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1 **From apparent competition to facilitation, impacts of consumer**
2 **niche construction on the coexistence and stability of consumer-**
3 **resource communities**

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9 Summary

10 1. In addition to their direct trophic effects, some consumers have a positive indirect
11 effect on their resource, due to niche construction. A predator can facilitate its prey
12 resource acquisition, through prey transport, or through modifications of nutrient cycling.
13 Other predators defend their prey against other predators, or actively manage it, as in
14 agriculture, which is found in numerous taxa such as humans, but also ants, beetles, fishes
15 and microbes.

16 2. Here we investigate the ecological consequences of considering such positive
17 effects in a simple two resource–one predator module, in which the consumer has a
18 positive effect on one of the resources.

19 3. We consider several scenarios, in which the positive effect of the resource is
20 either non costly, ie resulting from a by-product of the consumer phenotype such as
21 nutrient cycling, or costly. The cost either decreases the exploitation of the helped
22 resource or the opportunity to forage the alternative resource.

23 4. We show that by modifying the trophic interactions in the module, niche
24 construction alters the apparent competition between the resources, thereby impacting
25 their coexistence.

26 5. We investigate how the intensity of niche construction impacts species
27 coexistence, the distribution of biomass among the three species, and the stability of the
28 community. When niche construction has little or no cost, it leads to higher consumer and
29 helped resource densities, while decreasing the alternative resource density. Alternatively,
30 when niche construction has a strong cost, the alternative resource can increase in density,
31 niche construction thereby leading to the emergence of facilitative interactions among
32 resource species.

33 Keywords

34 niche construction, consumer-resource theory, apparent competition, facilitation,

35 agriculture, trophic module

36 Introduction

37 While most studies in network ecology consider only one interaction type (ie,
38 either food webs or mutualistic networks), the co-occurrence of different interaction types
39 within networks has been of increasing interest in the last decade, in both theoretical and
40 empirical studies (Fontaine et al., 2011; Kéfi et al., 2012; Mougi & Kondoh, 2012). In
41 particular, positive interactions that co-occur with antagonistic interactions may originate
42 from mutualism, facilitation (Bruno, Stachowicz, & Bertness, 2003), ecosystem
43 engineering (Jones, Lawton, & Shachak, 1994) and niche construction (Odling-Smee,
44 Laland, & Feldman, 1996). They can either directly affect the partner of interaction (as in
45 mutualism) or alter the environment (as in ecological engineering) (Kéfi et al., 2012).

46 Importantly, the co-occurrence of multiple interaction types may affect predictions
47 on general ecological questions such as ecosystem functioning, community stability and
48 persistence (Fontaine et al., 2011; Kéfi et al., 2012). For instance, positive interactions
49 can increase the persistence of a consumer under resource-limited conditions (Kylafis &
50 Loreau, 2008) thus facilitating the coexistence and increasing community diversity
51 (Gross, 2008). Positive interactions can notably occur when a given species has both
52 trophic and non-trophic effects on the same partner of interaction. For instance, ant
53 species that simultaneously tend aphids and prey on them can provide benefits to aphids
54 by eating honeydew and protecting them from predators (Stadler & Dixon, 2005). Note
55 that the frontier between a consumer helping its resource and a mutualist exploiting its
56 partner is not clear, and the examples we cite later on could often belong to either
57 categories (Bronstein, 2001; Offenberg, 2001). The net demographic effect of the
58 interaction theoretically allows a complete classification but is not always measurable.

59 Indirect positive effects can emerge from a variety of consumer behaviours that
60 improve some components of the resource growth rate (Brown, Ferris, Fu, & Plant, 2004
61 and references within). A first intuitive case would be a consumer facilitating its resource

62 nutrient acquisition. For instance, while grazing, herbivores recycle nutrients to the soil,
63 and may under some conditions increase primary productivity. An intermediate level of
64 herbivory then leads to an optimal primary productivity (grazing optimization hypothesis,
65 (de Mazancourt, Loreau, & Abbadie, 1998)). Predators may also reduce prey mortality,
66 when they protect it against other predators (through interference with or predation of
67 alternative predators) or inhibits the prey's competitors. For instance, in devil's gardens,
68 ants kill competitors of their host plant species (Frederickson, Greene, & Gordon, 2005).
69 Finally, a consumer may help its resource dispersal and reproduction (eg, seed dispersal
70 linked to granivory, (Davidson, 1977)), or reduce prey intraspecific competition. The
71 nematode *Caenorhabditis elegans* for instance transports its prey bacteria and inoculate
72 them to unexploited resource pools (Ingham, Trofymow, Ingham, & Coleman, 1985;
73 Thutupalli et al., 2017).

74 Such helping behaviours can occur at a cost for the consumer or not. This
75 distinction ultimately changes the way the positive effect affects the demography of the
76 consumer species in the system, altering the prey-consumer feedback. We call the positive
77 effect passive if it results from a by-product of the consumer phenotype, with no direct
78 metabolic cost. Nutrient cycling, as in the grazing optimization hypothesis (de
79 Mazancourt et al., 1998), seed dispersal or passive transport of the resource to
80 unexploited areas as in the nematode-bacteria interaction would all fall in this category
81 (Thutupalli et al., 2017). Dissuading other predators from attacking the resource through
82 the mere presence of the consumer could also be a passive positive effect.

83 When the positive effect on the resource is active, its negatively affects another
84 consumer fitness component. For example, active resource management, that we refer
85 loosely to as "agriculture", incurs a cost in terms of time and energy. Agriculture -
86 cultivation of plants, algae, fungi and animal herding - is found in humans, but also ants,
87 beetles, fishes and even microbes (Boomsma, 2011; Hata & Kato, 2006; Mueller,
88 Gerardo, Aanen, Six, & Schultz, 2005; Rowley-Conwy & Layton, 2011; Smith, 2016).

