

1 **Community structure and collapses in multi-channel food webs: role of consumer body sizes and**
2 **mesohabitat productivities.**

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27

28 **Abstract**

29 Multi-channel food webs are shaped by the ability of apex predators to link asymmetric energy flows in
30 mesohabitats differing in productivity and community traits. While body size is a fundamental trait
31 underlying life histories and demography, its implications for structuring multi-channel food webs are
32 unexplored. To fill this gap, we develop a framework that links population responses to predation and
33 resource availability to community-level patterns using a tri-trophic food web model with two
34 populations of intermediate consumers and a size-selective top predator. We show that asymmetries in
35 mesohabitat productivities and consumer body sizes drive food web structure, merging previously
36 separate theory on apparent competition and emergent Allee effects (i.e., abrupt collapses of top predator
37 populations). Our results yield theoretical support for empirically observed stability of asymmetric
38 multi-channel food webs and discover three novel types of emergent Allee effects involving
39 intermediate consumers, multiple populations or multiple alternative stable states.

40 **Introduction**

41 Non-random distribution of trophic links underlies the persistence and stability of food webs (Otto *et al.*
42 2007; Rooney *et al.* 2006). Most food webs rely on the linkage of alternative, asymmetric energy sources
43 by predators at higher trophic levels (Rooney *et al.* 2008; McCann & Rooney 2009; Barnes *et al.* 2018).
44 Asymmetric energy flows strengthen the resilience of food webs (Rooney *et al.* 2006; Wolkovich *et al.*
45 2014), e.g., by reducing population fluctuations and subsequent extinction cascades due to the paradox
46 of enrichment (Otto *et al.* 2007; Dolson *et al.* 2009). Asymmetric energy flows often arise in freshwater
47 ecosystems when mobile generalist predators link different mesohabitats, such as the littoral, pelagic
48 and benthic habitats in lentic systems (Schindler & Scheuerell 2002; Dolson *et al.* 2009; Marklund *et*
49 *al.* 2018) or downstream and upstream areas in lotic systems (Lapointe *et al.* 2010; Rosenblatt &
50 Heithaus 2011). Energy in these mesohabitats often comes from different sources and the flows differ
51 in turnover and production rates (Rooney & McCann 2012). In lentic systems, energy flow driven by
52 photosynthesis in the more productive ‘green’ pelagic mesohabitat is usually faster than the flow driven
53 by decomposers that depend on detritus and dissolved organic carbon in the ‘brown’ benthic mesohabitat
54 (Zou *et al.* 2016).

55 Asymmetries in regulatory processes within multi-channel food webs can influence the
56 coexistence of competing species at intermediate trophic levels. Such asymmetries can arise in bottom-
57 up regulatory processes from differences in basal productivity rate and prey biomass (Chesson & Kuang
58 2008; DeCesare *et al.* 2010) or in top-down processes stemming from differences in the feeding
59 behaviour of the top predator (Post *et al.* 2000; Marklund *et al.* 2019) and hence asymmetric predation
60 pressure (Rooney *et al.* 2006; Wolkovich *et al.* 2014). In particular, linkage by top predators may
61 influence communities in different mesohabitats in a way that either permits their coexistence or makes
62 the least resilient community vulnerable to extinctions as suggested by earlier work on apparent
63 competition in simple food web modules (Holt *et al.* 1994; Chase 1999).

64 Asymmetric energy flows in multi-channel food webs relate to the limiting similarity hypothesis
65 (MacArthur & Levins 1967), which posits that increasing niche overlap of co-occurring species
66 diminishes their ability to coexist (Mesz ena *et al.* 2006; Abrams & Rueffler 2009). For example, species
67 competing for a common resource and sharing the same predator can only coexist if they differ

68 sufficiently in morphological or physiological traits, niche overlap and environmental requirements
69 (Leibold 1996, 1998). Other studies, however, highlighted possible coexistence of similar species due
70 to symmetric predation pressure (Holt *et al.* 1994) or due to varying fitness caused by variable
71 phenotypes (Godoy *et al.* 2018; McPeck 2019) or variable body sizes.

72 Food webs can also undergo abrupt ecological regime shifts when they exceed their ecological
73 stability boundaries, leading to a switch between alternative stable states (May 1977; Scheffer *et al.*
74 2001). These shifts occur in response to external perturbations such as eutrophication in freshwater
75 (Folke *et al.* 2004; Scheffer & van Nes 2007) and marine habitats (Möllmann & Diekmann 2012;
76 Muthukrishnan *et al.* 2016), or in response to intrinsic perturbations inherent to population dynamics
77 such as Allee effects (de Roos & Persson 2002; Beisner *et al.* 2003; Oliver *et al.* 2015). Alternative
78 stable states in food webs can be generated by various mechanisms including intraguild predation,
79 apparent competition, prey size refugia, cannibalism and legacy effects during community assembly
80 (reviewed in Schröder *et al.* 2005 and Gårdmark *et al.* 2015). For example, prey size refugia can lead to
81 alternative stable states at intermediate nutrient levels in a food web consisting of two consumers sharing
82 the same resource and predator (Chase 1999, 2003). However, the propensity of multi-channel food
83 webs to ecological regime shifts has not yet been addressed.

84 Body size and resource productivity are ubiquitous drivers of community structure (Persson *et*
85 *al.* 2014). Empirical data show that differences in community size spectra underlie the existence of fast-
86 and slow-energy channels in aquatic food webs (Mehner *et al.* 2018). That is, pelagic habitats are
87 dominated by small-bodied phytoplankton and zooplankton, while benthic habitats host mainly larger-
88 bodied macroinvertebrates (McCann & Rooney 2009). Altogether, the combined asymmetries in
89 consumer body size and energy partition across mesohabitats could stabilize multi-channel food webs
90 (Rooney & McCann 2012) or promote population collapses (de Roos & Persson 2002) and alternative
91 stable states (Chase 2003), but we lack quantitative theory to resolve these interacting roles of consumer
92 body size and resource productivity in the structuring of multi-channel food webs.

93 To fill these gaps, we modelled the effect of varying body sizes and mesohabitat productivities
94 on multi-channel food webs. We focused on a case in which a top predator integrates two tri-trophic
95 chains with size-structured populations of intermediate consumers that differ in body size using a

96 modified tri-trophic chain model by de Roos & Persson (2002). This food chain model exhibits an
97 emergent Allee effect due to predation-induced competitive release in the prey (Gårdmark *et al.* 2015)
98 and the possibility of sudden predator collapse. Integrating two such food chains in different
99 mesohabitats with a shared top predator opens the possibility for additional, qualitatively different
100 community structures and steady state transitions. We thus examined how differences in productivity
101 and consumer body sizes affect consumer life histories, the structure of each food chain, apparent
102 competition between the intermediate consumers, and the persistence of the top predator. We were
103 particularly interested in the combinations of consumer body sizes and habitat productivities that (1)
104 enabled coexistence of the intermediate consumers when linked by the top predator and (2) lead to
105 alternative stable states and possible collapses of top predator or intermediate consumer populations.

