

# The evolutionary dynamics of plastic foraging and its ecological consequences: a resource-consumer model.

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## Abstract

Phenotypic plasticity has important ecological and evolutionary consequences. In particular, behavioural phenotypic plasticity such as plastic foraging (PF) by consumers, may enhance community stability. Yet little is known about the ecological conditions that favor the evolution of PF, and how the evolutionary dynamics of PF may modulate its effects on community stability. In order to address these questions, we constructed an eco-evolutionary model in which resource and consumer niche traits underwent evolutionary diversification. Consumers could either forage randomly, only as a function of resources abundance, or plastically, as a function of resource abundance, suitability and consumption by competitors. PF evolved when the niche breadth of consumers with respect to resource use was large enough and when the ecological conditions allowed substantial functional diversification. In turn, PF promoted further diversification of the niche traits in both guilds. This suggests that phenotypic plasticity can influence the evolutionary dynamics at the community-level. Faced with a sudden environmental change, PF promoted community stability directly and also indirectly through its effects on functional diversity. However, other disturbances such as persistent environmental change and increases in mortality, caused the evolutionary regression of the PF behaviour, due to its costs. The causal relationships between PF, community stability and diversity are therefore intricate, and their outcome depends on the nature of the environmental disturbance, in contrast to simpler models claiming a direct positive relationship between PF and stability.

**Keywords:** phenotypic plasticity, adaptive foraging, plastic foraging, eco-evolutionary dynamics, community stability

Author contributions: SI, JG and LL originally formulated the project; SI, JG, EF and LL developed the model; LL and OG performed the numerical analyses; all authors participated in writing the manuscript

# 28 1 Introduction

29 Phenotypic plasticity has become central to evolutionary theory (West-Eberhard, 2003; Pfennig, 2021),  
30 but the interplay between its evolutionary dynamics and ecological consequences remains under-  
31 explored. Such an interplay occurs when a variety of resources are available to consumers investing  
32 more or less time on each resource according to its suitability, which depends on the (mis)match  
33 between the resources' defensive and consumers' counter-defensive traits (e.g. Clissold et al., 2009)  
34 and the nutritional quality of the resources and the requirements of the consumers (e.g. Behmer and  
35 Joern, 2008). The relative time spent on each resource (relative foraging efforts, sensu Abrams, 2010)  
36 sometimes corresponds to the best compromise between suitability and abundance, an outcome called  
37 *optimal foraging* (MacArthur and Pianka, 1966; Loeuille, 2010). However optimal foraging might be  
38 difficult to achieve when the identity and abundance of resources vary over time and space, because for-  
39 aging optimization is not instantaneous (Abrams, 1992, 2010). Under such circumstances, consumers  
40 may nevertheless redirect their relative foraging efforts towards more profitable resources in order to  
41 increase their energy intake. The ability to adjust relative foraging efforts is a type of behavioural  
42 plasticity which has been called *adaptive foraging* in the literature (Valdovinos et al., 2013; Loeuille,  
43 2010). However, this term can be misleading because "*adaptive*" generally refers to traits shaped by  
44 natural selection. Here, the term *plastic foraging* (PF) will be used for clarity, moreover because its  
45 evolutionary dynamics will be explored.

