These trajectories terminate when a dimorphism  
 521 emerges or the cycle resets (which is assumed to happen via a downwards  
 522 movement). The probability to become dimorphic along a given trajectory  
 523 is equal to the product of the transition probabilities of the steps in that tra-  
 524 jectory. The overall probability of reaching a dimorphic state is then given  
 525 by summing over all trajectories which reach this state.

526 *Complex Community Dynamics.* In region III we observe food webs that  
 527 contain coevolutionary, and occasionally single morph, cycles. We have pre-  
 528 viously observed that the cycles in distinct trophic levels are independent. As  
 529 such the behaviour of single morph cycles, even in a polymorphic system, can  
 530 be adequately understood in a monomorphic context, see above. Moreover,  
 531 the dynamic patterns of coevolutionary cycles can be understood in terms of  
 532 the evolutionary behaviour of morphs in a single trophic level. The increase  
 533 of a morph's bodysize in a coevolution cycle is due to the same mechanism as  
 534 in single morph cycles. The asymmetry in the feeding kernel  $\gamma(\cdot)$  (Eq. (3)),  
 535 creates an evolutionary ratchet, which drives the morphs to higher bodysizes  
 536 (see Fig. 3). However, the evolution of the morphs is limited by interference  
 537 competition. Each morph, except the largest and the smallest morph, have  
 538 two neighbours at a bodysize distance slightly bigger than the competition  
 539 range  $\beta$ . Therefore mutants of the intermediate morphs inevitably compete  
 540 with these neighbours and can not invade. While the smallest morph has only  
 541 a larger neighbour, smaller mutants are not viable due to the decreasing abil-  
 542 ity to feed on the lower trophic level and high intra trophic level predation.  
 543 The largest morph in an coevolution cycle has only a smaller neighbour,  
 544 thus it can increase its bodysize through the evolutionary ratchet. All other  
 545 morphs follow one after another, since they are not bounded upwards any  
 546 more. Therefore coevolution is a top-down process in this model. However,  
 547 just as in the single morph case, increasing bodysize results in the largest  
 548 morph reaching an unstable state where it can be invaded and outcompeted  
 549 by smaller mutants. This is analogous to the jump point of a single morph

550 cycle.

551 In contrast to single morph cycles, the largest resident is not outcompeted  
552 by a new offspring of its own, but by a mutant of the second largest resident.  
553 The second largest resident is replaced by a slightly larger mutant, which is  
554 within competition range  $\beta$  of the largest resident. (Time-points, at which  
555 the two largest residents compete are marked by grey vertical lines in Figs. 2c  
556 and 3.) This mutant is close enough to the optimal feeding distance that it  
557 can outcompete, and thus replace, the largest resident. Thus the interference  
558 competition from above is removed, allowing each of the resident morphs to  
559 increase its bodysize. A new mutant, descended either from the smallest  
560 resident, or from a resident in a lower trophic level, can invade either close  
561 to the end, or at the beginning, of a cycle; when the interference competition  
562 from the smallest resident is lowest.

#### 563 4. Discussion

564 The model introduced by Loeuille and Loreau [20] is well known for evo-  
565 lutionarily static food webs. We investigated a larger range of competition  
566 parameters, and found novel evolutionary states: cycling of single morphs  
567 (region II), cycling of complete food webs (region III), and transitory states  
568 from single morph cycles to polymorphic food webs (region IV). We want to  
569 discuss six main implications of our study:

570 First, the observed evolutionary cycles are based on coevolution, which is  
571 driven by competition and trophic interactions between resident morphs and  
572 also the invader. These coevolutionary processes are observed in empirical  
573 studies, where they can also be driven by competition [9, 23] or trophic in-  
574 teractions [1]. However, it is hard to study coevolution empirically in larger  
575 communities, due to the high number of complex interactions which make  
576 identification of the evolutionary dynamics and the coevolving traits very  
577 difficult [33]. Our findings show that it is not necessary to consider all inter-  
578 actions between species within the community to explain cycling. Instead,  
579 it is sufficient to consider interactions between smaller, independently coe-  
580 volving, subgroups. In our system, each trophic level represents a subgroup,  
581 since each level evolves independently with a different frequency.

