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1 **Coevolution of species colonization rates controls food-chain length in spatially**
2 **structured food webs**

3

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13

14 **Abstract**

15 The complexity of food webs and how it depends on environmental variables is a long-
16 standing question in ecology. Food-chain length depends on many factors, such as
17 productive space, disturbance and spatial processes. It is not clear though how food-chain
18 length should vary with adaptive evolutionary changes of the constitutive species. Assuming
19 that each trophic level is subject to a competition-colonization trade-off, we model the
20 adaptive evolution of their colonization rates and its consequences on equilibrium
21 occupancies and food-chain length. When colonization rates are allowed to evolve, longer
22 food chains can persist. Extinction, perturbation and habitat loss all affect the evolutionary-
23 stable colonization rates, but trade-off strength (costs of dispersal) has a major role: weaker
24 trade-offs yield longer chains. Our results suggest a strong link between within-trophic level
25 competition, spatial occupancies and food-chain length. Although these eco-evo dynamics
26 partly alleviate the constraint on food-chain length in metacommunities, we show it is no
27 magic bullet: the highest, most vulnerable, trophic levels are also those that least benefit
28 from evolution. Our model generates qualitative predictions regarding how trait evolution
29 affects the response of communities to disturbance and habitat loss. This highlights the
30 importance of eco-evolutionary dynamics at metacommunity level in determining food-chain
31 length.

32

33

34 **Key words:** dispersal; eco-evolutionary dynamics; habitat destruction; metacommunity;
35 patch occupancy model

36

37 Introduction

38 An important puzzle in ecology is how food web topology, and in particular food-chain length,
39 is determined (Hutchinson, 1959, Pimm, 1982, May, 1983, Cohen and Briand, 1984,
40 Stenseth, 1985, Cohen and Newman, 1988, Williams and Martinez, 2000, 2004). Food-chain
41 length is a measure of the number of feeding links between resources and top predators
42 (e.g. Sabo et al., 2009). Ecological theory has long tried to understand what limits this length
43 (Hutchinson, 1959, May, 1972, Hastings and Conrad, 1979, Pimm, 1982, Menge and
44 Sutherland, 1987). For instance, the energetic constraint hypothesis (Hutchinson, 1959)
45 invokes imperfect transfers of energy and resources along food chains, the dynamics
46 constraint hypothesis (May, 1972, Pimm and Lawton, 1977) argues that long food chains are
47 more vulnerable to perturbation than short ones, and the community area hypothesis
48 combines the diversity-area relationship obtained by the theory of island biogeography
49 (MacArthur and Wilson, 1967) with the link scaling law (Cohen and Briand, 1984) to predict a
50 concave increase in food-chain length with habitat area (Cohen and Newman, 1991). Recent
51 empirical studies have identified three major determinants of food-chain length: productive
52 space (*i.e.* ecosystem size \times productivity), disturbance, and ecosystem size (Post, 2002).
53 While confirming the roles of resource limitation and perturbation, these results argue
54 against single explanations, and also stress the need to incorporate space in theoretical
55 models. Indeed, despite ample evidence that food-chain length correlates with habitat area
56 or ecosystem size (Schoener, 1989, Cohen and Newman, 1991, Post et al., 2000, Takimoto
57 et al., 2008), spatial processes are still understudied in theoretical models of food webs
58 (Holt, 2002, Amarasekare, 2008). Calcagno et al. (2011) extended the model of Holt (2002)
59 to provide predictions under a range of conditions encompassing top-down effects of any
60 sorts and habitat selection effects, while Pillai et al. (2011) studied the effect of colonization
61 rates on the complexity of food webs at the metacommunity level. More recently, Wang et al.
62 (2021) reanalyzed a similar ecological model of spatial food chains in order to study how
63 metacommunity dynamics should influence maximum food-chain length. They rendered the
64 model spatially realistic and provided some empirical support for its predictions in a butterfly-
65 parasitoid system.

66
67 The spatial structure of populations, on the other hand, has inspired one of the most prolific
68 research lines in evolutionary biology, namely the evolution of dispersal (for reviews, Bowler
69 and Benton, 2005; Ronce, 2007; Duputié and Massol, 2013). Indeed, there has been an
70 early realization that spatial structure, beyond its population dynamical consequences, also
71 imposed strong selection pressures, and that the key parameter in this context, the
72 colonization, dispersal, or migration rate, could be shaped by evolutionary adaptation. A
73 range of selective forces should act on the dispersal rate, and determine its evolutionarily
74 stable (ES) value, depending among others on patch size, connectivity, spatio-temporal
75 environmental variability and dispersal costs. In the case of metapopulation occupancy
76 models, following the seminal work of Levins (1969), Slatkin (1974), Hastings (1980), Hanski
77 (1983), Tilman (1994) and others, one can translate a purely ecological statement of the
78 problem (“what is the occupancy of competing species when they obey a competition-
79 colonization trade-off?”, Calcagno et al. 2006) into an evolutionary question (“how should
80 this competition-colonization trade-off drive the evolution of colonization rates of coexisting
81 species?”, Aubrée et al. 2020), and thence investigate the eco-evolutionary dynamics of
82 adaptation of colonization rates in a metacommunity.

83
84 The purpose of this article is to connect these two important aspects of spatially structured
85 communities, namely the ecological limit they impose on food-chain length on the one hand,
86 and the evolutionary dynamics of dispersal on the other hand, and to determine how they
87 could interact and influence one another. In Calcagno et al. (2011), two distinct constraints
88 on food-chain length arising from metacommunity structure were identified. First, finite
89 colonization rates limit predator occupancy to a subset of prey-occupied sites. Second,
90 extinction rates accumulate along food chains. Both processes thus concur to decrease
91 maximal and average food-chain length in metacommunities. However, in an eco-

92 evolutionary dynamics framework, the evolution of colonization rates, in response to
93 competition within trophic levels, will affect the first constraint (by either increasing or
94 decreasing colonization rates), and hence will likely change trophic level occupancies and
95 food-chain length. Here, we investigate this question theoretically by plugging an adaptive
96 dynamics-based model of colonization evolution into the food-chain metacommunity model
97 of Calcagno et al. (2011). This model allows us to assess how habitat availability and
98 extinction and perturbation rates select for colonization rates, and how this selection
99 changes prediction between a metacommunity that evolves and one that does not. The
100 parameters of the competition-colonization trade-off provide us with another lever quantifying
101 the strength of intra-trophic level competition. Ultimately, this model allows us to predict how
102 food-chain length changes with environmental variables in response to selection on
103 colonization rates.