46 Indeed, phenotypic plasticity often results from evolution by natural selection (Nussey et al., 2005;  
47 Peluc et al., 2008; Van Kleunen and Fischer, 2001). In particular, phenotypic plasticity may help  
48 populations to cope with environmental changes (Chevin et al., 2013; Vedder et al., 2013; Charmantier  
49 et al., 2008), although empirical evidence is sometimes questionable (Merilä and Hendry, 2014). From  
50 a theoretical point of view, the extent to which phenotypic plasticity is adaptive has not been tested in  
51 the context of PF because previous works ignored the evolutionary dynamics of PF, focusing instead  
52 on food-web stability (Kondoh, 2003; Uchida and Drossel, 2007; Heckmann et al., 2012) or food web  
53 structure (Beckerman et al., 2006). Abrams (2003) modelled the evolution of the general foraging  
54 effort, corresponding to the overall amount of time and energy invested in foraging (e.g. Dill, 1983), in  
55 function of the trade-off with predation risk. *General* foraging effort differs from PF, that in contrast  
56 focuses on the adjustment of *relative* foraging efforts, i.e. how the general foraging effort is distributed  
57 across the different resources. Although the PF strategy ~~tends to increase fitness, in some situations PF~~  
58 ~~may reduce it~~ increases energy intake, it may also be costly, e.g. by increasing predation risk (Abrams,  
59 2003; Pangle et al., 2012; Wang et al., 2013; McArthur et al., 2014; Costa et al., 2019), preventing  
60 efficient thermoregulation (du Plessis et al., 2012; Van de Ven et al., 2019) or increasing searching time  
61 for resources (Randolph and Cameron, 2001; Bergman et al., 2001; Fortin et al., 2004). Since PF faces  
62 several trade-offs with life-history components, its evolution should depend on ecological parameters  
63 such as mortality rate, resource searching time or consumer niche width.

64 The first aim of the present study is therefore to understand, using a theoretical model, under  
65 which ecological conditions the ability of consumers to forage plastically is subject to evolution by  
66 natural selection. In short: is plastic foraging adaptive? We define PF as a change in relative foraging  
67 efforts that directly increases *energy intake*, but not necessarily *fitness*. This contrasts with Loeuille  
68 (2010) who defined adaptive foraging as "changes in resource or patch exploitation by consumers that  
69 give the consumer a higher fitness compared with conspecifics that exhibit alternative strategies". Our  
70 restricted definition is justified by the need to explore how the trade-off between energy intake and  
71 other life-history components modulates the evolution of PF. Moreover, consumers are affected by  
72 environmental changes, either directly (Bale et al., 2002; Staley and Johnson, 2008; Scherber et al.,  
73 2013) or indirectly through changes affecting their resources. For instance, environmental changes  
74 may induce a shift in resource phenology (Altermatt, 2010; Kerby et al., 2012; Portalier et al.) or  
75 alter resource chemistry (Bidart-Bouzat and Imeh-Nathaniel, 2008; Rasmann and Pellissier, 2015).  
76 As a result, the diet preferences of consumers may be altered (Rasmann et al., 2014; Rosenblatt  
77 and Schmitz, 2016; Boersma et al., 2016), suggesting that environmental disturbances should lead to  
78 the evolution of PF. However as disturbances may also reduce the functional diversity of available  
79 resources (Thuiller et al., 2006; Buisson et al., 2013), the evolutionary response of the PF strategy to  
80 environmental changes is unclear.

81 Although phenotypic plasticity generally results from evolution by natural selection, as outlined  
82 above, it also generates evolutionary changes (Simpson, 1953; Baldwin, 1896; Laland et al., 2014), with  
83 genes acting as followers (West-Eberhard, 2003). In the context of PF, the consumption of novel or  
84 unusual resources through behavioral plasticity might trigger subsequent adaptations that favour the  
85 use of these resources. This would increase the diversity of the traits involved in resource use, such  
86 as counter-defences and nutritional requirements. The second motivation is therefore to investigate  
87 how PF can alter the evolution of these consumer traits, as well as those of their resources (defenses,  
88 nutritional quality). In particular, we expect PF to affect the functional diversity of consumers and  
89 resources, through its effects on diet breadth.

90 The evolutionary dynamics of phenotypic plasticity has important ecological consequences (Miner  
91 et al., 2005; Turcotte and Levine, 2016), which in turn can feed back into the evolutionary dynamics.  
92 In the case of PF, behavioural plasticity in diet choice can favour the persistence of consumers in  
93 unusual environments and rescue them in the face of environmental changes (e.g. Varner and Dearing,  
94 2014; Kowalczyk et al., 2019). Previous theoretical studies have indeed shown that PF promotes  
95 community stability (Křivan and Schmitz, 2003; Abrams and Matsuda, 2004; Kondoh, 2003; Uchida  
96 and Drossel, 2007). The third motivation is to test if this positive relationship holds when both PF  
97 and the functional traits of consumers and resources are subject to evolutionary dynamics. In this  
98 eco-evolutionary context, it is uncertain whether the evolution of PF stabilises communities directly,  
99 by altering food-web structure or indirectly, through its effects on functional diversity.