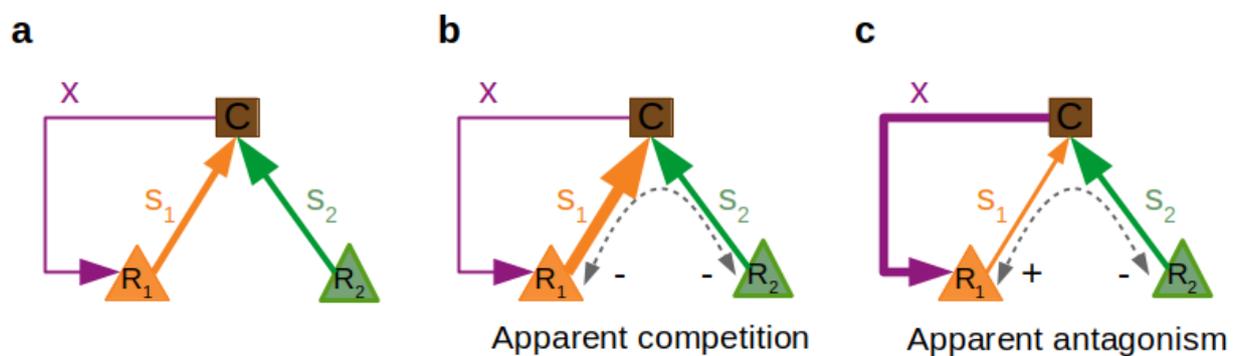
89 The cost of agriculture can be envisioned through foraging theory (Charnov, 1976), where
90 spending time on one resource reduces the available time to forage another resource,
91 leading to an “opportunity cost”. Another type of cost can emerge if actively defending a
92 resource against other predators or competitors implies moving away from this resource
93 site or decreasing its consumption (eg, by allocating time to defense rather than
94 consumption). Then, an “exploitation cost” scenario emerges with a trade-off between
95 resource consumption and resource protection.

96 We here investigate the ecological consequences of considering such positive
97 effects in a simple trophic module. We consider a consumer that feeds on a helped
98 resource while also foraging on a second (non-helped) resource. Such simple trophic
99 modules have been extensively used in ecology to understand mechanisms promoting
100 coexistence and stability in ecological networks (Bascompte & Melián, 2005; Holt, 1997;
101 Stouffer & Bascompte, 2010). We assume the consumer has a positive effect on one of the
102 resources (the “helped” one). We consider three scenarios that cover passive positive
103 effects (“no cost” scenario) and two types of active positive effects (“exploitation cost”
104 and “opportunity cost” scenarios). “No cost” scenarios assume that niche construction
105 only has an effect on the resource growth rate with no allocative cost (nutrient recycling,
106 cross-feeding). In “exploitation cost” scenarios, we assume that investment in niche
107 construction decreases the direct consumption of the helped resource. This may occur
108 when time devoted to defense against predators constrains consumption (for instance, ants
109 protecting aphids against ladybirds (Stadler & Dixon, 2005). “Opportunity cost” scenarios
110 assume that niche construction decreases consumption of the alternative resource. This
111 scenario is tightly linked to optimal foraging theory (Charnov, 1976; Pyke, Pulliam, &
112 Charnov, 1977)(Charnov, 1976; Pyke et al., 1977) and exploitation-exploration trade-offs
113 (Monk et al., 2018). It relates to transitions between predation and breeder behaviours,
114 found in numerous species that specialize partly (facultative aphid rearing ants) or fully
115 on cultivated resources (humans, obligate aphid rearing ants (Ivens, von Beeren,

116 Blüthgen, & Kronauer, 2016), fungus growing ants (Chapela, Rehner, Schultz, & Mueller,
117 1994)).

118 We investigate how niche construction impacts species coexistence, the distribution
119 of biomass among the three species, and the stability of the community. Predictions can
120 be made considering the indirect effects occurring in the system. In our module, the two
121 resource species do not directly compete but engage in apparent competition through their
122 interactions with the shared predator (Holt, 1977). Any increase in biomass of a given
123 prey has an indirect negative effect on the other prey as it increases predator density.
124 Previous works show that the winner of the competition is the species that sustain the
125 highest density of predator, leading to a P^* rule similar to the R^* of exploitative
126 competition (Holt, Grover, & Tilman, 1994). Because we consider that one species
127 receives an additional positive effect from the consumer, indirect effects are altered. If the
128 net effect of the consumer on the helped resource is positive, then the apparent
129 competition may become an apparent antagonism as the alternative resource has a
130 positive indirect effect on the helped resource (see figure 1). In “no cost” scenarios, we
131 predict that niche construction increases the growth rate of the helped resource, hence
132 negatively impacting the alternative resource through increased apparent competition.
133 Eventually, such an effect may lead to the loss of coexistence. Considering a trade-off
134 with the consumption of either resource may modify these predictions by affecting the
135 balance of indirect effects. In the “exploitation cost” scenario, niche construction
136 decreases the consumption of the helped resource, hence makes it less vulnerable to
137 predation: we predict that it would win the competition because it suffers less from the
138 indirect negative effects received from the alternative resource. We therefore predict that
139 niche construction should eventually negatively impact coexistence. In the “opportunity
140 cost” scenario, niche construction decreases the consumption of the alternative resource,
141 hence the effects of apparent competition should be more balanced among prey species,
142 promoting coexistence.

143 Predictions can also be made regarding the effects of niche construction on the
144 stability of the system. In the “exploitation cost” scenario, niche construction should
145 reduce the energy flux from the resource to the consumer, relative to the consumer loss.
146 Such limited energy fluxes should be stabilizing, as long as the net interaction remains
147 trophic (Rip & McCann, 2011). Considering the whole three-species module, niche
148 construction is expected to be stabilizing when it increases interaction heterogeneity
149 among prey species (McCann, Hastings, & Huxel, 1998), for instance due to costs on the
150 consumption of either species. However, if the net interaction between the consumer and
151 the helped resource becomes mutualistic due to large positive effects, we expect it to be
152 destabilizing, because a negative trophic feedback loop then becomes a positive feedback
153 loop (May, 1973).