104
105

106 **Model and Methods**

107

108 ***Spatial food chain model***

109 We use a model of spatial food chain identical to that in Calcagno et al. (2011), and very
110 close to that of Wang et al. (2021). It is best formulated in terms of the dynamics of q_i , the
111 fraction of patches that contain trophic level i , and thus all the lower trophic levels too,
112 regardless of the presence/absence of upper trophic levels (Fig. 1). These dynamics can be
113 expressed in a way similar to Levins' classical metapopulation model:

$$114 \frac{dq_i}{dt} = c_i q_i (q_{i-1} - q_i) - (\langle e_i \rangle + \mu) q_i \quad (1)$$

115 where for the first trophic level ($i=1$), $q_0 = h$ is the proportion of habitat (patches) available
116 (level 0 is therefore not counted in food-chain length). As a simple example, a fully
117 developed set of equations is described in Supplementary Material for a two-level trophic
118 chain.

119

120 This equation assumes that patches experience perturbation at rate μ , which causes all
121 trophic levels to disappear simultaneously (perturbation-driven extinction). An additional
122 fraction of extinctions, called the effective extinction rate $\langle e_i \rangle$, is experienced independently
123 by each trophic level, and incorporates a basal extinction rate e , potentially modified by
124 bottom-up and top-down effects. Bottom-up effects reflect the fact that if a given trophic level
125 goes extinct in a patch, all upper trophic levels must go extinct too. Top-down effects
126 represent how the presence of upper trophic levels may increase the extinction rate of the
127 focal trophic level (parameter e_{TD}), for instance through a reduction of local population size.

128 We assume that in the fraction of sites that contain the $i+1$ trophic level ($= q_{i+1} / q_i$) top-down
129 effects increase the extinction rate by a constant. Applying this rule to all trophic levels, this
130 yields $\langle e_i \rangle$ to be expressed as $e + (i-1)(e + e_{TD}) + e_{TD} q_{i+1} / q_i$ (see Calcagno et al. 2011;
131 Wang et al. 2021).

132

133 ***Evolutionary dynamics of colonization rate***

134 The above model has been thoroughly studied for arbitrary, fixed, colonization rates of the
135 different trophic levels (Calcagno et al. 2011). In this article, we further let colonization rate
136 values evolve under the effect of natural selection (the basal extinction rates and the
137 strength of top-down effects are fixed). Metapopulation structure is known to impose strong
138 selection pressures on dispersal, and hence on the colonization rate (Duputié & Massol
139 2013). Dispersal is selected for by the presence of empty available patches (Comins et al.
140 1980), and, for low enough population sizes, kin competition. On the other hand, dispersal is
141 counter-selected by competitive trade-offs, *i.e.* the fact that high dispersal rates come at the

142 expense of local growth and/or competitive strength, which is the case when dispersal is
143 costly (Supplementary Material). We here use a simple representation of these evolutionary
144 dynamics, that can be derived from competition-colonization trade-offs (Calcagno et al.
145 2017), or alternatively from spatially structured population models (Supplementary Material).
146 It incorporates the three selective forces listed above. The derivation yields the following
147 equation for the dynamics of c_i :

$$148 \quad \frac{dc_i}{dt} = V_G \left[q_{i-1} - q_i + (\phi + 2c_i\psi_0)q_i \right] \quad (2)$$

149 V_G is a parameter representing the genetic variance in colonization (from a quantitative
150 genetics perspective, Lande 1979; see Dieckmann & Law 1996 for an alternative
151 interpretation). The other two evolutionary parameters describe the strength of the trade-off
152 between local competitiveness and colonization (Supplementary Material). ϕ is the
153 probability that immigrants replace residents when they have the same colonization rate
154 (between 0 and 1), and ψ_0 is the (negative) slope quantifying how much increasing
155 colonization rate comes at the expense of decreased local competitiveness (*i.e.* there is a
156 cost of dispersal). The first two terms in the brackets represent positive selection for
157 dispersal caused by the presence of empty available patches (fraction $q_{i-1} - q_i$), and the
158 third term $(\phi + 2c_i\psi_0)q_i$ represents the usually negative selection on colonization rate
159 caused by local competition. More specifically, the ϕ term represents the (weak) positive
160 selection caused by kin competition (Supplementary Material), whereas the term involving
161 ψ_0 represents the counter-selection imposed by competitive trade-offs and costs of
162 dispersal. As shown in Supplementary Material, eq. (2) admits a unique positive equilibrium
163 in the cases of interest; this singular strategy is always convergence stable, and is an
164 evolutionarily stable strategy (ESS) provided one condition is met by the trade-off function.
165 The ESS is attained when the selective forces for and against colonization cancel out.
166

167 **Computing equilibria and maximum food-chain length**

168 The dynamics of (1) can be used directly, with fixed colonization rates, to compute food-
169 chain length in the absence of evolution (Calcagno et al. 2010; Wang et al. 2021). To
170 introduce evolution, we study the coupled dynamics of eq. (1) and (2), using the common
171 simplification that eq. (1) was at equilibrium, *i.e.* that metapopulation dynamics was faster
172 than evolutionary dynamics. Given the nature of the ecological and evolutionary attractors,
173 the assumption is not expected to have important consequences (Sanchez et al. 2011). For
174 numerical examples with small numbers of trophic levels, we numerically integrated eq. (2)
175 through time, keeping eq. (1) at equilibrium. For larger numbers of trophic levels and to
176 compute maximum food-chain length, we assumed eq. (2) was at equilibrium (ESS), and
177 implemented an iterative algorithm allowing to jointly solve eq. (1) and (2) (see
178 Supplementary Material for details on the algorithm). Using this algorithm, we computed the
179 maximum food-chain length, defined as the maximum number of trophic levels that can
180 persist, where persistence is defined as having equilibrium occupancy greater than some
181 small threshold level ϵ . In practice, we used 10^{-3} , meaning that any trophic level should
182 occupy at equilibrium at least one patch in one thousand in order to persist.
183

184
185 In all figures, we used the following reference parameter values, unless stated otherwise or a
186 parameter was systematically varied: $h = 1$, $e = 1$, $\mu = 1$, $\phi = 0.5$, $\psi_0 = -0.1$.