100 The main questions outlined earlier are sketched in Figure 1:

- 101 • Question 1. Under which ecological conditions is PF evolutionary adaptive?
- 102 • Question 2. When PF evolves, what are its effects on the diversity of the traits involved in the  
103 resource-consumer interaction?
- 104 • Question 3. What is the effect of the evolution of PF on the stability of the resource-consumer  
105 system, in response to environmental changes? Are these effects direct (Q3a) or indirect, medi-  
106 ated by the influence of PF on functional diversity (Q3b)?

107 To address these issues, we build an eco-evolutionary model in which a consumer species feeds  
108 on a resource species. Both species are characterized by an ecological trait; the resource is the most  
109 suitable for the consumer when both traits match. In addition, the consumers carry a foraging trait  
110 measuring the extent to which they select the resources allowing the largest intake, or instead forage  
111 randomly and consume the resources as a function of their abundance. Ecological and foraging traits  
112 are subject to evolution; starting from monomorphic initial conditions, they rapidly diversify and  
113 reach a stationary regime characterized by a stable diversity of ecological and foraging traits. The  
114 stationary regime is then subjected to various environmental disturbances, to test how the evolution  
115 of PF responds to environmental changes, and how this cascades down on the ecological properties of  
116 the resource-consumer system.

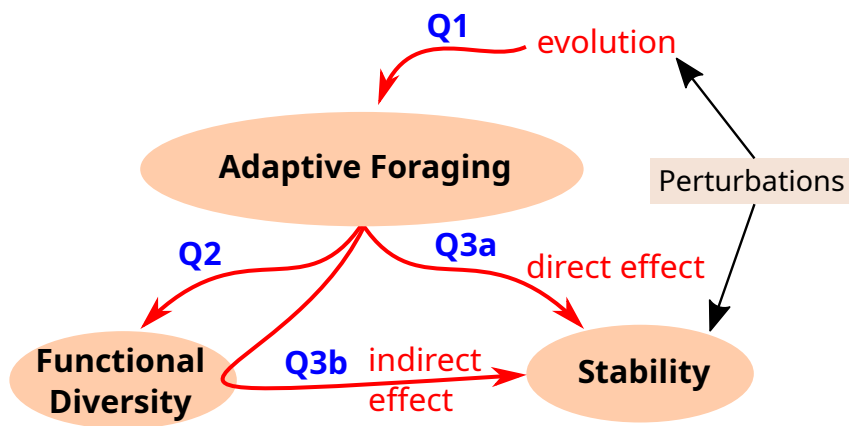


Figure 1: Overview of the main questions: (Q1) Under which ecological conditions does PF evolve? (Q2) Does the evolution of PF increases the diversity of traits involved in the resource-consumer interaction? (Q3) Does the evolution of PF enhances the stability of the resource-consumer system, either directly (Q3a) or through its effects on functional diversity (Q3b)?

## 117 2 Model description

### 118 2.1 A resource-consumer niche model

119 An eco-evolutionary model is developed to describe the dynamics of a consumer population feeding,  
 120 with various individual foraging strategies, on a resource population. Consumers compete for resources  
 121 both directly and indirectly. Individuals are characterized by quantitative traits: the niche traits  $x$  and  
 122  $y$  of consumers and resources, respectively, and the plastic foraging trait  $z$  of consumers. The niche  
 123 traits affect competition between individuals as well as interactions between consumer and resource  
 124 individuals. The foraging trait  $z$  affects the foraging strategy of the consumers through their foraging  
 125 efforts  $\phi$ . The model describes the time dynamics of the trait densities of resources  $R(t, y)$  and  
 126 consumers  $C(t, x, z)$ ; the components of the model are detailed in the following sections.