154 *Figure 1: Presentation of the three-species model and indirect effects occurring*
155 *between the resources. a Direct interactions: the consumer C consumes both resources R₁*
156 *and R₂ depending on its specialization on each resource (s₁ and s₂). It increases the*
157 *growth of resource R₁ by a factor x, which is the niche construction investment trait. b*
158 *When the outcome of the C-R₁ interaction is negative (s₁>x), resources are limited by*
159 *apparent competition. c When the outcome of the C-R₁ interaction is positive (s₁<x), the*
160 *resources engage in apparent antagonism.*

161 Model presentation

162 Ecological dynamics are modeled using ordinary differential equations (eq 1):

$$\begin{cases} \frac{dC}{dt} = C(e_1 s_1 R_1 + e_2 s_2 R_2 - m) \\ \frac{dR_1}{dt} = R_1(b_1 - g_1 R_1 - s_1 C + w x C) \\ \frac{dR_2}{dt} = R_2(b_2 - g_2 R_2 - s_2 C) \end{cases} \quad 1$$

163 The consumer C *per capita* growth rate depends on its consumption of resources
164 (modelled by specialization on resource R_i , s_i , and conversion efficiency of resource R_i , e_i)
165 and on its *per capita* death rate m . Resources have a logistic growth in the absence of the
166 consumer (allowing for their coexistence in such situations): b_i is the *per capita* birth rate
167 and g_i is the intraspecific competition rate for resource R_i . We do not consider any direct
168 competition between resources so that their coexistence can be entirely understood based
169 on variations of indirect effects inherent to the consumer species. To this logistic growth
170 is added a consumption rate scaled by the specialization of consumer on the resource, and
171 a niche construction effect for resource R_i . All interactions are linear. In particular, in this
172 first model, niche construction is proportional to the investment trait x , and the consumer
173 density, modulated by a niche construction efficiency w . Such simple linear functions
174 allow for an analytical study of the system. In the Supplementary Information, we
175 consider a saturating response for the niche construction effects and discuss the
176 robustness of the results we present in the main text. We assume that e_i , s_i , b_i , g_i , x are
177 positive, so that niche construction is facultative for the maintenance of resource 1.

178 The ecological analysis of the system focuses on the feasibility and linear stability
179 criteria applied on the different possible equilibria. Feasibility conditions require the
180 positivity of all equilibrium densities. The stability analysis relies on the analysis of the

181 Jacobian matrix (thereby assessing the return time to equilibrium following a small
182 disturbance) and of the invasibility of considered equilibrium by species that are not
183 present at equilibrium. All figures and computations were made using Mathematica 11.

184 Results

185 The model displays community states (equilibria) at which resources can subsist
186 without the consumer, or the consumer coexists with one or both resources. We sum up
187 the general stability and feasibility conditions for the “no cost” scenario, and study how
188 niche construction impacts these coexistence and stability conditions. We then investigate
189 how the addition of a cost modifies those results in the “exploitation cost” and
190 “opportunity cost” scenarios. The detailed mathematical analysis can be found in the
191 Supplementary Information.

192 **1) Coexistence and stability under the “no cost” scenario ($s_1'(x)=s_2'(x)=0$)**

193 In this scenario, the positive effect of the consumer on its resource happens through
194 a passive effect, as a by-product of metabolism or activity of the consumer. There is no
195 direct cost for the consumer. For instance, the large effects on nutrient recycling by the
196 wildebeest in the Serengeti ecosystem (McNaughton, 1976) could be considered as a
197 motivation for such a scenario. The positive effect only impacts the growth rate of
198 resource 1 through the consumer density-dependent factor, and predation rates s_1 and s_2
199 are constant.

200 We show that the consumer-helped resource ($C-R_1$) equilibrium is feasible and
201 stable when the interaction between the two species remains trophic, (ie, positive effects
202 are not too high). The ratio between the resource birth rates and their vulnerabilities
203 determines the invasion potential for resource R_2 : if it has a high birth to vulnerability
204 ratio, it can invade the consumer-helped resource system. In this ($C-R_1$) subsystem, niche
205 construction has no effect on the resource density but increases the consumer density. The
206 increase in growth rate is compensated by an increase in predation rate, so that the
207 resource remains top-down controlled.

208 Regarding the (C - R_2) equilibrium, our analysis reveals that niche construction does
 209 not have an impact on the equilibrium densities, as the helped resource is absent. Niche
 210 construction is destabilizing, as large x allows an invasion of the equilibrium by resource
 211 R_1 . Conditions of coexistence of the three species can therefore be expressed as upper and
 212 lower limits of the positive effect intensity. Hence, niche construction favors coexistence
 213 at intermediate values.

214 Niche construction affects the distribution of species densities. Given the dynamical
 215 system 1, species densities at the coexistence equilibrium in the “no cost” scenario can be
 216 written:

$$\begin{aligned}
 C^* &= \frac{b_1 e_1 g_2 s_1 + b_2 e_2 g_1 s_2 - g_1 g_2 m}{e_1 g_2 s_1 (s_1 - w x) + e_2 g_1 s_2^2} \\
 R_1^* &= \frac{b_1 - (s_1 - w x) C^*}{g_1} \\
 R_2^* &= \frac{b_2 - s_2 C^*}{g_2}
 \end{aligned}
 \tag{2}$$

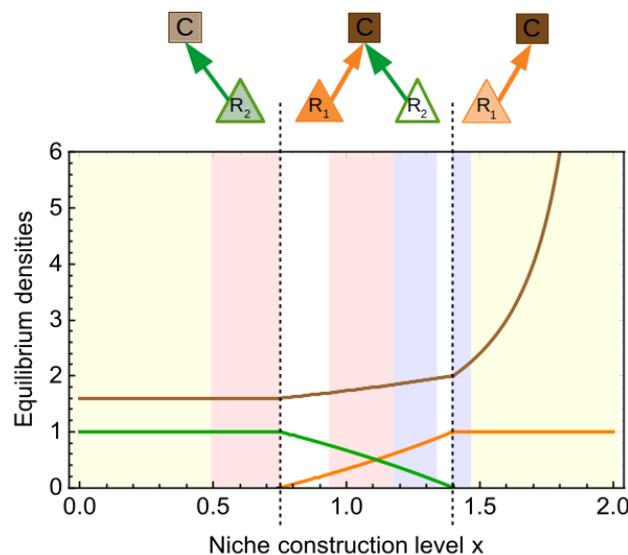
217 It is then possible to show how species densities vary depending on the intensity of niche
 218 construction:

$$\begin{aligned}
 \frac{\partial C^*}{\partial x} &= \frac{g_2 C^*(x) e_1 s_1}{g_2 e_1 s_1 (s_1 - w x) + e_2 g_1 s_2^2} > 0 \\
 \frac{\partial R_1^*}{\partial x} &= \frac{e_2 C^*(x) s_2^2}{g_2 e_1 s_1 (s_1 - w x) + e_2 g_1 s_2^2} > 0 \\
 \frac{\partial R_2^*}{\partial x} &= \frac{-C^*(x) e_1 s_1 s_2}{g_2 e_1 s_1 (s_1 - w x) + e_2 g_1 s_2^2} < 0
 \end{aligned}
 \tag{3}$$

219 As predicted, niche construction has a positive effect on the helped resource
 220 density, leading to a positive bottom-up effect on its consumer, negatively affecting the
 221 alternative resource density through apparent competition (figure 2). Equilibrium
 222 densities at the C - R_2 equilibrium do not vary with the intensity of niche construction, but

223 the invasion potential of R_1 increases up until R_1 can invade, eventually leading to
224 coexistence.

225 Niche construction also affect the resilience of the system (measured as the
226 negative real part of the dominant eigenvalue (Pimm & Lawton, 1977)). The stability
227 measure varies abruptly around the ecological states frontiers (see Rip & McCann,
228 (2011)), and we focus on variation for intermediate densities. For the coexistent
229 equilibrium (as predicted from the mathematical conditions, see (S12)), niche
230 construction is initially destabilizing then stabilizing, as it eventually increases
231 interaction heterogeneity (McCann et al., 1998). Concerning the C - R_1 equilibrium, niche
232 construction is stabilizing, as it decreases the *per capita* energy flux from the resource
233 to the consumer (Rip & McCann, 2011).



234 Figure 2: Effects of niche construction on the stable equilibrium densities and stability in
235 the “no cost” scenario. The consumer density is in brown, resource 1 density in orange,
236 resource 2 density in green. Above the plot, the different states of the module are
237 represented. An empty box means that density decreases, light box means that density
238 does not vary, while a dark box means that density increases. Within the plot, the
239 background shows stability variation: no variation (yellow), destabilization (red),

240 *stabilization (blue). Stability is non-monotonous in white areas (transition between*
 241 *ecological states). $e_1=e_2=0.5$, $g_1=g_2=0.8$, $m=1$, $b_1=2$, $b_2=4$, $s_1=2$, $s_2=2$.*

242 **2) Effects of costly niche construction on coexistence and stability**

243 We now assume that niche construction is costly for the consumer. This cost may
 244 decrease the consumption of either the helped resource (“exploitation cost”), or the
 245 alternative resource (“opportunity cost”). “Exploitation cost” scenarios include situations
 246 where higher positive effects on the helped resource (eg agriculture) decreases the
 247 exploitation of the same resource. This can happen because the time or energy devoted to
 248 protection of the resource against predators cannot be used for consumption (for instance,
 249 ants protecting aphids against ladybirds (Stadler and Dixon 2005)). “Opportunity cost”
 250 scenarios correspond to situations where the foraging on an alternative resource
 251 decreases, implying a trade-off between predation and agriculture activities.

252 From eq 1, it is easy to show that niche construction affects the distribution of
 253 species densities as (see Supplementary Information (S14)):

$$R_1^*(x) = \frac{((-s_1+x)C^*)'(x)}{g_1} = -\frac{(s_1(x)-x) C^*(x) + (s_1'(x)-1)C^*(x)}{g_1}$$

$$R_2^*(x) = \frac{(-s_2 C^*)'(x)}{g_2} = -\frac{s_2(x) C^*(x) + s_2'(x)C^*(x)}{g_2}$$
4

254 These derivatives are made of two terms. The first one shows the ecological
 255 consequences of niche construction (its impact on consumer population $C^*(x)$), while the
 256 second term embodies the effect of each cost, $s_1'(x)$ and $s_2'(x)$.

257 a) “Exploitation cost” scenario ($s_1'(x) < 0$, $s_2'(x) = 0$)

258 In the “exploitation cost” scenario, niche construction directly lowers the
 259 consumption of R_1 . Intuitively, such a decrease in consumption reinforces the positive

260 effect of niche construction on R_1 . In turn, this should increase apparent competition and
 261 harm R_2 . In such a scenario, we obtain that:

$$\begin{aligned} \frac{\partial C^*}{\partial x} &= \left[\frac{\partial C^*}{\partial x} \right]^{(1)} + s_1'(x) \frac{g_2 e_1 (-C^*(x) s_1(x) + g_1 R_1^*(x))}{g_2 e_1 s_1(x) (s_1(x) - x) + e_2 g_1 s_2^2} \\ \frac{\partial R_1^*}{\partial x} &= \left[\frac{\partial R_1^*}{\partial x} \right]^{(1)} - s_1'(x) \frac{e_2 C^*(x) s_2^2 + g_2 e_1 R_1^*(x) (s_1(x) - x)}{g_2 e_1 s_1(x) (s_1(x) - x) + e_2 g_1 s_2^2} \\ \frac{\partial R_2^*}{\partial x} &= \left[\frac{\partial R_2^*}{\partial x} \right]^{(1)} + s_1'(x) \frac{e_1 s_2 (C^*(x) s_1(x) - g_1 R_1^*(x))}{g_2 e_1 s_1(x) (s_1(x) - x) + e_2 g_1 s_2^2} \end{aligned} \quad 5$$