187

188

189 **Results**

190

191 ***The evolution of dispersal in a spatial food chain***

192 Fig. 2a-b presents results for the simplest possible case with only two trophic levels: one
193 prey and one predator. In the figure, the basal extinction rate is gradually increased, causing
194 the occupancy of the two trophic levels to decline, eventually going extinct one after the
195 other. This basically mimics a continuous degradation of the environment which becomes
196 harsher and harsher in time, as expected for example if the taxa are challenged by climate
197 change or anthropisation. In the absence of evolution, the figure was parameterized in order
198 to replicate the results of Wang et al. (2021)'s figure 1, thus including top-down control of the
199 predator. In that case, our mathematical model faithfully reproduces these spatially realistic
200 simulation results. Occupancy decreases markedly for the higher trophic level, which
201 disappears at rather low extinction rates. The lower trophic level can maintain itself at much
202 larger extinction rates. Due to the absence of trait dynamics, the colonization ratio (c/e)
203 curves remain identical, until the higher trophic level disappears.

204
205 Fig. 2c-h shows the impact of evolution on these results. Important quantitative and
206 qualitative differences emerge. If evolution is slow (Fig. 1c-d), *i.e.* if parameter V_G is low in
207 eq. (2), evolution has little impact, and does not significantly “delay” the extinction of the
208 predator (*i.e.* allows it to survive at higher values of e). Despite the predator evolving higher
209 colonization rate when approaching extinction, eventually outpacing the increase in
210 extinction rate (*i.e.* the colonization ratio c/e increases), this is not sufficient to prevent
211 extinction. Following the predator's extinction however, the prey manages to persist despite
212 the continuous increase in extinction rate, through a gradual increase in its colonization rate,
213 and thus its colonization ratio c/e (Fig. 2d). Its occupancy declines, but the decline is
214 mitigated by evolution, preventing extinction in the range of extinction rates considered.

215
216 When evolution is faster, the predator can evolve sufficiently to delay its extinction (Fig. 2e-
217 f), and ultimately it also manages to escape extinction (albeit at low occupancy), just like the
218 prey (Fig. 2g-h). Note that when the prey is not threatened with extinction, evolution in the
219 prey can initially decrease its equilibrium occupancy, which is detrimental to predator
220 persistence and counteracts the effects of evolution in the latter.

221
222 From eq. (2), it can be seen that as a species approaches extinction, $q_i \rightarrow 0$, c_i always
223 increases, acting to counteract extinction in all cases. However, comparing among trophic
224 levels when they are on the verge of extinction ($q_i \approx \epsilon$), one can deduce that (i) the positive
225 selection pressure caused by available habitat is lower for higher trophic levels (since q_{i-1}
226 decreases with i), and (ii) the negative selection pressure caused by local competition is
227 stronger (since the colonization rate c_i will generally be increasing with trophic position).
228 Both effects make selection for larger colonization rates less efficient at higher trophic levels,
229 providing a rationale for the results shown in Fig. 2.

230
231 Overall, the evolution of colonization rate is beneficial to species persistence and thus food-
232 chain length. Higher trophic levels will be selected for larger colonization rates than lower
233 trophic levels. However, while all trophic levels are selected for higher colonization when
234 approaching extinction, the intensity of the effect increases with trophic level, putting a
235 higher evolutionary challenge on higher trophic levels. Furthermore, evolution at low trophic
236 levels, when they are not threatened by extinction, is often detrimental to the persistence of
237 upper trophic levels. For these two reasons, the beneficial effects of evolution are not as
238 effective as one might expect to promote food-chain length. Basically, a fast evolution of
239 predators is more efficient at maintaining the integrity of the food chain than a fast evolution
240 of their prey; fast evolution in prey becomes necessary to maintain the system only in
241 conditions where the prey would be threatened even in the absence of predation.

242
243 Since results go in the same direction with fast and slow evolution and since assuming the
244 ESS allows for much easier mathematical analysis and faster computing (Supplementary

245 Material), in the following we will consider fast evolution only, and compare results with the
246 “no evolution” scenario. Our results can be taken as giving an upper bound on the potential
247 consequence of evolution on food-web dynamics, and capturing the two extreme possible
248 situations, most actual situations probably falling somewhere in between them.

249

250 **Maximum food-chain length under habitat degradation**

251 We considered two forms of habitat degradation: (i) an increase in extinction rate (as in the
252 previous section), and (ii) habitat destruction (*i.e.* a decrease in the fraction of available
253 patches h ; see equation [1]).

254

255 As expected, increasing the extinction rate decreases the maximum food-chain length in the
256 absence of evolution (Fig. 3a, see also Calcagno et al. 2011; Wang et al. 2021). In the
257 presence of evolution, however, the decline is much reduced. This is caused by an increase
258 in the colonization rate of the upper trophic levels, which are selected for high values, even
259 though this does not suffice to overcome the increasing extinction rate and the reduced
260 occupancy of lower trophic levels (Fig. 3b). Note that, with or without evolution, the decline of
261 maximum food-chain length with extinction rate always has an overall convex shape (rapid
262 loss of many trophic levels followed by gradual loss of the remaining levels as extinction rate
263 increases).

264

265 When destroying habitat patches (reducing h), the same tendency is observed: evolution
266 allows longer food chains to persist, compared to the reference case with no evolution (Fig.
267 3c). Note, however, that all trophic levels jointly evolve higher colonization rates, even the
268 lower ones (Fig. 3d). This is because decreasing h affects the first trophic level just as
269 strongly as the others, unlike increasing the extinction rate, which has a disproportionately
270 stronger effect on the higher trophic levels. We also remark a qualitative impact of evolution:
271 the decline of food-chain length with habitat destruction follows a convex sequence in the
272 absence of evolution (first many losses, then more gradual losses), as it does when
273 manipulating extinction rate. However, with evolution, increasing habitat destruction causes
274 a concave declining sequence of food-chain length, with two trophic levels (out of four) going
275 extinct when habitat destruction attains values of 0.8-1.0 (Fig. 3c).