582 Second, we found that food web characteristics are remarkably robust  
583 towards evolution. The network structure, number of morphs and links are  
584 relatively constant during evolution. In addition, the network structures  
585 of solely coevolving food webs and static food webs are similar. Therefore

586 they are not distinguishable on the time scale of the population dynamics.  
587 However for mixed evolutionary food webs the network structure changes: the  
588 number of species contained in each trophic level and the distance between  
589 each level loses its regularity.

590 Third, our results are in agreement with Cope's rule [10]: During an  
591 evolutionary cycle, morphs increase their bodysize, since a slightly larger  
592 morph has a higher fitness than a smaller morph. In addition, our study  
593 suggests a more natural explanation of the "Endless trends to gigantism"  
594 paradigm [16] than mass extinction [18]. Large bodysizes are advantageous  
595 over a wide range, especially towards similar sized morphs, but result in a  
596 lower ability to consume the original resource, which finally increases the  
597 vulnerability towards invasion of better adapted morphs.

598 Fourth, single morph cycles have similar characteristics to taxon cycles  
599 [34, 45], suggesting that the down-regulation of the environmental quality  
600 for the resident (decreasing resource consumption) is also responsible for  
601 the arising evolutionary cycling: the increase in bodysize of the resident,  
602 due to coevolution with invaders, results in morphs that are progressively  
603 less suited to their environment. Thus, morphs that are better adapted to  
604 the environment can invade. Furthermore, theoretical studies of competing  
605 species on a niche axis have shown that this class of evolutionary community  
606 cycles is related to the asymmetry in the competitive interaction (Rummel  
607 and Roughgarden [35], Taper and Case [41], Matsuda and Abrams [24]). In  
608 our study an asymmetry is introduced naturally via trophic interactions and  
609 therefore we suggest that evolutionary cycling is an intrinsic phenomenon in  
610 the model of Loeuille and Loreau [20], which can also occur in the absence  
611 of competition. Evolutionary cycling might be a general phenomenon in  
612 evolutionary size-structured food web models.

613 Fifth, our study provides a new avenue for the debate of whether ongoing  
614 evolutionary changes and Red Queen dynamics are ecologically realistic.  
615 Dieckmann et al. [12] proposed evolutionary limit cycles, e.g between predator  
616 and prey species, as a theoretical framework for Red Queen dynamics,  
617 but our study suggests an alternative mechanism. Thereby, in the simplest  
618 case of single morph cycles, the resident species is evolutionarily driven towards  
619 unfavourable positions in niche space, which reduces its viability and  
620 ultimately leads to self-extinction - so that the community can be colonized  
621 again by a mutant or invader at a different, more favorable, phenotypic trait.  
622 In contrast, in even the simplest predator-prey limit cycle, both species are  
623 present at all times.



624 Sixth, we propose that taxon cycles might be a transitory phase of island  
 625 colonisation: we observe that single morph cycles can be transitory states,  
 626 after which the community becomes polymorphic and large food webs emerge.  
 627 These webs can be either static or dynamic. The latter can be a possible  
 628 representation of cycling of larger communities – continental taxon cycles –  
 629 which are hypothesised, but hard to study empirically, due the intertwining of  
 630 the invasion processes [29]. Note that within the model used, the estimation  
 631 of the time scale considered is not possible without relating it to empirical  
 632 data, since all variables are treated as dimensionless.