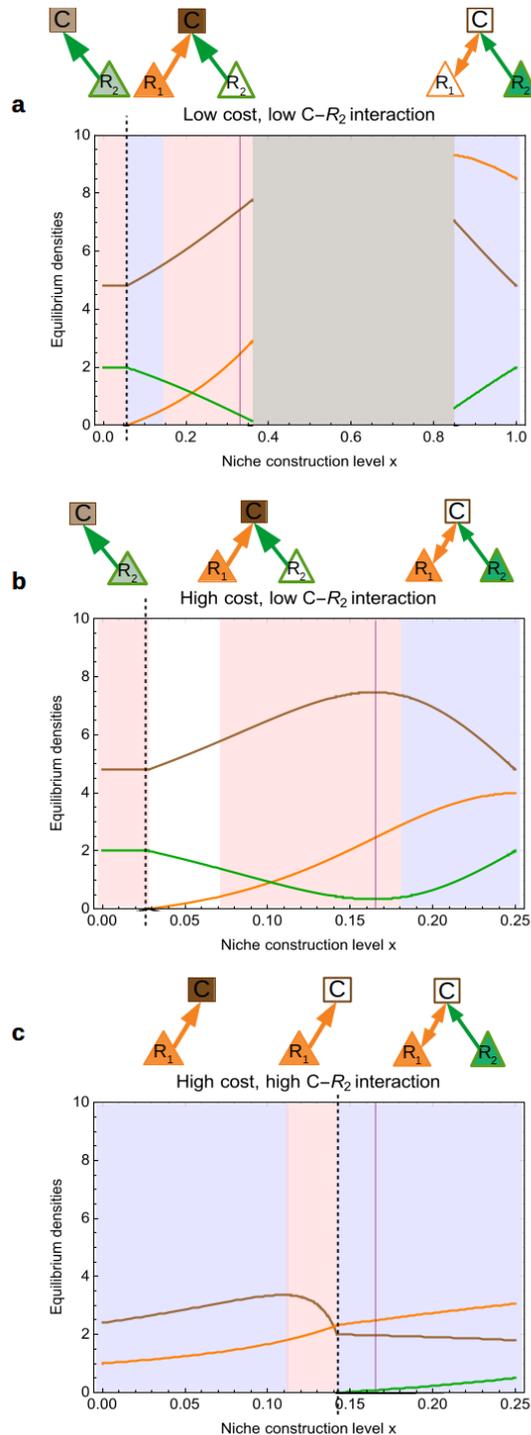
262 $\left[\frac{\partial R_1^*}{\partial x} \right]^{(1)}$, $\left[\frac{\partial R_2^*}{\partial x} \right]^{(1)}$ and $\left[\frac{\partial C^*}{\partial x} \right]^{(1)}$ are density variations in the “no cost” scenario
 263 (see eq. 3). These derivatives can either be all positive or all negative. Because niche
 264 construction comes at a cost for the consumer, the overall effect on C^* may be negative.
 265 Consumption is then relaxed on the alternative resource so that it may also benefit from
 266 niche construction.

267 On figure 3, we illustrate these outcomes assuming a linear trade-off: $s_1(x) = s_1 - \beta_1$
 268 x , with different trade-off strengths (β_1) and interaction intensity s_2 . At low niche
 269 construction, when the alternative interaction is low (panels a and b), variations are
 270 similar to the no cost scenario (equation 3 and 5). On panel a, note that intermediate niche
 271 construction does not allow the stable maintenance of a coexistent system (grey area).
 272 Starting from a coexistent state, dynamics lead to the extinction of resource R_2 and the
 273 exponential growth of the C - R_1 system. An initial C - R_1 subsystem ($R_2=0$) would lead to
 274 the extinction of the consumer. This may be explained by the fact that in the first case, the
 275 transient dynamics during which R_2 is present allows large consumer populations that
 276 ever increase due to the positive feedback with R_1 (the interaction C - R_1 is mutualistic, as
 277 $s_1 < x$ in this area). In the second case, the initial state does not allow such an infinite
 278 growth as populations are too small. Because x is intermediate, the cost on the consumer
 279 growth rate is not high enough to stabilize the dynamics: the energy intake from the

280 consumption of resource 1 is still high. Hence, we obtain typical unstable mutualistic
281 dynamics with exponential growth of the consumer and the helped resource (those
282 dynamics are illustrated in supplementary information, figure S1). When niche
283 construction x is high (fig 3a, right), it decreases consumer density (reduced energy
284 intake). Since the interaction is mutualistic, this also decreases R_1 density. From the
285 helped resource perspective, the positive effect of niche construction (increasing x and
286 reducing attack rate s_I) is compensated by the negative density-dependent effect on the
287 consumer. Considering equation 4 helps visualizing this balance: the first part of the
288 equation is negative because $C^*(x) < 0$ and $s_I(x) - x < 0$ (the interaction is mutualistic).
289 The second part corresponds to a positive effect stemming from the reduction in attack
290 rate $s_I(x)$. On the contrary, variations in R_2 density is only driven by the consumer density
291 effect (equation 4). We would like to draw the attention on an important consideration
292 here: for high values of niche construction, the C - R_1 interaction is mutualistic but it is not
293 symmetrical. In particular, when x is high enough, $s_I(x)$ tends towards 0 so that the
294 interaction tends to commensalism (null effect of R_1 on C while R_1 benefits from niche
295 construction). In panel c, because the alternative interaction is high, R_1 dominates the
296 apparent competition when there is low niche construction. Increasing x first increases
297 both R_1 and C but eventually heightens the cost of niche construction. R_2 can eventually
298 invade the system when consumer density goes below its P^* . Niche construction then
299 favors both resources densities while harming the consumer density.

300 Effects of niche construction on stability are largely consistent with the “no cost”
301 scenario (compare Fig3a,b vs Fig2). However, note that for higher x values, niche
302 construction is stabilizing. Niche construction costs there reduce the attack rate on R_1 and
303 makes the interaction tend to commensalism. This reduces the positive feedback between
304 R_1 and C thereby explaining the stabilization of the system. As a corollary, intermediate
305 niche construction levels lead to unstable dynamics such as in the grey area of Fig3a.