276

277 **The consequences of trade-off intensity**

278 Increasing the intensity of the trade-off between colonization and local competitiveness (*i.e.*
279 decreasing the basal competitiveness of immigrants ϕ and/or making the slope ψ_0 more
280 negative) increases the negative selection pressure on the colonization rates (eq. 2), and
281 should thus select for lower values of the latter. This should in turn negatively affect

282 maximum food-chain length. This is indeed what we find (Fig. 4a), except that parameter ϕ
283 has very little impact. The latter result is consistent with Calcagno et al. (2017). If the trade-
284 off slope is very shallow, colonization rates are free to evolve to quite high values, which
285 allows much longer food chains to persist (Fig. 4b). Conversely, if the slope is very negative,
286 selection favours low colonization values, especially at lower trophic levels, at the expense
287 of population persistence and food-chain length (Fig. 4b). Costs of dispersal (trade-off
288 intensity) are therefore a critical aspect for predicting the consequences of dispersal
289 evolution for food-chain length.

290

291 **The relationship between food-chain length and the proportion of empty patches**

292 As demonstrated by Calcagno et al. (2011) and Wang et al. (2021), in the absence of
293 evolution, a negative correlation is expected between food-chain length and the fraction of
294 empty patches. In other words, long food chains can be observed only if the total occupancy
295 is high enough, as shown in Fig. 5. When varying the extinction rate e , we again find that
296 evolution changes the pattern quantitatively, but not qualitatively (Fig. 5a-b). Things are
297 different when the amount of habitat destruction varies: in this case, we observe concave
298 negative relationships between food-chain length and the fraction of empty patches, but only

299 with evolution. Without evolution, we observe the classic convex relationships observed
300 otherwise or, at best, linear relationships (Fig. 5c-d). Such a qualitative difference in the
301 shape of the relationships could be looked for in empirical or experimental data in order to
302 infer the action of evolutionary dynamics. Interestingly, this difference is reminiscent of the
303 one we have observed between food-chain length and habitat destruction (Fig. 3c-d). We
304 checked that varying other parameters (specifically the perturbation rate μ) could not
305 produce concave relationships, with or without evolution (Supplementary Fig. 2). It therefore
306 seems that habitat destruction has a specific action that brings up a qualitative difference
307 between evolved and unevolved food chains. Specifically, with evolution, relationships that
308 are otherwise convex can be turned concave.

309 310 **Discussion**

311
312 As previous studies have shown, metacommunity dynamics impose an intrinsic constraint on
313 food-chain length, and the persistence of long food-chains in spatially structured habitats
314 thus requires specific conditions (Holt, 2002; Calcagno et al. 2011). Higher trophic levels are
315 vulnerable to extinction from multiple processes, and, paraphrasing Robert May, they must
316 arguably deploy “devious strategies” in order to persist. The most obvious strategy in this
317 context is the adoption of systematically higher colonization rates by higher trophic levels,
318 but there are also other strategies, such as behavioural ones (Calcagno et al. 2011).

319
320 As shown here, the evolutionary dynamics of colonization rates, *i.e.* the evolution of
321 dispersal at individual trophic levels, is yet another way to alleviate the constraint on food-
322 chain length. Natural selection does favour larger colonization rates at upper trophic levels
323 and an evolutionary increase in colonization rate can, if fast enough, allow the persistence of
324 longer food chains than when species traits are constant. The selection pressures imposed
325 on colonization rates by trophic relationships and spatial structure cause evolutionary
326 responses that can sustain the persistence of more trophic levels in the face of habitat
327 degradation, such as increased disturbances or habitat destruction.

328
329 It would seem at first glance that such eco-evolutionary dynamics could be the ultimate
330 devious strategy, by allowing the colonization rates of species to evolve larger values as
331 needed. They could potentially alleviate any limit on food-chain length, as spatial persistence
332 is ensured provided a sufficiently large colonization rate. This would be similar to
333 evolutionary rescue, in another context and at a larger scale. However, our results show that
334 things are not so simple. Indeed, when all trophic levels are allowed to evolve in such a way,
335 two factors limit the efficiency of evolution in rescuing food-chain length. First, the lowest
336 trophic levels, which are typically not facing the greatest danger of spatial extinction,
337 experience little selection for increased colonization as their effective extinction rates are
338 low. Quite the opposite, they can readily be selected for lower colonization rates, because of
339 intraspecific competition or, equivalently, costs of dispersal. Such a negative selection
340 pressure lowers their spatial occupancy, directly jeopardizing the persistence of the superior
341 trophic levels. Second, the strength of selection for larger colonization rates typically
342 declines, all else being equal, as trophic level increases. This is because positive selection
343 declines as the fraction of hospitable patches decreases, while at the same time, the larger
344 colonization rates that higher trophic levels must adopt increase the strength of selection
345 against dispersal caused by intraspecific competition (see the gradient equation [2]).
346 Combined, these two factors make eco-evolutionary dynamics at lower trophic levels
347 potentially detrimental to maximum food-chain length, and not so effective at rescuing higher
348 trophic levels. In short, even if very efficient, evolutionary dynamics is not the silver bullet to
349 ensure the persistence of higher trophic levels. This is why, even with no particular
350 constraint on the speed or extent of adaptive evolution, eco-evolutionary dynamics does not
351 totally suppress the spatial constraint on maximum food-chain length. Even when it permits
352 longer food-chains to persist, the higher trophic levels are typically kept at low spatial
353 occupancies, thus vulnerable to environmental perturbations or other random events.

354

355 In the evolutionary context we have considered here, the question of understanding what
356 devious strategies higher trophic levels must deploy to persist remains, though the range of
357 available strategies is more precisely defined. Theoretically, factors that could favour the
358 persistence of longer food-chains are: (i) higher trophic levels have faster evolution rates, or
359 (ii) competition-colonization trade-off intensities are weaker at higher trophic levels. These
360 two possibilities remain to be investigated empirically. We can nonetheless remark that one
361 of the components affecting trade-off intensity is local population size (Supplementary
362 Material). The larger the local population size, the less steep the trade-off, all else being
363 equal. Since we would quite often expect higher trophic levels to have smaller local
364 population sizes, this should make ψ_0 more negative as trophic level goes up. If so, this
365 would be yet another factor detrimental to food-chain length under eco-evolutionary
366 dynamics. Regarding heterogeneity in evolution rates among trophic levels, the good news
367 is that, if evolution proceeded more quickly in prey than predators or vice versa for all traits
368 under selection, such a heterogeneity should leave a clear mark on the population dynamics
369 series of both predator and prey (Yoshida et al. 2003; Hiltunen et al. 2014), thus providing us
370 with an empirical test of this hypothesis.