106

107 **Methods**

108 *Food web structure*

109 Our minimal multi-channel, tri-trophic food web includes seven possible communities differing in the
110 presence of the intermediate consumers and the top predator (communities 0–6 in Fig. 1). For
111 convenience, we refer to the mesohabitats as pelagic ($i = 1$) and benthic ($i = 2$), each with its own basal
112 resource R_i and intermediate consumer species C_i , and apex predator P integrating both habitats. We
113 begin by outlining expected transitions between these communities. Increasing productivity in each
114 mesohabitat should lead to lengthening of the food chain and successful establishment of the consumer
115 followed by the top predator (Oksanen *et al.* 1981; Fretwell 1987) (community state transitions 0→1→4
116 and 0→3→6 in Fig. 1). Benthic and pelagic consumers coexist in the absence of the top predator if each
117 mesohabitat is sufficiently productive (community 2). Successful invasion of the top predator in this
118 community (transition 2→5) may subsequently affect consumer coexistence and lead to the exclusion
119 of the less resilient consumer due to apparent competition (transitions 5→4 or 5→6 in Fig. 1). Possible
120 alternative stable states involving two or more of these communities are described in Results.

121

122 *Population structure and dynamics*

123 In our model, the top predator P with a fixed body size feeds indiscriminately on the size-structured
 124 populations of intermediate consumers C_1 and C_2 , while each consumer population feeds on its own
 125 basal resource that follows a semi-chemostat dynamics with carrying capacity K_i and flow-through rate
 126 ρ_i ($i = 1, 2$). We keep the parameter values used in de Roos & Persson (2002) as a baseline scenario for
 127 the benthic food chain R_2 - C_2 - P and modify them for the pelagic food chain R_1 - C_1 - P (see below and
 128 Appendix S1 for details). We also assume that the pelagic resource R_1 has a faster turnover rate than the
 129 benthic resource R_2 (Fortier *et al.* 1994) and set $\rho_1 = 2 \rho_2$.

130 Individual consumers are born at length $l_{b,i}$, mature at length $l_{j,i}$ and can grow to the maximum
 131 length $l_{m,i}$ under unlimited resources ($i = 1, 2$). For simplicity, we assume that both consumers differ by
 132 a given size ratio in all three traits

$$133 \frac{l_{b,1}}{l_{b,2}} = \frac{l_{j,1}}{l_{j,2}} = \frac{l_{m,1}}{l_{m,2}} = \beta \quad (1)$$

134 (i.e., pelagic consumers are larger than benthic ones if $\beta > 1$ and smaller if $\beta < 1$) and that all processes
 135 regulating their populations are qualitatively identical, i.e., any differences arise only through their
 136 difference in body size and resource availability. Consumer individuals are characterized by size- and
 137 resource-dependent feeding rates $I_i(R_i, l_i)$ growth rates $g_i(R_i, l_i)$ and fecundities $b_i(R_i, l_i)$ and size- and
 138 predator-dependent mortality rates $\mu_i(P, l_i)$. Their individual biomass scales with l^3 with a proportionality
 139 constant ω . Individuals of both consumers die with the same size-independent background mortality
 140 rate μ_b and are further vulnerable to predation until reaching a vulnerability size threshold l_v . This
 141 vulnerability window provides a qualitatively correct description, e.g., for many fish population
 142 (Andersen & Beyer 2006). Ingestion rates of individual consumers with length l_i feeding on the
 143 respective basal resource R_i follow type II functional response, $I_i(R_i, l_i) = I_m l_i^2 R_i / (R_h + R_i)$ with the
 144 proportionality constant I_m and half-saturation constant R_h . Individuals of both consumers follow a von
 145 Bertalanffy growth curve with resource-dependent asymptotic size, $g_i(R_i, l_i) = k(l_{m,i} R_i / (R_h + R_i) - l_i)$,
 146 where k is the growth rate coefficient. They produce offspring after maturation at a *per capita* rate $b_i(R_i,$
 147 $l_i) = r_m l_i^2 R_i / (R_h + R_i)$, with a proportionality constant r_m . Finally, the top predators feed indiscriminately
 148 on vulnerable individuals from both consumer populations when present and follow a Holling type II

149 functional response with constant attack rate a and handling time h . We assume constant conversion
 150 efficiency ϵ of ingested prey biomass to predator biomass and background mortality rate δ of the top
 151 predators.

152 In sum, both tri-trophic food chains in our model have identical properties except the
 153 mesohabitat productivity and the ratio of consumer body sizes, although the model could be easily
 154 modified to further explore the consequences of, e.g., consumer-specific functional response parameters.
 155 The five-species community dynamics is described by the following set of ordinary and partial
 156 differential equations ($i = 1, 2$):

$$\begin{aligned}
 157 \quad \frac{dR_i}{dt} &= \rho_i (K_i - R_i) - \int_{l_{b,i}}^{l_{m,i}} I_i(R_i, l_i) c_i(t, l_i) dl \\
 158 \quad \frac{\partial c_i(t, l_i)}{\partial t} + \frac{\partial g_i(R_i, l_i) c_i(t, l_i)}{\partial l} &= -(\mu_b + dP) c_i(t, l_i) \\
 159 \quad g_i(R_i, l_i) &= \int_{l_{b,i}}^{l_{m,i}} b_i(R_i, l_i) c_i(t, l_i) dl \quad (2) \\
 160 \quad C_i &= \int_{l_{b,i}}^{l_v} \omega l_i^3 c_i(t, l_i) dl \\
 161 \quad \frac{dP}{dt} &= \left(\epsilon \frac{a(C_1 + C_2)}{1 + h(C_1 + C_2)} - \delta \right) P
 \end{aligned}$$

162 We focus on three key properties that can affect the community structure and transitions
 163 including the emergent Allee effects: consumer size ratio β and the productivity in each mesohabitat,
 164 which we attribute to the resource carrying capacities K_1 and K_2 . We first quantify the impact of
 165 consumer body size and habitat productivity on its ontogeny including predation risk, population growth
 166 rate, and birth rate with and without predation. We then examine the effects of consumer body size and
 167 habitat productivity on the structure of each food chain and the whole food web to understand how
 168 asymmetries in consumer body size and mesohabitat productivity influence the apparent competition
 169 between intermediate consumers and the whole community structure (Fig. 1). We solve Eq. 2
 170 numerically using the R package *PSPManalysis* version 3.1.2 (de Roos 2014, 2020) to track the system
 171 equilibria and detect thresholds associated with successful establishment or collapse of intermediate
 172 consumers and the top predator.