633 As with all modelling studies, our results depend on the choice of pro-  
 634 cess formulations and simplifications used in the model. Here, we have  
 635 chosen to closely follow the formulation as defined by Loeuille and Loreau  
 636 [20]. While many compelling refinements of this model have been proposed  
 637 [21, 20, 4, 8, 5], our study shows that evolutionary community cycles are  
 638 already a natural outcome in the original model. Using extensive numerical  
 639 simulations we have confirmed that our main model results also hold in more  
 640 refined model variants. We briefly mention the two most influential changes:  
 641 to the competition and feeding kernels. First, following Loeuille and Loreau  
 642 [20] we have used a box-shaped kernel  $\alpha(\cdot)$  with a finite competition range  $\beta$   
 643 to describe the interference competition (Eq. (3)). Therefore, morphs either  
 644 compete with a fixed, well-defined strength, or competition is absent. More  
 645 realistically, competition strength should change continuously with bodysize  
 646 distance which could be described by link overlap (e.g. a Gaussian kernel)  
 647 sensu [22], as applied by [5, 8, 30]. Using numerical simulations we verified  
 648 that evolutionary cycling still occurs if the box-shaped interference competi-  
 649 tion is replaced by link overlap competition. Furthermore, the range of link  
 650 overlap competition is closely related to the feeding range  $\sigma$  of the compet-  
 651 ing morphs ( $\propto \sqrt{2}\sigma$ ). Comparing link overlap competition with box-shaped  
 652 competition shows that link overlap competition occurs over a wider bodysize  
 653 distance. This justifies the investigated competition range  $\beta$  in our studies.

654 Second, following Loeuille and Loreau [20], our chosen feeding kernel  $\gamma(\cdot)$   
 655 consists of a truncated Gaussian. This discontinuity could be responsible for  
 656 the cycling behaviour observed. However, when the discontinuous feeding  
 657 and competition kernels were replaced with continuous functions, we still  
 658 observed cycling see Fig. A.7. In particular, we note that it was necessary  
 659 to use an asymmetric feeding kernel (the ability to consume morphs with a  
 660 larger bodysize decreases faster than the ability to consume smaller morphs)  
 661 e.g. the Ricker function [44], in order to obtain this behaviour. Thus, we

662 conclude that cycling behaviour arises from strong asymmetries in the feeding  
663 kernel.

664 We have shown that evolutionary cycles occur in the evolutionary food  
665 web model used, it is robust towards variation in the shape and range of the  
666 feeding and competition kernels, and can manifest in various ways. However,  
667 the underlying mechanism, leading to evolutionary cycling, is not restricted  
668 to the model used. We suggest that evolutionary cycles might be a general  
669 phenomenon in evolutionary food web models and also empirical food webs  
670 and therefore conclude that evolutionary cycling in food webs may be more  
671 frequent than commonly believed.