371

372 We obviously did not impose any restriction on the range of colonization rates that could
373 evolve. This may be unrealistic and other selective forces or constraints could of course
374 interfere with the effects presented here. For instance, colonization rates may have upper
375 bounds (see Supplementary Material for an example resulting from maximum reproductive
376 investment). If the upper bound is low enough, this could constrain the possibility of at least
377 some trophic levels to persist through the evolution of greater colonization rates. Large
378 colonization rates are especially selected for at higher trophic levels, so the latter would
379 need to have less stringent bounds.

380

381 One direct way to test our predictions is to use an experimental approach, with suitable
382 biological systems such as ciliates or other microorganisms in which both dispersal and
383 competition have been thoroughly studied (Fox & Morin, 2001; Pennekamp et al. 2014) and
384 for which the definition of trophic levels, patches and dispersal are simple to establish. More
385 generally, we might use observational data from the field to evaluate whether some of the
386 qualitative patterns / trends we have identified here actually occurs – these patterns could
387 indeed be diagnostic of whether the type of eco-evolutionary dynamics modelled are at play
388 or not. Of course, natural communities and food chains experience processes and
389 contingencies left out in models (e.g. autocorrelation and/or clustering of perturbations,
390 species occurring at more than one trophic level). This would often complicate the task, but
391 datasets such as the one used in Wang et al. (2021) exist and are extremely useful in this
392 context, especially if they extend to three or more trophic levels. The patterns reported in
393 Fig. 3 and 5 appear especially valuable for empirical assessments. Indeed, we found that
394 among systems differing in their level of habitat destruction, either spontaneously or upon
395 experimental manipulation, the maximum food-chain length declines in a generically convex
396 manner in the absence of eco-evolutionary dynamics, whereas it could have a concave
397 decline with such dynamics (Fig. 3c). Such a concave shape is never observed without
398 evolutionary dynamics, and is not observed when manipulating the extinction rate. The
399 existence of a concave relationship would therefore be a strong indication that eco-
400 evolutionary dynamics are at play.

401 Alternatively, the correlation between total occupancy (and thus the fraction of unoccupied
402 patches) and maximum food-chain length offers the same prediction (Fig. 5): it could
403 assume a concave shape only with eco-evolutionary dynamics, not in their absence, and
404 only if habitat destruction is the underlying varying parameter. A concave shape is observed
405 upon varying the extinction rate e or the perturbation rate μ (Supplementary Fig. 2). It thus
406 seems that datasets or experiments documenting the impact of habitat destruction on

407 maximum food-chain length and overall occupancy offer great promises to evaluate the
408 importance of eco-evolutionary dynamics in shaping food webs.

409

410 Our results were derived in a simple spatially homogeneous and mean-field patch-
411 occupancy model. Interestingly, such a simple model faithfully reproduces the results
412 presented in Wang et al. (2021), who used stochastic simulations of a spatially realistic
413 model. This gives additional credence in the predictions we derived here. Our results could
414 be extended in many different ways, possibly including more complex food-web topologies
415 (“how would omnivory affect model predictions?”), introducing several species per trophic
416 level (leading to the study of apparent predation at the scale of the metacommunity) or even
417 using trophic level-specific definitions of a patch (e.g. McCann et al. 2005), but they reveal
418 some fundamental ways in which the evolution of dispersal and spatial food-webs dynamics
419 are interconnected. In any case, they suggest a lot is to be gained from bringing more eco-
420 evolutionary dynamics into the realm of food-web ecology.

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424 **Author contributions**

425 The initial idea of this work originated from FM during his PhD thesis with PJ and PD. VC
426 and FM designed and conducted the research. VC and FM wrote the initial manuscript, all
427 co-authors contributed to manuscript preparation.

428

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434 function from a spatially structured population model to the dearly missed Isabelle Oliveri,
435 who hinted at it in a split sentence in 2005, as he was doing his PhD under her supervision.

436

437 **Conflicts of interest**

438 The authors declare no conflict of interest.

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Figure legends

Figure 1.

443 A graphical illustration of the spatial food chain model. The habitat consists of many
444 interconnected patches. Each patch can be colonized by one or more trophic levels. The first
445 trophic level can colonize any empty available habitat patch, whereas the second trophic
446 level can only colonize patches where the first trophic level is found, etc. Each trophic level
447 can disappear from a patch at some basal extinction rate e , and local extinction of one
448 trophic level causes the local extinction of all upper trophic levels. Patches can also undergo
449 catastrophic perturbation events, at rate μ , causing all trophic levels to be removed at once.
450 The dynamical variables of interest in eq. (1) are the q_i , *i.e.* the proportion of patches
451 occupied by the i -th trophic level (and possibly upper trophic levels too), as illustrated at the
452 bottom of the figure.

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Figure 2.

456 Increasing extinction rate in a system with two trophic levels. **(a-b)** No evolution. The
457 extinction rate is gradually increased from its baseline value ($e=1$). The equilibrium
458 occupancies of the prey (*blue*) and the predator (*green*) gradually decline until extinction (a),
459 as the colonization ratios (c/e) decline with the increase in e (b). These results very closely
460 reproduce Wang et al. (2021) fig. 1 results. **(c-d)** Introducing evolution at low speed relative
461 to the change in e ($V_G = 0.1$). **(e-f)** Introducing evolution at an intermediate speed relative
462 to the change in e ($V_G = 1$). **(g-h)** Introducing evolution at a large speed relative to the change
463 in e ($V_G = 100$). The two trophic levels initially had colonization rates $c = 10$; without
464 evolution they retained these values throughout, whereas with evolution the values gradually
465 changed according to eq. (2). Other parameters were at default values, except $\mu = 0$ and e_{TD}
466 $= 2 e$.

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Figure 3.