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Results

Effects of body size and habitat productivity on consumer life history

Body size has a strong effect on nearly all aspects of the intermediate consumer life history (Fig. 2). Larger consumers take longer time to reach their asymptotic size but benefit from an earlier escape from predation, while very small consumers ($\beta < 0.24$) stay vulnerable to predation even as adults (Fig. 2A). In the absence of predation, larger consumers have faster population growth rates (Fig. 2B) but lower birth rates than smaller consumers (Fig. 2C). Size-dependent predation releases the survivors from intraspecific competition and leads to higher birth rates relative to the non-predated population if some juvenile consumers are invulnerable to predation (ca. $\beta > 0.24$; red vs. black lines in Fig. 2C). As expected, consumers birth rates and population growth rates increase with habitat productivity at any given body size (Fig. 2B-C). In what follows, we constrain our analyses to sufficiently large consumers for which the adults are not vulnerable to predation ($\beta \geq 0.24$).

Tri-trophic chain: role of intermediate consumer body size and mesohabitat productivity

For a wide range of consumer body sizes, the food chain lengthens as the habitat productivity increases and exhibits an emergent Allee effect in the top predator with two alternative stable states at intermediate habitat productivity levels (community state 1/4; Fig. 3A). That is, a relatively high habitat productivity is required for the top predator population to establish, but established top predators can sustain lower habitat productivity as they modify the stage structure of the consumer population (de Roos & Persson 2002; also Fig. 4A for $\beta = 1.2$). The food chain collapses abruptly to a stable consumer-resource equilibrium when the habitat productivity decreases below the top predator persistence level (Fig. 4A). The productivity threshold required for consumer establishment is essentially independent of consumer body size, but those associated with top predator establishment and collapse are highly sensitive to consumer body size as top predators feeding on larger consumers require significantly higher resource productivity to survive (Fig. 3A). Finally, the top predator cannot survive when consumers become invulnerable to predation ($\beta > ca. 3.8$; Fig. 3A).

201 *Multi-channel food web: role of asymmetries in intermediate consumer size and mesohabitat*
202 *productivities*

203 Coexistence and exclusion of apparent competitors are determined by their relative ability to
204 sustain predation pressure. Here we analyse the effects of varying mesohabitat productivities and
205 consumer body size on the structure of the multi-channel food web, with emphasis on the coexistence
206 of both intermediate consumers. We found surprisingly complex patterns of consumer body size ratios
207 and habitat productivities required for their coexistence with the top predator. We first outline the range
208 of habitat productivity levels that maintain both benthic and pelagic consumers of a given size ratio in
209 the food web, and subsequently provide more detailed results on body size differences that enable
210 consumer coexistence and top predator persistence at given productivity levels in one of the
211 mesohabitats (community state 5 and states 2/5, 4/5, 5/6, 2/4/5 and 2/5/6 that include state 5 as one of
212 the alternatives; see Fig. 1).

213 For a given consumer body size ratio β , the food web structure is driven by the ratio of the
214 pelagic and benthic habitat productivity and the total effective productivity. The latter can be close to
215 the sum of resource carrying capacities K_1+K_2 (hereafter ‘total carrying capacity’, abbreviated as TCC)
216 irrespective of the relative contribution of the pelagic habitat $K_1/(K_2 + K_1)$ (hereafter abbreviated as PB
217 ratio) as in Fig. 3B, or depend on both the PB ratio and TCC (see below). Resource carrying capacity in
218 the given habitat determines the invasion threshold of each intermediate consumer (Fig. 5), while the
219 total effective productivity determines the invasion and collapse thresholds of the top predator (Fig. S1).
220 Competitive exclusion and coexistence of the two intermediate consumers when linked by the top
221 predator is driven mainly by the PB ratio (Figs. 3B and S3).

222 Consumer coexistence along the habitat productivity gradients is promoted by larger body size
223 differences. That is, the coexistence of all five species is constrained to a narrow range of PB ratios and
224 sufficiently high TCC values for same-sized intermediate consumers ($\beta \approx 1$; community states 5 and 2/5
225 in Figs. 5 and S3D). When one of the consumers is substantially larger ($\beta \ll 1$ or $\beta \gg 1$) and hence
226 competitively superior (see above), all five species can coexist only if its habitat is moderately
227 productive. Higher productivity values in that habitat lead to competitive exclusion of the smaller
228 consumer, while lower productivity values cannot support the larger consumer. On the other hand,

229 coexistence is almost independent of the productivity in the smaller consumer's habitat as long as it can
230 support the top predator (ca. $K_1 > 1.5 \times 10^{-4}$ to 4×10^{-4} g.L⁻¹ in Fig. S4A-C and $K_2 > 9 \times 10^{-5}$ g.L⁻¹ in Fig.
231 S3E-I).

232 Unequal consumer body sizes also underpin asymmetric roles of habitat productivities in the
233 fate of the top predator. TCC values required for top predator persistence are nearly independent of the
234 PB ratio for most consumer body size ratios β , and increase with PB only when the pelagic consumers
235 are much larger ($\beta = 3$ in Fig. S1A). TCC thresholds associated with predator invasion are more sensitive
236 to β and PB ratios: they decline with the PB ratio when $\beta \leq 1$ and increase otherwise (Fig. S1B). This
237 asymmetric role of the pelagic and benthic habitat productivities is caused by the habitat-specific
238 consumer vulnerability to predation as both consumers are equivalent in terms of contribution to the
239 critical prey biomass required by the top predator (Fig. S2). That is, a more productive pelagic habitat
240 is required to sustain the top predator as β increases and the pelagic prey becomes less vulnerable (Fig.
241 S1A).

242 At low benthic productivities K_2 , all five species therefore coexist if pelagic consumers are
243 sufficiently small and pelagic productivity sufficiently high (community state 5; ca. $\beta < 0.66$ for $K_1 >$
244 10^{-4} g.L⁻¹ in Fig. 5A). Surprisingly, coexistence is also possible if the pelagic consumers are larger and
245 pelagic productivity intermediate (community state 2/5; up to $\beta = 1.5$ for K_1 between ca. 10^{-5} g.L⁻¹ and
246 10^{-4} g.L⁻¹ in Figs. 3B and 5A; see also Figs. 4B and S4A-D). Coexistence at high benthic productivity
247 K_2 requires sufficiently large pelagic consumers (ca. $\beta > 0.9$ in Fig. 5B) in a moderately productive
248 pelagic mesohabitat; the range of pelagic productivity leading to possible coexistence increases with β
249 (community states 5, 4/5 and 2/4/5; Figs. 5B and S4G-I; see also Fig. 4C). Intermediate benthic
250 productivities K_2 combine the outcomes for low and high K_2 , i.e. all five species can coexist when
251 sufficiently high pelagic productivity supports small pelagic consumers or when large pelagic
252 consumers are constrained by intermediate pelagic productivity (community states 5, 2/5, 4/5 and 2/4/5,
253 Fig. S4EF).