$$\partial_t R(t, y) = R(t, y) \left( \overbrace{\rho(t, y)}^{\text{resource growth}} - \overbrace{F_R(t, y)}^{\text{resource consumption}} \right) + \overbrace{\mathcal{M}_R(t, y)}^{\text{niche trait mutations}} \quad (1)$$

$$\partial_t C(t, x, z) = C(t, x, z) \left( \overbrace{F_C(t, x, z)}^{\text{resource absorption}} - \overbrace{\delta(t)}^{\text{mortality and competition}} \right) + \overbrace{\mathcal{M}_C(t, x, z)}^{\text{niche and PF traits mutations}} \quad (2)$$

127 **Resource growth and niche trait.** In the absence of consumers, resources grow logistically

$$\rho(t, y) = g \left( 1 - \frac{r_e(t, y)}{K(y - y_0)} \right) \quad (3)$$

128 with an intrinsic rate  $g$ , independent from the niche trait  $y$ , and a carrying capacity that depends  
 129 on the difference between the niche trait  $y$  and the optimal niche trait  $y_0$ . Competition between  
 130 resources depends on the niche trait  $y$  through the carrying capacity  $K(y - y_0)$  of individuals with  
 131 trait  $y$  and  $r_e(t, y)$ , the effective population density perceived by an individual with trait  $y$  at time  $t$ .  
 132 The effective density depends on the phenotype distribution of the population and the competition  
 133 strength  $K_e(y - y')$  exerted by an individual with trait  $y'$  on an individual with trait  $y$ :

$$r_e(t, y) = \int K_e(y - y') R(t, y') dy' \quad (4)$$

134 The functions  $K$  and  $K_e$  are normally distributed around  $y = 0$  with variances  $\sigma_K$  and  $\sigma_C$  respectively  
 135 (Table SI.1 and Fig. SI.1).

136 **Resource consumption and absorption.** In the presence of consumers, resources are exploited  
 137 at rate  $F_R$ , whereas the consumer density increases through resource absorption at a rate  $F_C$ . On  
 138 the one hand, these rates depend on the consumers foraging efforts  $\phi(t, x, y, z)$ , which characterize the  
 139 time spent by a consumer of niche trait  $x$  and foraging trait  $z$  on a resource of trait  $y$  during a period  
 140  $t$ . On the other hand, they vary with the effective interaction strength  $\Delta(x, y)$  between consumer  
 141 and resource individuals. The function  $\Delta$  is normally distributed around 0 with a variance  $\sigma$ , which  
 142 measures the extend to which consumers can deal with a variety of resource types (Table SI.1). The  
 143 variance parameter  $\sigma$  is chosen similarly to previous models (see e.g. Dieckmann and Doebeli, 1999;  
 144 Egas et al., 2005), but it is not subject to evolution as in Egas et al. (2005). The interactions are  
 145 described by a Holling type II functional response, which provides the following consumption and  
 146 absorption rates:

$$F_R(t, y) = \iint U(t, x, y, z) C(t, x, z) dx dz \quad \text{and} \quad F_C(t, x, z) = \alpha \int U(t, x, y, z) R(t, y) dy \quad (5)$$

$$\text{with } U(t, x, y, z) = \frac{b\phi(t, x, y, z)\Delta(x, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)R(t, y)dy} \quad (6)$$

147 with  $\alpha$  the conversion coefficient,  $b$  the extraction coefficient and  $s(z)$  the searching time, which depends  
 148 on the foraging trait  $z$  as explained below. The quantity  $U$  corresponds to the uptake per resource of  
 149 type  $y$  from a consumer of traits  $(x, z)$ .

150 **Consumer mortality and competition.** Moreover, consumer density is affected by mortality at  
 151 a constant rate  $d$  and by direct intraspecific competition between consumers for other limiting factors  
 152 than resources, at a rate  $I$ .

$$\delta(t) = \left( d + I \iint C(t, x, z) dx dz \right) \quad (7)$$

153 where the integrals correspond to the total biomass of consumer.