470 Maximum food-chain length under habitat deterioration. **(a-b)** The effect of increasing the
471 extinction rate on maximum food-chain length (a), without evolution (*orange*) and with
472 evolution (*blue*). In the case of evolution, the colonization ratio values at each trophic level
473 are shown in (b). **(c-d)** Same as (a-b), except that the level of habitat destruction ($1-h$) was
474 increased instead of e . Initially (*i.e.* for $e=0$ or $h=1$), species have the same colonization
475 rates in the two scenarios (with or without evolution), set at the corresponding ES values.
476 These values do not change in the no evolution scenario, whereas they changed in the other
477 scenario.

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Figure 4.

481 Consequences of varying the competitive trade-off intensity. **(a)** A contour plot of maximum
482 food-chain length, with evolution, as a function of the two competitive trade-off parameters
483 (ϕ ; y-axis) and (Ψ_0 ; log scale, x-axis; $-100 < \Psi_0 < -0.01$). **(b)** For a fixed $\phi = 0.5$
484 (corresponding to the dotted line in panel a), the colonization ratios of the different trophic
485 levels as a function of Ψ_0 .

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Figure 5.

489 The relationship between food-chain length and the fraction of empty patches without
490 evolution (left panels) and with evolution (right panels). **(a-b)** Each dot represents a different
491 parameter value, where the extinction rate varies between 0.01 and 100, under three
492 different values of Ψ_0 . **(c-d)** Each dot represents a different parameter value, where the
493 habitat destruction level $1-h$ varies between 0 and 1, under three values of Ψ_0 . In all panels,

494 the three values of Ψ_0 were -1 (gray dots), -0.1 (orange dots) and -0.01 (blue dots). As in
495 Fig. 3, species had colonization rates set at the ES values for the initial parameter value, and
496 these values remained constant in the no evolution scenarios, whereas they adapted in the
497 evolution scenarios. Points were slightly jittered vertically for better readability.