254 We observe similar patterns for fixed pelagic productivities K_1 : coexistence is possible if benthic
255 consumers are substantially larger and occupy a less productive habitat or if they are substantially
256 smaller and live in a more productive habitat than the benthic consumers (community states 5, 2/5, 4/5,

257 5/6, 2/4/5 and 2/5/6; Figs. 5CD and S5). Coexistence is less likely, i.e. occurs for a smaller range of β
258 and K_2 , as the pelagic productivity becomes very low (Fig. S5A) or very high (Figs. 5D and S5G-I). At
259 intermediate values of pelagic productivity, even similarly sized benthic and pelagic consumers may
260 however coexist within a range of intermediate benthic productivity (community state 2/5 in Fig. 5C
261 and states 5 and 2/5 in Fig. S5B-F).

262

263 *Emergent Allee effects and alternative stable states in the multi-channel food web*

264 We identified nine possible alternative stable state configurations in the food web and classify them into
265 four groups. First, they include the ‘classical’ *emergent Allee effect in the top predator* associated with
266 its sudden collapse (de Roos & Persson 2002; Fig. 6A) when one or both consumer populations are
267 present (community states 1/4, 3/6 and 2/5 in Figs. 1 and 5). Second, an *emergent Allee effect in an*
268 *intermediate consumer* represents the collapse of a competitively inferior consumer population due to
269 apparent competition when all other species are present (community states 4/5 and 5/6 in Fig. 1). Third,
270 an *emergent two-species Allee effect* is associated with the invasion of the competitively inferior
271 consumer species upon the sudden collapse of the top predator or its disappearance after the top predator
272 establishes in the trophic food chain (community states 2/4 and 2/6 in Fig. 1). Finally, the community
273 can have *three* alternative stable states: presence of the top predator with one or both consumer
274 populations, or both consumer populations without the top predator (community states 2/5/4 and 2/5/6
275 in Fig. 1). This outcome combines the emergent Allee effects in the top predator and in an intermediate
276 consumer; we call it a *cascading emergent Allee effect* characterised by consecutive (Fig. 6B) or nested
277 (Fig. 6C) population collapses of the top predator and one or both consumers. While the consecutive
278 collapses enable the food web structure pass through all three alternative stable states through gradual
279 change of the environmental conditions alone, the nested collapses make one of the stable states
280 unreachable by gradual change.

281 We observed emergent Allee effects across a wide range of habitat productivities (Figs. 3 and
282 S3) and consumer size ratios (Figs. 5 and S4-S5). Emergent Allee effects in the top predator and the
283 two-species Allee effects (community states 1/4, 2/4, 2/5, 2/6 and 3/6), occurred at all consumer size
284 ratios β but were restricted to intermediate TCC levels; the exact TCC range varied with the PB ratio

285 when β deviated strongly from unity (Figs. 5 and S3). Emergent Allee effects in intermediate consumers
286 (community states 4/5 and 5/6) occurred only when β deviated strongly from unity and TCC levels were
287 high enough for the top predator to persist (Figs. 5B and S3-S5). Cascading emergent Allee effects
288 (community states 2/5/4 and 2/5/6) appeared mainly for sufficiently dissimilar consumer body size ratios
289 and intermediate TCC levels (Figs. 5AD, S3B, S3E-I, S4E-G and S5B and S5E-I). They almost always
290 included consecutive population collapses (Figs. S6B and S7AC) and very rarely the nested collapse
291 (community states 2/4 and 2/5/4 in Fig. S4CD).

292 Emergent Allee effects in our simulations predominately affected communities in which the top
293 predator gained a feeding link to the pelagic or both consumers (community states 1/4, 2/4, 2/5 and
294 2/4/5) or in which apparent competition drove benthic consumers extinct (4/5; Fig. 5BD). We varied
295 body size of pelagic consumers while keeping the size of benthic consumers constant in our analyses.
296 Thus, the range of environmental conditions giving rise to the emergent Allee effect in the benthic food
297 chain (community state 3/6) was independent of β , while the other emergent Allee effects in the top
298 predator (1/4 and 2/5) and the two-species Allee effect associated with the loss of the benthic consumer
299 (2/4) became more common as β increased (Figs. 3B, 4D and S4; see also Fig. 5AD). Alternative stable
300 states in which the top predator could gain access to the benthic consumers (community states 2/6, 3/6
301 and 2/5/6) were less common and limited to sufficiently small pelagic consumers living in a moderately
302 productive mesohabitat (states 2/6 and 2/5/6 in Figs. 5C, S3A-F, S4FG and S5A-D) and to food webs
303 with intermediate benthic productivity K_1 and pelagic productivity K_2 below the pelagic consumer
304 persistence threshold (state 3/6 in Figs. 3B, S3 and S4FG). Finally, we found the emergent Allee effect
305 in which the top predator drove the pelagic consumers to extinction (community state 5/6) only for very
306 small pelagic consumers ($\beta < 0.5$) and a narrow range of moderate benthic productivity ($K_2 \approx 10^{-4} \text{ g.L}^{-1}$,
307 Figs. 5CD, S3AB, S4FG, and S5).

308

309 **Discussion**

310 Variation in predator-prey body size ratios underpins the structure and stability of food webs (Brose *et*
311 *al.* 2006; Petchey *et al.* 2008). Furthermore, individual growth in size plays an important role in predator-
312 prey interactions as large prey often become invulnerable to predation (de Roos & Persson 2002;

313 Andersen & Beyer 2006). However, the importance of varying body sizes in multi-channel food webs
314 that arise in many aquatic and terrestrial ecosystems has not been explored. Here we provided theoretical
315 support for the key role of asymmetric body sizes and resource productivities in the empirically observed
316 stability of multi-channel food webs (Rooney *et al.* 2006). We also showed that alternative stable states
317 in these food webs can go beyond the emergent Allee effect in the top predator (de Roos & Persson
318 2002) and mutual exclusion via apparent competition (Holt *et al.* 1994; Chase 1999) as we discovered
319 three new types of emergent Allee effects affecting intermediate consumers or multiple populations, or
320 involving multiple alternative stable states. Our results emphasize the need to jointly consider the
321 strength of bottom-up regulatory processes, individual ontogeny and size-dependent interactions to
322 improve our understanding of the responses of multi-channel food webs to environmental change.