306



307 *Figure 3: Effect of niche construction in the “exploitation cost” scenario for cost values*
 308 *and alternative resource interactions. The color code is the same as for figure 1. The grey*
 309 *area corresponds to no stable equilibria. The purple line indicates the value of niche*
 310 *construction where interaction between C and R_1 switches from trophic to mutualistic.*
 311 *$e_1=e_2=1$, $g_1=g_2=0.8$, $m=1$, $b_1=2$, $b_2=4$. In panel a, $s_1(x)= 0.5 - 0.5 x$, $s_2 = 0.5$. In b,*
 312 *$s_1(x)= 0.5 - x$, $s_2 = 0.5$. In c, $s_1(x)= 0.5 - x$, $s_2 = 2$.*

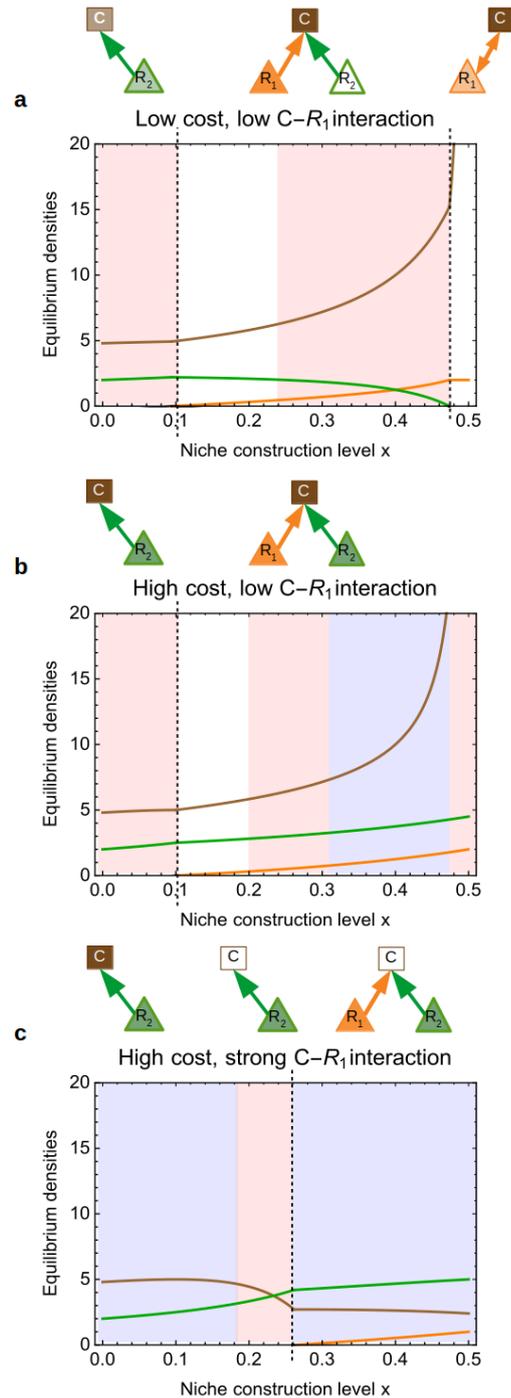
313 b) “Opportunity cost” scenario ($s_2'(x) < 0$, $s_1'(x) = 0$)

314 Given “opportunity costs”, niche construction decreases predation on the
 315 alternative resource. We can expect this to dampen the effects of apparent competition: as
 316 x increases, benefits on resource R_1 increase, and predation on R_2 is relaxed. We thus
 317 expect coexistence to be facilitated in this scenario compared to the previous ones.

318 We obtain that:

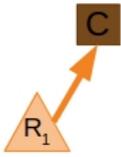
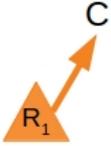
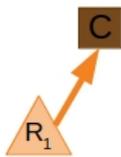
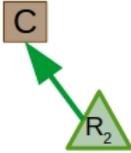
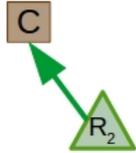
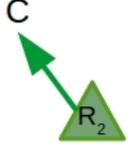
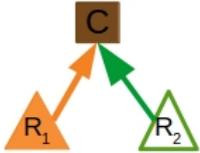
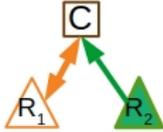
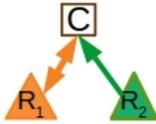
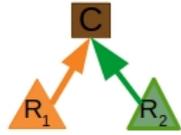
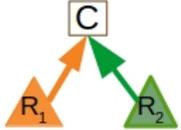
$$\begin{aligned} \frac{\partial C^*}{\partial x} &= \left[\frac{\partial C^*}{\partial x} \right]^{(1)} + s_2'(x) \frac{e_2 g_1 (g_2 R_2^*(x) - s_2(x) C^*(x))}{g_2 e_1 s_1 (s_1 - x) + e_2 g_1 s_2(x)^2} \\ \frac{\partial R_1^*}{\partial x} &= \left[\frac{\partial R_1^*}{\partial x} \right]^{(1)} - s_2'(x) \frac{e_2 (s_1 - x) (g_2 R_2^*(x) - s_2(x) C^*(x))}{g_2 e_1 s_1 (s_1 - x) + e_2 g_1 s_2(x)^2} \\ \frac{\partial R_2^*}{\partial x} &= \left[\frac{\partial R_2^*}{\partial x} \right]^{(1)} - s_2'(x) \frac{e_2 g_1 R_2^*(x) s_2(x) + e_1 s_1 C^*(x) (s_1 - x)}{g_2 e_1 s_1 (s_1 - x) + e_2 g_1 s_2(x)^2} \end{aligned} \quad 6$$

319 As in the “exploitation scenario”, we illustrate the effects of the cost, assuming a
 320 linear trade-off $s_2(x) = s_2 - \beta_2 x$ (Fig4), varying the intensity of the cost and interaction s_1 .
 321 From system 6, $s_2'(x)$ modifies the density variations expected from the “no cost
 322 scenario”. When this cost is low ($\beta_2 \sim 0$), qualitative patterns are consistent with the no cost
 323 scenario, both in terms of density and stability variations (Fig4a). Higher costs benefit all
 324 densities, as predicted (Fig4b). Niche construction also stabilizes the system, as it
 325 increases the asymmetry between the two interactions (Fig4b,c). Results in Fig4c, where
 326 both the cost and the alternative interaction are high, are consistent with those of figure
 327 3c, that also assumed a high cost and a high alternative interaction. R_1 can only invade
 328 when high niche construction reduces the consumer density under its P^* . The two
 329 resource densities then increase with x , while consumer density slightly decreases. At low
 330 x values, for the consumer- R_2 equilibrium, niche construction is first stabilizing then
 331 destabilizing (eventually allowing the invasion of R_1). Results are also similar at higher
 332 levels of niche construction (fig 4c vs 3c).