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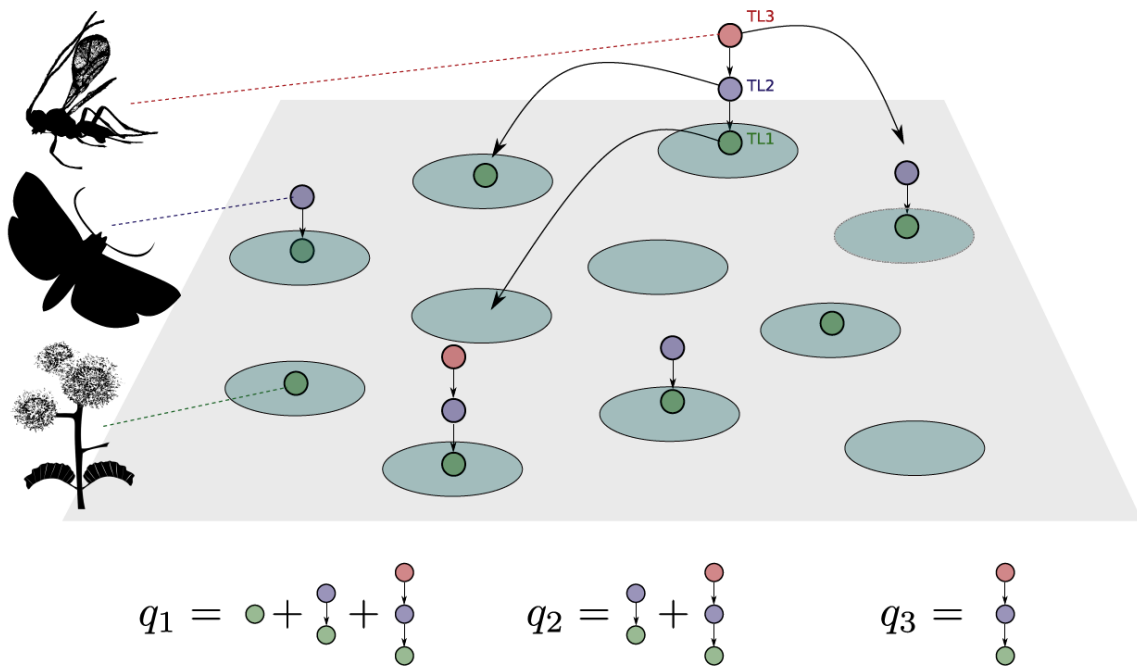
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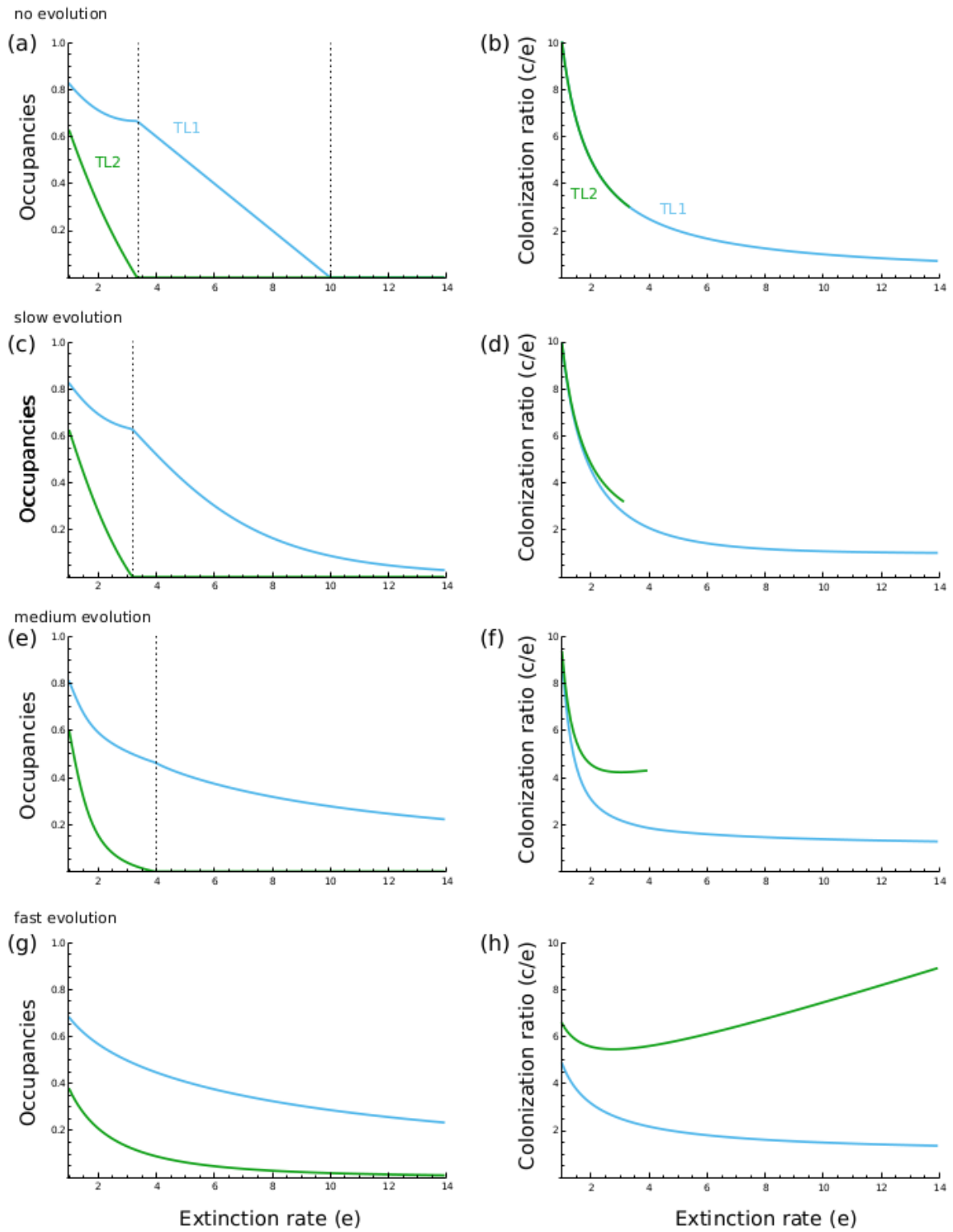
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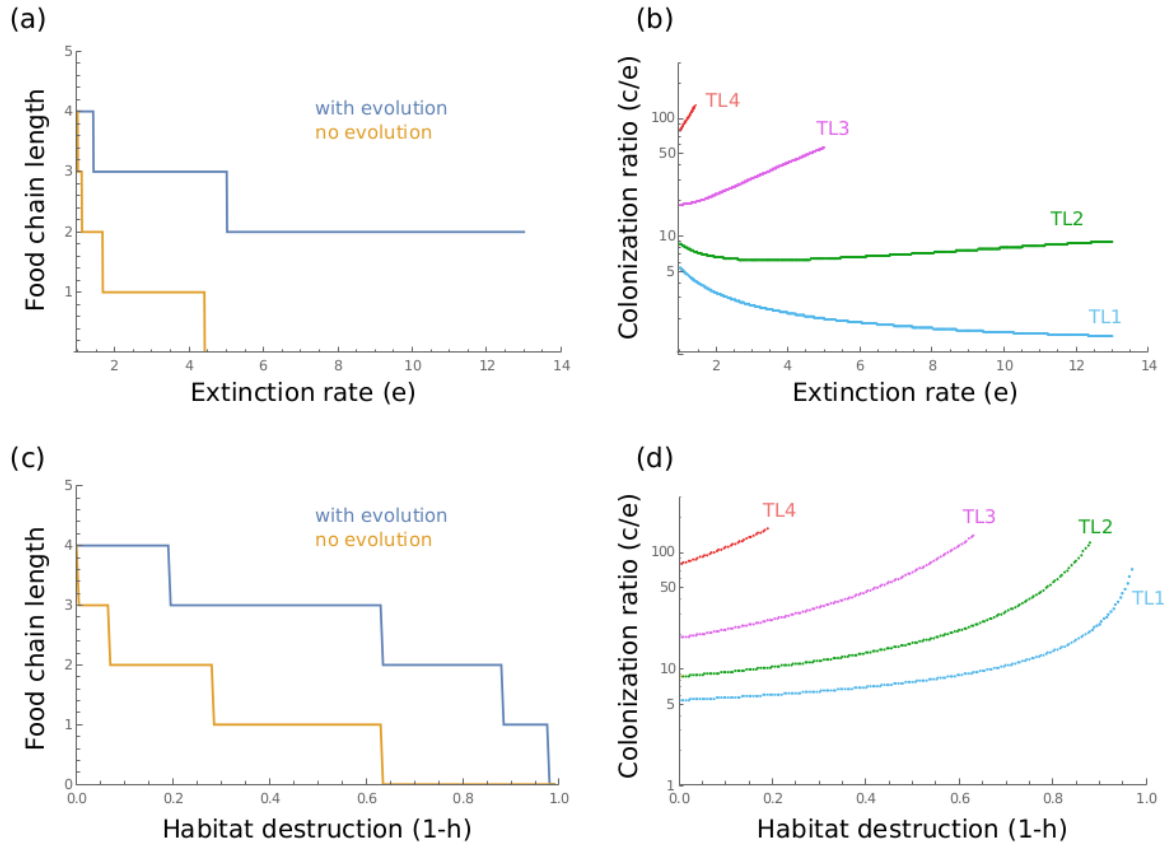
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Figure 1