323

324 *Multi-channel food webs and apparent competition*

325 We showed that intermediate consumer body sizes and energy partition between mesohabitats jointly
326 determine the limits of species coexistence in multi-channel food webs. Classic theory of apparent
327 competition between two consumers sharing a predator predicts that the prey resilient to the highest
328 predation pressure prevails (Holt *et al.* 1994). Further extensions examining the combined roles of
329 apparent and exploitative competition found that consumer coexistence requires a trade-off in the ability
330 to dominate in each type of competition (Holt *et al.* 1994) and that habitat productivity drives the
331 outcome (Leibold 1996; Chase 1999). That is, species dominating in exploitative competition should be
332 gradually replaced by species resistant to predation as productivity increases, with coexistence possible
333 at intermediate productivity levels (Leibold 1996). This will often mean that small and large species will
334 respectively dominate at low and high habitat productivity if predators cannot feed on large prey (Chase
335 1999, 2003).

336 The lower vulnerability of larger consumers to predation was not traded off against higher
337 resource requirements in our model. However, larger consumers did not always prevail as expected in
338 apparent competition because of the additional role of bottom-up regulatory processes. That is,
339 consumer coexistence in our model was primarily driven by the ratio of productivity in both linked
340 mesohabitats when both consumers were similarly sized and by productivity in the larger consumer's

341 mesohabitat (i.e., similar to the findings by Chase (1999) and Leibold (1996)) when their sizes differed
342 substantially. We conclude that a “symmetry in asymmetries” is required for consumer coexistence in
343 multi-channel food webs: asymmetry in body size must compensate for a mirror asymmetry in energy
344 partitioning such as smaller consumers living in a more productive mesohabitat.

345 These combination of asymmetries occur frequently between pelagic and benthic mesohabitats
346 in freshwater systems (Rooney *et al.* 2006). The pattern of (i) smaller organisms and high
347 photosynthetic-driven productivity in pelagic mesohabitats and (ii) larger organisms and low
348 allochthonous productivity in benthic mesohabitat (Baird & Ulanowicz 1989; Rooney *et al.* 2008)
349 corresponds to the observations for $K_2 < K_1$ and $\beta < 1$ in our model (Figs. S3–S5). This implies that these
350 multi-channel food webs rely on the above compensatory asymmetries to ensure stable coexistence of
351 apparent competitors in different food-web channels (Rooney *et al.* 2006). Interestingly, our model also
352 predicts stable coexistence if the larger organisms and lower productivity occur in the pelagic
353 mesohabitat, i.e. the observed coexistence patterns are not primarily driven by higher resource turnover
354 rate in the pelagic mesohabitat ($\rho_2 > \rho_1$).

355 *Emergent Allee effects, alternative stable states and catastrophic collapses*

356 Increasing anthropogenic pressure on fish stocks through eutrophication and harvesting
357 (Möllmann & Diekmann 2012) has led to catastrophic declines of two thirds of freshwater and marine
358 predatory fish, with an acceleration of 54% over the past 40 years (Christensen *et al.* 2014; Otto 2018).
359 While these declines can be reversible (Hutchings 2000; Persson *et al.* 2007), they require
360 disproportionately large efforts if the collapses associate with Allee effects that affect populations
361 resilience and recovery, promote alternative stable states in the system (Scheffer *et al.* 2001; van Kooten
362 *et al.* 2005), and make the food webs vulnerable to sudden collapse (Möllmann & Diekmann 2012;
363 Gårdmark *et al.* 2015).

364 Here we demonstrated that multi-channel food webs can become disconnected not only by the
365 loss of top predator, but also by the loss of populations at intermediate trophic levels in response to
366 increased productivity in the other mesohabitat, e.g. due to eutrophication. Our results imply that multi-
367 channel food webs show the highest propensity for alternative stable states at highly unequal consumer

368 body sizes and intermediate habitat productivity levels, which may guide future empirical studies on
369 alternative stable states in such food webs. Intermediate levels of habitat productivity are also
370 indispensable for alternative stable states in the diamond and intraguild predation food web modules
371 (Chase 1999, 2003; Diehl & Feißel 2000), suggesting that this pattern is independent of food web
372 topology.

373 Without exploitative competition, we did not observe alternative stable states affecting
374 consumers via priority effects (Chase 1999, 2003). However, we identified other novel types of
375 community transitions leading to the loss of the inferior consumer through an emergent Allee effect
376 when (i) the top predator invades the system and the system shifts from separate consumer-resource
377 pairs to a trophic chain, (ii) increased or decreased productivity in one mesohabitat disrupts the energy
378 balance and the system changes from a multi-channel food web to a trophic chain, and (iii) cascading
379 emergent Allee effects arise. In the latter case, we predict that the system can alternate between multiple
380 stable states involving separate consumer-resource pairs, a trophic chain and the complete multi-channel
381 food web. This additional complexity may contribute to the limited evidence of alternative stable states
382 on whole-ecosystem level (Schröder *et al.* 2005; but see Möllmann & Diekmann 2012).

383

384 *Implications for food web resilience in a changing world*

385 Anthropogenic impacts now account for most perturbations of natural ecosystems (Schindler &
386 Scheuerell 2002; Otto 2018). In particular, eutrophication (Oksanen *et al.* 1981; Otto *et al.* 2007) and
387 removal or introduction of species (DeCesare *et al.* 2010) essentially impact food web and community
388 structure (Möllmann & Diekmann 2012; Wollrab *et al.* 2012).

389 The impact of increased nutrient inputs on the structure of our multi-channel food web model
390 was contingent on the consumer size ratio, which underpins the importance of differences in species
391 traits between the energy channels. While increased nutrient loads in the mesohabitat occupied by the
392 smaller consumers stabilized the food web, increased productivity in the other mesohabitat was
393 potentially destabilizing as it disrupted the linkage between mesohabitats and excluded the weaker
394 competitor. On the other hand, the loss of one consumer population did not necessarily lead to the

395 extinction of the top predator as long the total system productivity remained sufficiently high, thereby
396 showing that multiple energy channels protect top predators.

397 To conclude, our predictions confirm empirical data on the resilience of natural systems due to
398 asymmetric patterns between heterogeneous habitats, which enable faster recovery of the system after
399 perturbation (Rooney *et al.* 2006; McCann & Rooney 2009). We have demonstrated that detailed
400 understanding of species traits such as body size and their impact on trophic interactions are required to
401 understand the structure and persistence of multi-channel, tri-trophic food webs when facing
402 environmental stressors. Further studies of the role of species traits in multi-channel food webs could
403 help identify communities and species vulnerable to regime shifts (Gårdmark *et al.* 2015) and suggest
404 possible restoration approaches.

405

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409

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531

532 **Legends**

533

534 **Fig. 1: Classification of all possible scenarios of community assembly in the multi-channel food**
535 **web.** Populations and trophic links: top predator (black circle), consumers (diamonds) and resources
536 (circles) linked by stable (solid lines) or bistable (dotted lines) trophic links; pelagic species in green,
537 benthic species in brown. Transitions between possible community states (numbered rectangles)
538 correspond to the invasion/extinction threshold of one consumer (dark green or brown arrows), or top
539 predator (black arrows). Dotted arrows = transitions between communities with 2–3 alternative stable
540 states (multiple numbers separated by slashes). Grey arrows illustrate gradients of energy partitioning
541 among mesohabitats and total system productivity.