333 *Figure 4: Effects of niche construction in the “opportunity cost” scenario. The color code*
 334 *is the same as in figure 3. $e_1=e_2=1$, $g_1=g_2=0.8$, $m=1$, $b_1=2$, $b_2=4$. Panel a: $s_2(x) = 0.5 -$*
 335 *$0.5 x$, $s_1 = 0.5$, panel b: $s_2(x) = 0.5 - x$, $s_1 = 0.5$, , panel c: $s_2(x) = 0.5 - x$, $s_1 = 1$*

336 The general results for the stock variations of the densities with x in the three
337 scenarios are summed up in the Table 1. We note that, when variations can be determined,
338 the consumer is usually positively affected by niche construction, except in high cost
339 scenarios. Similarly, niche construction is often positive for the helped resource, and may
340 create positive facilitative effects on the second resource, when costs of niche
341 construction are included.

| | “No cost” scenario | “Exploitation cost” scenario | “Opportunity cost” scenario |
|-------------|---|---|---|
| $C-R_1$ | $\frac{\partial R_1^*}{\partial x} = 0, \frac{\partial C^*}{\partial x} > 0$  | $\frac{\partial R_1^*}{\partial x} > 0, \frac{\partial C^*}{\partial x} > 0 \text{ or } < 0$  | $\frac{\partial R_1^*}{\partial x} = 0, \frac{\partial C^*}{\partial x} > 0$  |
| $C-R_2$ | $\frac{\partial R_2^*}{\partial x} = 0, \frac{\partial C^*}{\partial x} = 0$  | $\frac{\partial R_2^*}{\partial x} = 0, \frac{\partial C^*}{\partial x} = 0$  | $\frac{\partial R_2^*}{\partial x} > 0, \frac{\partial C^*}{\partial x} > 0 \text{ or } < 0$  |
| $C-R_1-R_2$ | $\frac{\partial R_1^*}{\partial x} > 0, \frac{\partial R_2^*}{\partial x} < 0,$ $\frac{\partial C^*}{\partial x} > 0$  | <p>low x and low cost: same as in the no cost scenario</p> <p>high x, low cost:</p>  <p>high x, high cost :</p>  | <p>low x and low cost: same as no cost scenario</p> <p>high x, high cost, low $C-R_1$:</p>  <p>high x, high cost, high $C-R_1$:</p>  |

342 Table 1: General effects of niche construction on density distributions. Empty, dark, light
 343 and no boxes mean decrease, increase, no variation and indetermination, respectively .

344 **3) Robustness analysis**

345 While we assumed effects of niche construction to be proportional to average investment
346 x and consumer density, little information exists to link niche construction with species
347 demography. In the supplementary material, we study an alternative model where niche
348 construction eventually saturates. Effects of niche construction on the distribution of
349 biomasses are largely consistent with the linear model, though species density variations
350 are more moderate and stabilize because of the saturating response.

351 Discussion

352 The motivation for our study was to investigate how the addition of a non trophic
353 positive effect to a trophic interaction impacts the structure and functioning of a one-
354 consumer-two-resources module. We investigate three scenarios that differ in whether and
355 how the positive effect entails an allocative cost for the consumer. We discuss the three
356 questions that we addressed in the introduction: the effect of niche construction on
357 coexistence, on the distribution of densities within the module, and on stability.

358 When niche construction has no or little cost, we find that niche construction
359 generally favors coexistence when the alternative resource initially dominates the
360 apparent competition (for instance because it has a higher intrinsic growth rate or suffers
361 less predation) (Holt, 1977). Niche construction then benefits the helped resource and
362 allows coexistence, though increasing further eventually leads to the competitive
363 exclusion of the alternative resource. Such a pattern may be linked to various empirical
364 examples. For instance, devil's gardens are almost pure plantations of one tree species
365 maintained by ants killing other, more competitive plants (Frederickson et al., 2005). On
366 the contrary, if the two resources are initially equally competitive or the alternative
367 resource is less competitive, niche construction increases the asymmetry between the two
368 resources thereby limiting coexistence. These results are consistent with classic trophic
369 module studies (Holt & Lawton, 1994), with niche construction simply modulating
370 apparent competition.

371 Niche construction also alters the abundance distribution of the different species.
372 Intuitively, we expect that niche construction behaviour may benefit the consumer
373 population as well as the abundance of the helped species. When niche construction has
374 no or little cost, we indeed find such a pattern, and also find that the alternative resource
375 density is decreased. Such results are largely consistent with the direct effects of niche
376 construction: it has a positive effect on the helped resource density, while increasing

377 consumer density through bottom-up effects (increased resource availability). This
378 increase in consumer biomass leads to a negative top-down effect on the alternative
379 resource density. Consistent with such a mechanism, some studies where ant tend aphids
380 have noted an increased predation from ants on alternative non-tended aphid species
381 (Warrington & Whittaker, 1985). It is however not clear whether this negative effect
382 occurs from a consumer density increase or through changes in the foraging pattern.
383 Similarly, Wimp & Whitham (2001) show that the experimental removal of an aggressive
384 aphids-tending ant strongly increases the biodiversity of other arthropod species,
385 suggesting that the ant-aphid association has a negative impact on the abundance of other
386 species and may indeed limit species abundances and coexistence.