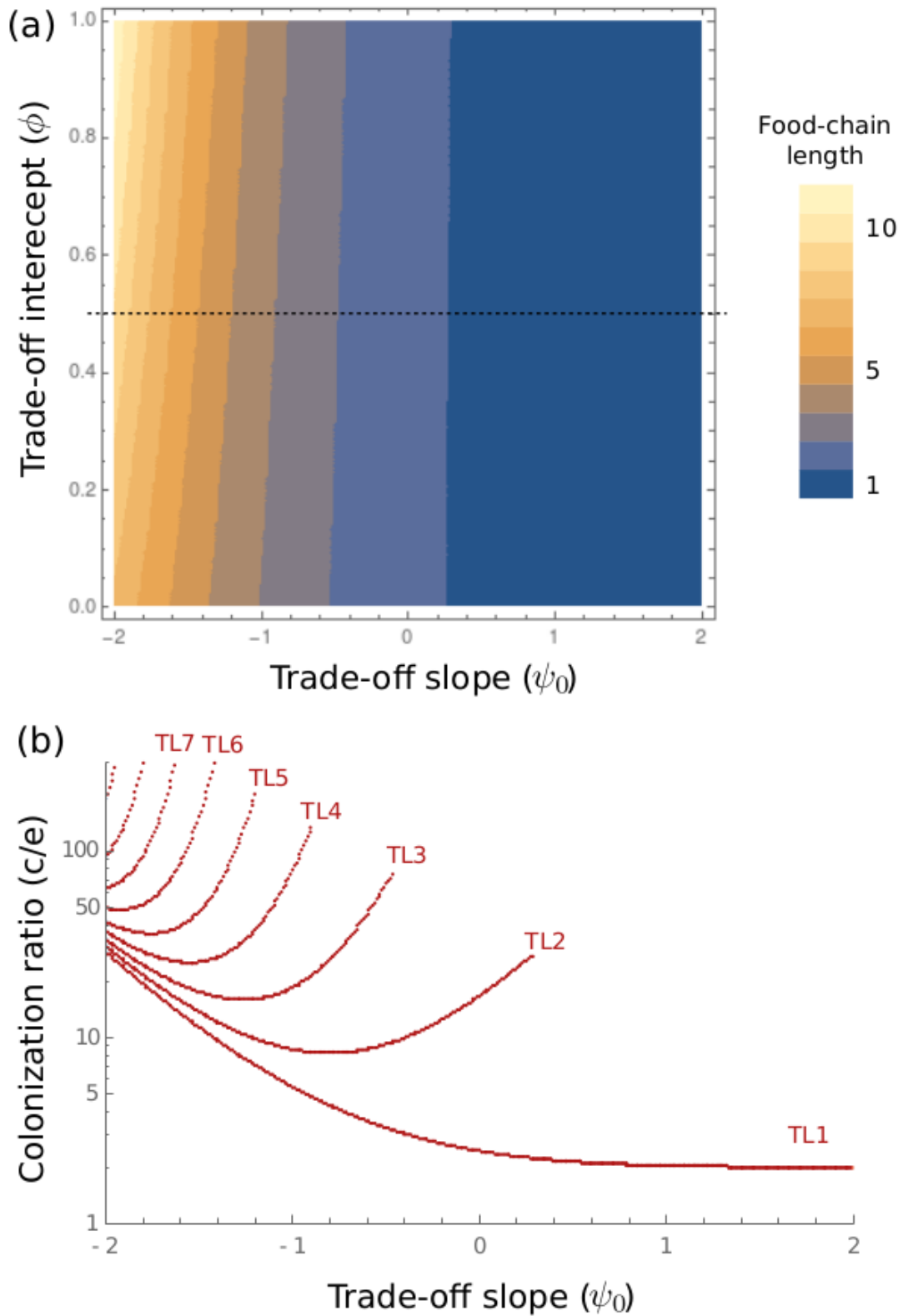
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Figure 2



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Figure 3



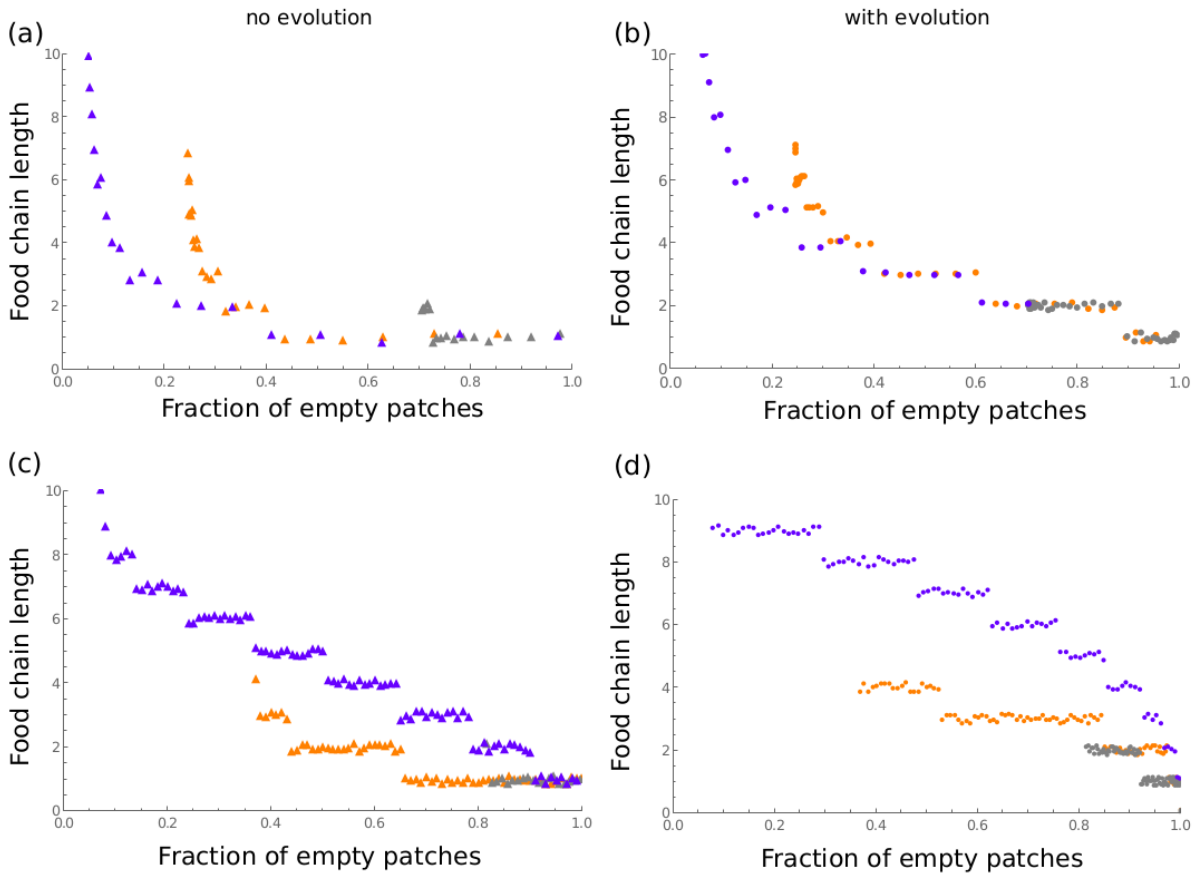


Figure 5

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