542

543 **Fig. 2: Influence of consumer relative body size β on key life history events (A), population growth**
544 **rate (B) and birth rate (C).** (A) Grey area: consumers vulnerable to predation (daily resolution); black
545 dotted line = maturation time; black solid line = time to reach maximum size, defined as age when
546 individual growth rate declines below 0.01 mm day^{-1} ; resource level R fixed at ca. $3 \times 10^{-4} \text{ g.L}^{-1}$. (B and
547 C) Population-level rates without predation (black lines, B and C) and with predation (red lines, C);
548 resource carrying capacity fixed at $K = 3 \times 10^{-5} \text{ g.L}^{-1}$ (thin lines), $8 \times 10^{-5} \text{ g.L}^{-1}$ (medium lines), and 3×10^{-4}
549 g.L^{-1} (thick lines). Other parameters as in Table S1. Community structure in panel C: solid lines = stable
550 equilibria dashed lines = unstable equilibria of the tri-trophic chain; black points = predator invasion
551 thresholds, red points = predator persistence thresholds; dash-dotted line = adult predation vulnerability
552 threshold.

553

554 **Fig. 3: Changes in community structure of the tri-trophic food chain (A) and the multi-channel**
555 **food web (B) along gradients of mesohabitat productivity and consumer body size.** Community
556 structures, numbered as in Fig. 1: resource-only equilibrium (0, white), consumer-resource equilibria
557 (green, 1–3), four-species equilibria (blue, 4 and 6), and coexistence of all five species (blue, 5). Solid
558 lines: invasion thresholds of pelagic (C_1 , dark green) and benthic (C_2 , brown) consumers and the top
559 predator (black). Dashed lines: invasion thresholds of pelagic (dark green) and benthic (brown)

560 consumers in an unstable equilibrium with top predator, and extinction threshold of top predator with
561 one or both consumers present (black). Parameters: (A) $K_2 = 5 \times 10^{-6} \text{ g.L}^{-1}$, (B) $\beta = 1.2$, other values as in
562 Table S1. Dotted lines: (A), β and K_2 values used in Fig. 4; (B), K_1 and K_2 values used in Fig. 5.

563

564 **Fig. 4: Emergent Allee effects in tri-trophic chain (A) and multi-channel food web (B), and**
565 **community transition between consumer coexistence and exclusion (C) along the pelagic**
566 **productivity gradient.** Parameter values: $\beta = 1.2$; $K_2 = 5 \times 10^{-6} \text{ g.L}^{-1}$ (A), $3 \times 10^{-5} \text{ g.L}^{-1}$ (B) and 3×10^{-4}
567 g.L^{-1} (C), i.e. benthic resource productivity increasing from A to C. Other parameters as in Table S1.
568 Solid lines: stable equilibria; dotted lines: unstable equilibria. Threshold productivity values marked by
569 vertical dotted lines: consumer invasion (blue points), top predator invasion (black points), top predator
570 collapse (red points). Top predator panel duplicated in (B) and (C) to enable comparison within each
571 mesohabitat. Community structures numbered as in Fig. 1. Axes scaling: x axis transformed as
572 $\log_{10}(x+10^{-5})$; y axis transformed as $\log_{10}(y+10^{-8})$ for juvenile and adult consumers and as $\log_{10}(y+10^{-6})$
573 for resources and top predator.

574

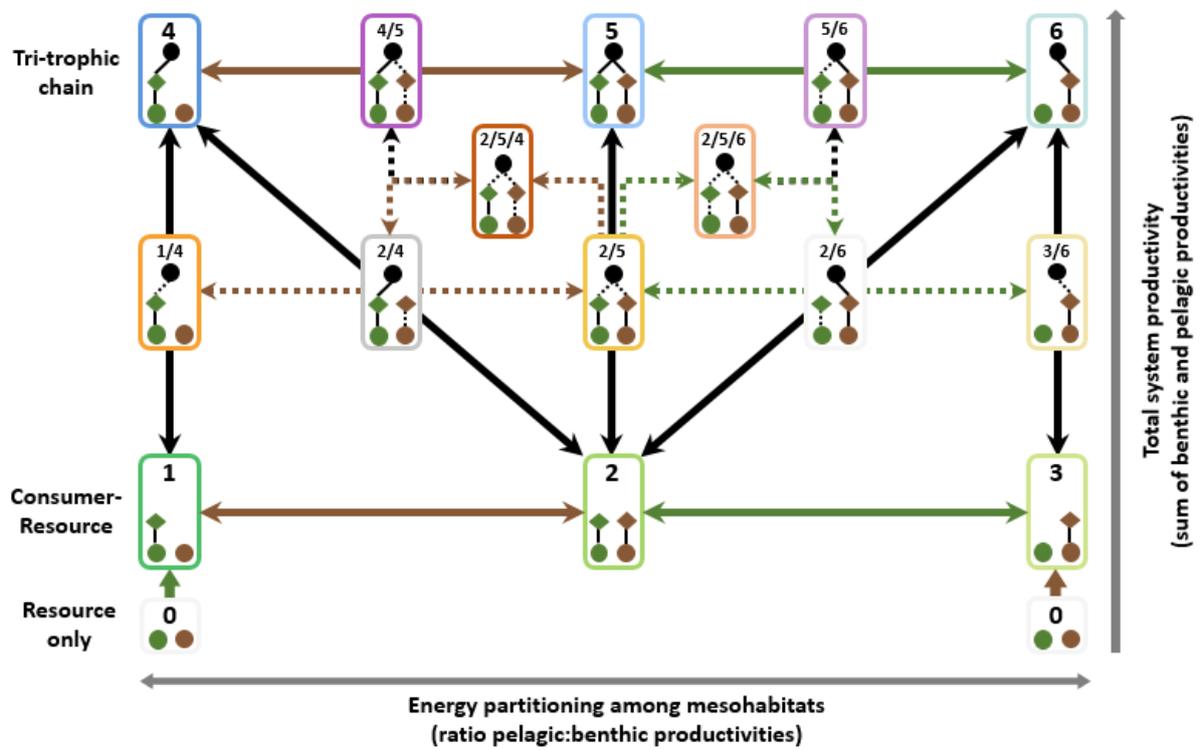
575 **Fig. 5: Dependence of community structure of the multi-channel system on resource productivity**
576 **and consumer relative body size β .** Resource carrying capacity always fixed in one habitat: $K_2 = 3 \times 10^{-5}$
577 g.L^{-1} (A) and $3 \times 10^{-4} \text{ g.L}^{-1}$ (B); $K_1 = 3 \times 10^{-5} \text{ g.L}^{-1}$ (C) and $3 \times 10^{-4} \text{ g.L}^{-1}$ (D). Other parameters as in Table
578 S1. Community structures numbered as in Fig. 1; coexistence of all five species denoted by '5'. Line
579 type and colour as in Fig. 3. Dotted lines ($\beta = 1.2$): results shown in Fig. 3B. Dash-dotted lines ($\beta = 3.8$):
580 predation vulnerability limit of the pelagic consumer.