154 **Mutation of traits and diffusion approximation.** Due to mutations, the niche traits and the  
 155 foraging trait can evolve independently. Foraging behaviour can indeed be heritable in nature (Wallin,  
 156 1988; Lemon, 1993). Since ecological and evolutionary dynamics occur on the same time scale, mutants  
 157 are constantly introduced through the diffusion of traits:

$$\mathcal{M}_R(t, y) = \frac{\mu\sigma_m^2}{2}\partial_y^2 R(t, y) \quad \text{and} \quad \mathcal{M}_C(t, x, z) = \frac{\mu\sigma_m^2}{2}\partial_x^2 C(t, x, z) + \frac{\mu\sigma_m^2}{2}\partial_z^2 C(t, x, z), \quad (8)$$

158 where  $\mu$  is the mutation frequency and  $\sigma_m^2$  is the variance of the mutational effects. This approach con-  
 159 trasts with the adaptive dynamic framework, in which a mutant phenotype is introduced sequentially  
 160 and persists only if its invasive fitness is positive (Geritz et al., 1998).

## 161 2.2 Foraging strategies and plastic foraging trait.

162 Consumers can use two different foraging strategies during their foraging time: Random Foraging (RF)  
 163 or Plastic Foraging (PF). The effective consumer foraging strategy depends on the consumer plastic  
 164 foraging trait  $z \in [0, 1]$ , which corresponds to the proportion of its general foraging effort spent using  
 165 the PF strategy. The effective consumer efforts are thus:

$$\phi = z\phi_{PF} + (1 - z)\phi_{RF} \quad (9)$$

166 where  $\phi_{PF}$  and  $\phi_{RF}$  are the foraging efforts resulting respectively from the plastic foraging strategy  
 167 and the random strategy.

168 **Random foraging strategy.** When using RF, the consumer randomly forages its environment  
 169 without selecting resources. The resulting efforts  $\phi_{RF}$  is proportional to the density of the resources:

$$\phi_{RF}(t, y) = \frac{R(t, y)}{\int R(t, y') dy'} \quad (10)$$

170 **Plastic foraging strategy.** Conversely, when using PF, consumers actively search for resources,  
 171 that maximize their energy intake. More precisely, they modify their foraging efforts according to the  
 172 potential resource uptake  $u$ , that corresponds to the amount of resource taken by the consumer, if its  
 173 foraging effort only focus on this resource. It depends on the resource availability and suitability (e.g.  
 174 Sundell et al., 2003). A consumer will reduce its effort on a resource if the uptake from that resource  
 175 is lower than the uptake from an other resource, that is if the difference between potential resource  
 176 uptakes is negative. The resulting relative foraging efforts  $\phi_{PF}$  may change over time according to  
 177 the average difference between resource uptake, weighted by the foraging effort per resource and the  
 178 amount of resource as follows:

$$\begin{aligned} \partial_t \phi_{PF}(t, x, y, z) = l_\phi C(t, x, z) & \left( \int R(t, y) \phi_{PF}(t, x, y', z) [u(t, x, y, z) - u(t, x, y', z)]_+ dy' \right. \\ & \left. - \int R(t, y') \phi_{PF}(t, x, y, z) [u(t, x, y', z) - u(t, x, y, z)]_+ dy' \right) \end{aligned} \quad (11)$$

179 where  $[u(y) - u(y')]_+ = \max\{(u(y) - u(y')), 0\}$  is the positive part of the difference between potential  
 180 resource uptake. The quantity  $\phi_{PF}$  is analogous to the behavioral trait  $z$  in Abrams and Matsuda

181 (2004). The potential resource uptake  $u(t, x, y, z)$  of a consumer with traits  $(x, z)$  on a resource with  
 182 trait  $y$  depends on its foraging efforts as well as the resource suitability and availability:

$$u(t, x, y, z) = \frac{b\Delta(x, y)R(t, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)R(t, y)dy} \quad (12)$$