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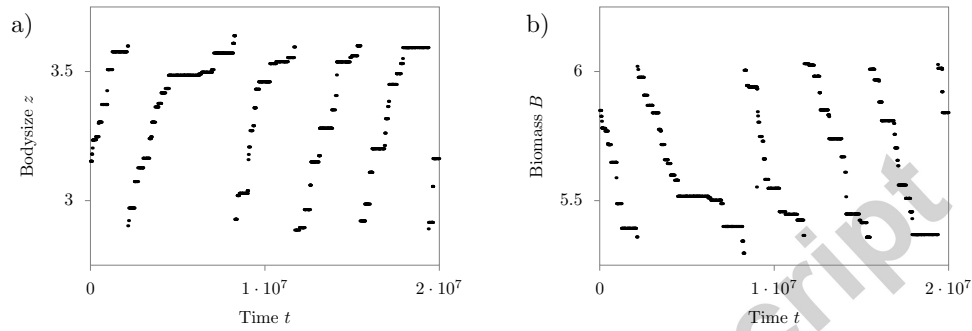
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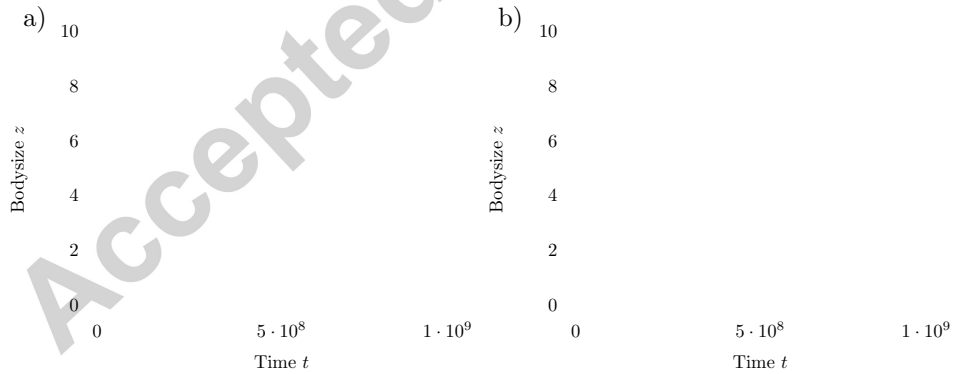
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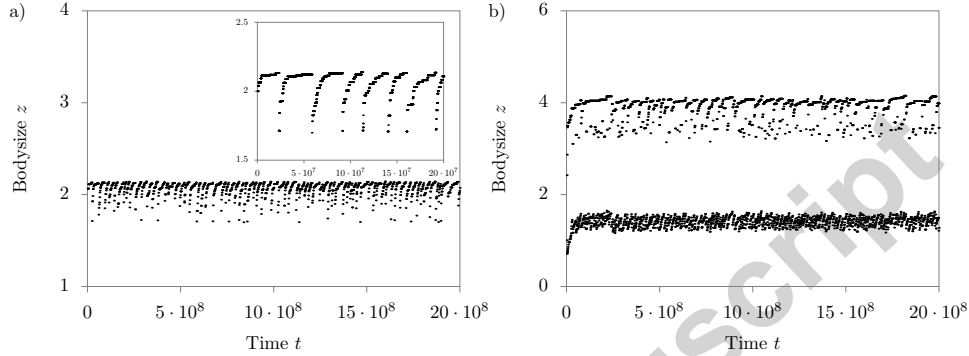
806 **Appendix A. Appendix**



**Figure A.5:** Evolutionary temporal behaviour of a single morph cycle (Fig. 2b)). **a, b:** Close-up of the biomass  $B$  and bodysize  $z$  during a single morph cycle shown in Fig. 2b.



**Figure A.6:** Transient dynamic. After a transient of single morph cycles the system becomes polymorphic. **a:** Mixed evolutionary behaviour of a food web is visible after the transition. The competition parameters are set to  $\alpha_0 = 0.1$  and  $\beta = 0.75$ . **b:** A static food web emerges after the transition. The competition parameters are set to  $\alpha_0 = 0.3$  and  $\beta = 0.58$ .



**Figure A.7:** Evolutionary food web behaviour for continuous feeding kernels. The interaction kernels are replaced by continuous functions. The original *feeding kernel*  $\gamma(\cdot)$  (Eq. 2) is replaced by a more ecologically accurate Ricker function [44],  $\gamma(z_i - z_j) = \frac{\gamma_0}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(\log(z_i - z_j) - \log(d))^2}{\sigma^2}\right)$ , which is asymmetric in respect to bodysize: the ability to consume larger morphs decreases faster than the ability to consume smaller morphs. The box shaped *competition kernel*  $\alpha(\cdot)$  (Eq. 3) is replaced by a Gaussian function,  $\alpha(|z_i - z_j|) = \frac{\alpha_0}{\beta\sqrt{2\pi}} \exp\left(-\frac{(z_i - z_j)^2}{\beta^2}\right)$ , similar to [8, 5, 30]. The Gaussian shape is motivated by competition due to link overlap as introduced by [22]. It is highest for identical bodysizes and decreases with the bodysize distance of the competing morphs. **a:** Single morph cycle for continuous interaction kernels, which is similar to the one observed in the original model, Fig. 2b ( $\sigma = 2.3, \alpha_0 = 0.2, \beta = 2$ ). **b:** Complex community cycles, that commemorate complex community cycles, see Fig. 2c,d ( $\sigma = 2.5, \alpha_0 = 0.2, \beta = 1.5$ ). All other parameters are set according to section 2.3.