581

582 **Fig. 6: Diagram of (A) emergent Allee effect and (B and C) cascading emergent Allee effects along**
583 **a productivity gradient.** Dashed arrows = sudden community transitions between alternative system
584 states; stable states (solid blue lines) separated by unstable equilibria (dotted lines). In cascading
585 emergent Allee effect, sudden community transitions follow in succession (B; e.g., community state
586 2/5/6 in Figs. S3B and S5B) or in a single event (C; community state 2/5/4 in Fig S4CD). Note that
587 stable state 2 cannot be reached by gradual changes in (C).

588 Figures

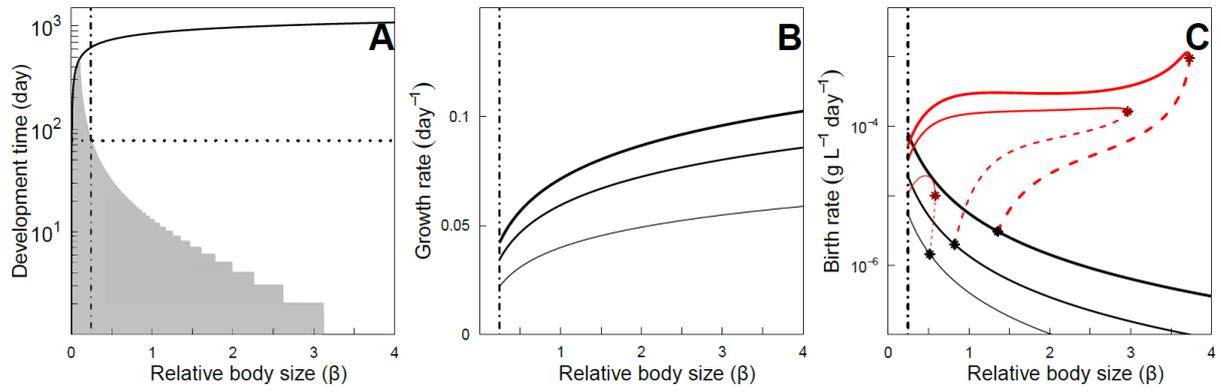
589 Fig. 1



590

591 **Fig. 2**

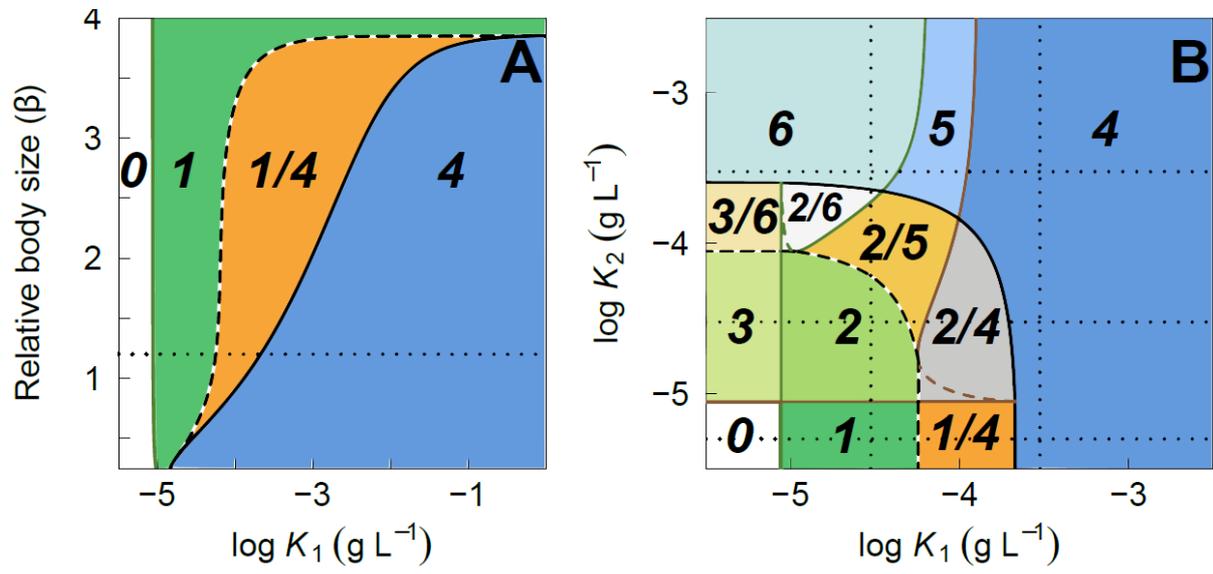
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594 **Fig. 3**

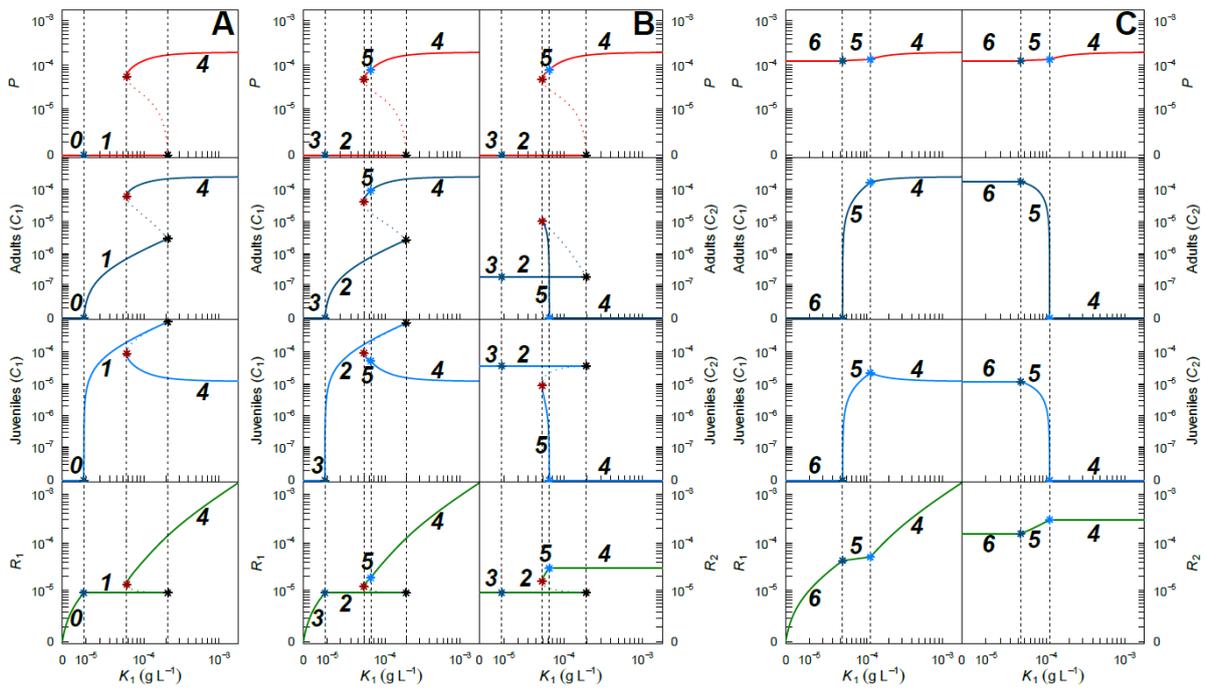
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597 **Fig. 4**