387 Interestingly, larger costs can strongly modify this intuitive pattern. The main effect
388 of a strong cost is, counter-intuitively, not dependent on where this cost occurs in our
389 trophic module. Whether this cost involves the exploitation of the helped resource (strong
390 “exploitation costs”), or of the alternative resource (strong “opportunity costs”), it leads to
391 a negative effect of niche construction on consumer density, and a positive effect on the
392 alternative resource. The effect on the helped resource varies depending on the balance
393 between the direct niche construction effect (through trait x) and the indirect effect on
394 consumer density. This general pattern can be interpreted in the following way: if the
395 interaction between the consumer and the helped resource becomes globally mutualistic
396 (ie, the positive effect is larger than the trophic effect of the consumer), then the consumer
397 and helped resource densities covary with the intensity of niche construction. Given a
398 high cost, niche construction then decreases both densities, helping the alternative
399 resource through relaxed predation (either because of the decrease in consumer density or,
400 in the case of opportunity costs, because of lower predation rates). If the interaction
401 remains mainly trophic, then niche construction generally decreases the consumer density
402 but increases both of the resource densities due to relaxed predation. Such overall positive
403 effects of niche construction on all resources can be linked to the notion of prudent

404 predation (Goodnight et al., 2008; Slobodkin, 1974) We also note, in the “exploitation
405 cost” scenarios, that consumer density reaches an optimum at intermediate niche
406 construction.

407 We note that such positive effect on the alternative resource, not directly helped,
408 may be seen as a facilitation of this species by the $C-R_1$ interaction. Such a facilitation
409 emerges when the interaction between the consumer and the helped resources becomes
410 mostly mutualistic. Assuming strong costs of niche construction, apparent competition is
411 then replaced by a dominant facilitation effect. Assuming strong costs, niche construction
412 leads to an increase in both resources because it relaxes predation impacts not only on the
413 helped resource, but also on the alternative resource species (either through a consumer
414 density-dependent effect, or through a decrease in the *per capita* attack rate). Our model
415 thus allows a continuum between competitive and facilitative interactions, whose
416 importance in ecology is increasingly recognized (Bruno et al., 2003; He, Bertness, &
417 Altieri, 2013; Kéfi et al., 2012). Because the balance between competition and facilitation
418 in our system depends on the levels of cost, this highlights the importance of investigating
419 the possible trade-offs associated to niche construction. We stress that the non-cultivated
420 resource is facilitated though it receives no direct benefit. Niche construction can modify
421 a foraging pattern in a way that is not necessarily costly: for instance, fire ants forage on
422 the ground but when they tend aphids they also forage on the arthropods present on the
423 host plant (Kaplan & Eubanks, 2005). Foraging on plants for preys only is not profitable
424 but foraging for honeydew makes foraging for nearby preys profitable. We here assume
425 that costs of niche construction act on predation rates. This assumption, based on
426 allocation of time and energy between different functions (niche construction on one side,
427 foraging on the other), could be generalized, for instance assuming a continuum between
428 our “exploitation cost” and “opportunity cost” scenarios.

429 Effects of niche construction on stability are less intuitive. When costs are low,
430 niche construction is first destabilizing then stabilizing. This can be explained thanks to

431 previous works on stability in trophic modules or networks. Notably, when it increases the
432 heterogeneity of interaction strengths (eg, due to costs), niche construction is stabilizing,
433 as found in food web modules (McCann et al., 1998). When only the helped resource is
434 present, increasing niche construction is also stabilizing, because it decreases the *per*
435 *capita* energy flux from the resource to the consumer, consistent with classical “paradox
436 of enrichment” results (Rip & McCann, 2011; Rosenzweig, 1971).

437 We chose to keep our model linear to allow for a better analytical tractability. We
438 assume no direct competition among resources focusing on apparent competition instead.
439 We believe that adding direct (or exploitative) competition between the resources would
440 give predictions similar to the P^*-R^* coexistence rule (Holt et al., 1994) with niche
441 construction modulating the P^* value of the resource species. We analyze the robustness
442 of the model regarding the assumption of a linear niche construction effect, investigating
443 a scenario where effects of niche construction progressively saturate. In terms of
444 equilibrium densities response, we find similar patterns in the linear and the saturating
445 model. The saturating response is generally stabilizing, as expected from previous studies
446 showing the stabilization of mutualism when considering saturating functional responses
447 (Holland & DeAngelis, 2010; Holland, DeAngelis, & Bronstein, 2002).

448 The explicit consideration of trophic interaction modifications has recently received
449 increased attention (Terry, Morris, & Bonsall, 2017 and references within). In this line of
450 work, our model investigates how positive niche construction effects interfere with
451 apparent competition, to constrain species coexistence and community stability. While
452 these small modules are by essence simplified compared to larger, natural networks,
453 ecology has a long tradition of using them to propose and test predictions on coexistence
454 or stability . We also assume that the consumer positively affected one of the two resource
455 species only. Note however that a consumer often has positive effects on several of its
456 resources, a case we can reasonably expect in the cases of nutrient cycling (Cargill &
457 Jefferies, 1984; de Mazancourt et al., 1998) and seed dispersal (Serrano-Cinca, Fuertes-

458 Callén, & Mar-Molinero, 2005; Thutupalli et al., 2017). Explicit simulations of these
459 more complex (ie, more species or more diffuse effects) scenarios are beyond the scope of
460 this article, but they would help to get a better understanding of the role of non trophic
461 interactions in larger networks, by allowing the accumulation of more indirect effects of
462 different types (Kéfi et al., 2012).

463 While the present study would benefit from being extended to multispecies
464 networks, we believe that even in such situations, some of our results would hold. For
465 instance, if a herbivore has a positive effect on many plants through recycling, such
466 positive effects will be larger for the most nutrient limited species. Our model should then
467 be seen as an approximation of such heterogeneities in the positive effects. Next to the
468 extension to complex networks, another important issue would be to explicitly consider
469 spatial dynamics. Indeed, local niche construction processes may create spatial
470 heterogeneities in nature. Obvious examples include ant gardens (Frederickson et al.,
471 2005) in which whole plant species communities are modified by the combination of
472 trophic and non trophic effects of ant species, or large scale patterns of vegetation as in
473 the termite-driven hypothesis for Namibian fairy circles (Juergens, 2013; Pringle &
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