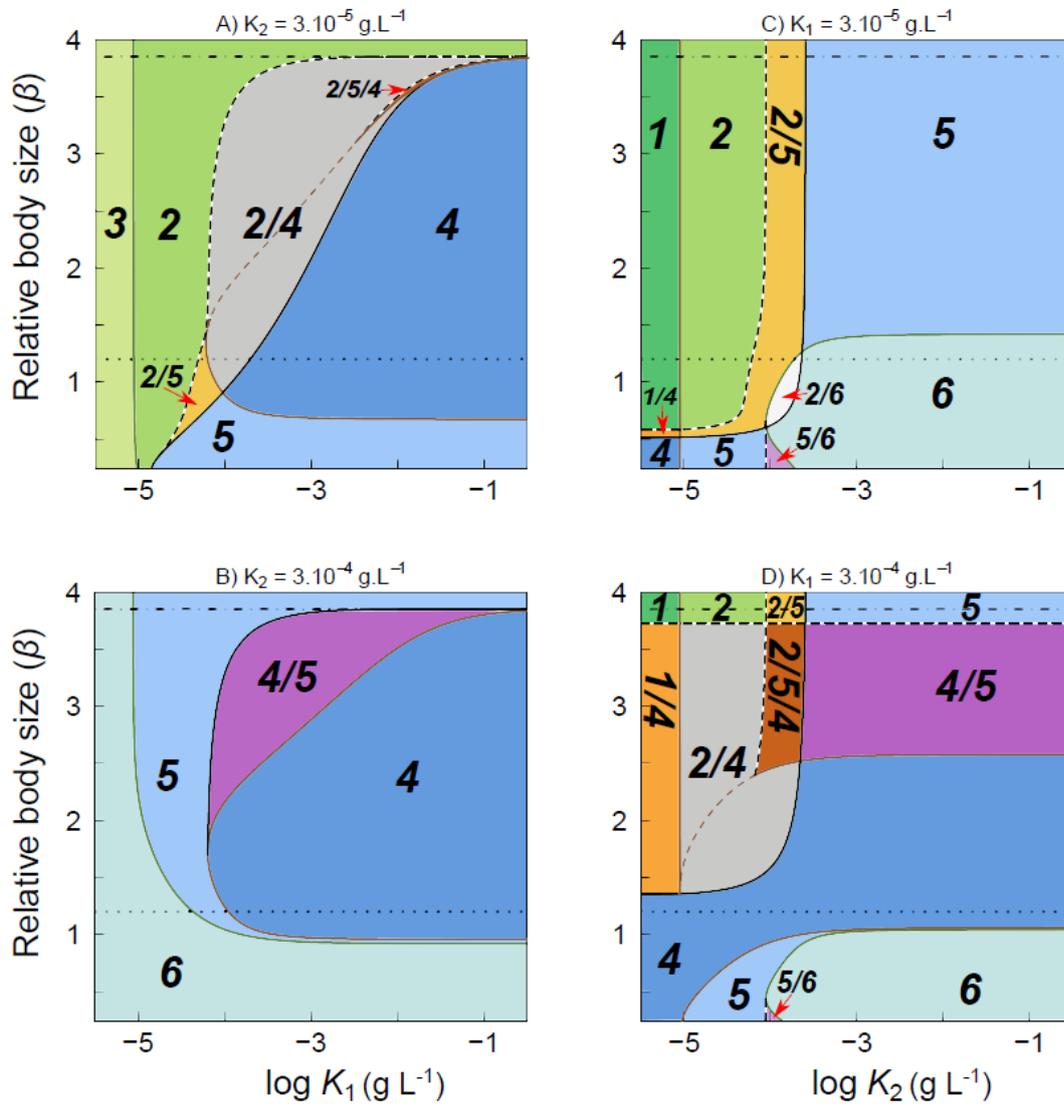
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600 Fig. 5

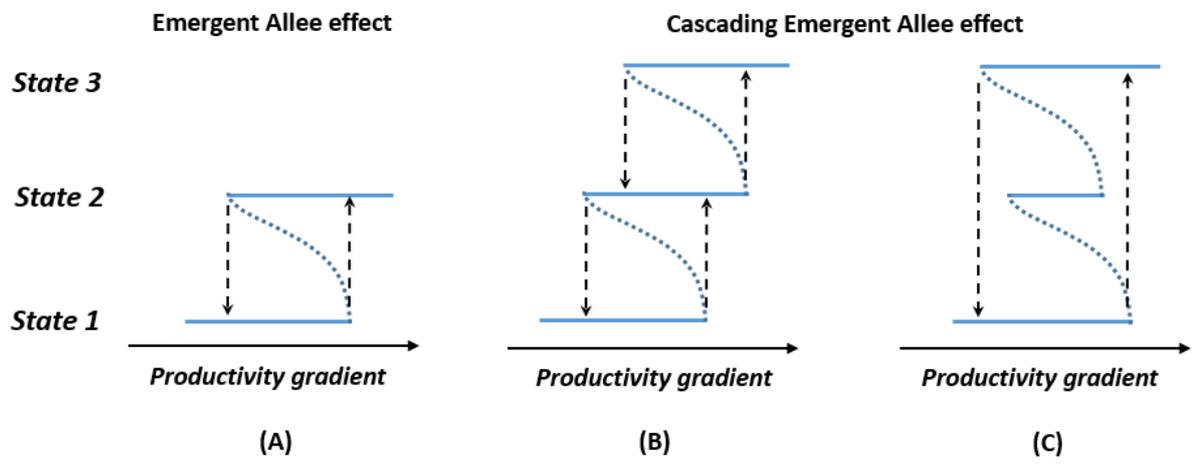
601



602

603 Fig. 6

604



605