183 The PF dynamics allow consumers to compare the benefits  $u$  received from different resources. More  
 184 precisely, for a given resource  $y$  and a given consumer with traits  $x$  and  $z$ , if the benefits  $u(t, x, y, z)$   
 185 from the resource  $y$  is larger than the benefit  $u(t, x, y', z)$  from the resource  $y'$ , that is  $[u(t, x, y, z) -$   
 186  $u(t, x, y', z)]_+ > 0$ , then the consumer will gain benefits by increasing its effort on resource  $y$ . Con-  
 187 versely, it will gain benefits by decreasing its effort on resource  $y'$ . Eq. (11) reflects the balance  
 188 between the positive effects  $[u(t, x, y, z) - u(t, x, y', z)]_+ > 0$  to increase the effort on resource  $y$  and  
 189 the negative effects  $-[u(t, x, y', z) - u(t, x, y, z)]_+ < 0$ , to do it. As a result, consumers increase their  
 190 efforts on the most beneficial resources and reduce them on sub-optimal resources. The comparison  
 191 of resources is assumed time consuming. The efforts are therefore not adjusted instantaneously but  
 192 exponentially fast at a rate that is proportional to the density of consumer  $C$ , with similar trait  $x$  and  
 193  $z$ , accounting for the use of social cues during foraging (Jones et al., 2018), and an intrinsic adjustment  
 194 rate  $l_\phi$ . When the intrinsic adjustment rate  $l_\phi$  becomes large, the plastic foraging strategy becomes  
 195 closer to the optimal foraging strategy maximizing the potential resource uptake  $u$  (MacArthur and  
 196 Pianka, 1966; Loeuille, 2010). Moreover, the searching time  $s(z)$  also increases with the foraging trait:  
 197  $s(z) = s_{min} + z(s_{max} - s_{min})$  (Figure SI.1d). This relationship introduces a trade-off between the PF  
 198 strategy and the searching time.

### 199 3 The evolution of plastic foraging

200 Previous models exploring the effect of PF on community dynamics assumed that PF was a fixed trait  
 201 of equal intensity for all consumers (Kondoh, 2003; Uchida and Drossel, 2007; Beckerman et al., 2010;  
 202 Heckmann et al., 2012; Valdovinos et al., 2013). In these models, the foraging efforts of consumers  
 203 changed in function of the availability and suitability of their resources, but whether foraging efforts  
 204 could change or not was itself not subject to evolution. Egas et al. (2005) modelled the evolutionary  
 205 dynamics of the consumers' niche width, but not of their foraging selectivity. Therefore, the first  
 206 motivation of this study was to explore under which conditions the capacity to forage plastically can  
 207 evolve by natural selection (Question 1 in the introduction).

#### 208 3.1 Diversification and emerging foraging strategy

209 The model is investigated numerically using MATLAB. The niche traits are discretized into 31 equally  
 210 distanced values (11 values for the foraging trait). In the simulations, when the density of a resource  
 211 or a consumer phenotype drops below the critical threshold  $\varepsilon = 10^{-4}$ , the density is set to 0 to  
 212 save computational time. The simulations start with monomorphic populations at the niche center  
 213 ( $y = x = 0$ ) and consumers have a purely random foraging strategy ( $z = 0$ ).

214 Given the parameter ranges of Table 1, the eco-evolutionary dynamics of the model lead to the  
 215 diversification of resources and consumers along the ecological gradient (Figure 2a). Although the  
 216 distribution of the consumer foraging trait reaches a unimodal distribution (Figure 2a), the consumers  
 217 positioned at the niche center forage randomly, while those at the niche edges forage plastically (Figure  
 218 2b). Indeed, scarce resources located at the niche edge are consumed significantly by plastic foragers  
 219 only, because random foragers cannot choose infrequent resources. Instead, abundant resources located  
 220 at the niche center can be consumed in large amounts by random foragers. This model prediction calls  
 221 for empirical testing, as we are not aware of any existing work reporting this pattern. In addition, the  
 222 distributions of the niche traits reach a stationary regime that vary over time due to the PF strategy  
 223 (Appendix A.1).

Parameters		Values for the response to disturbances	Ranges for the sensitivity analysis	PRCC values
$\sigma$	Consumers niche width	0.9	[0; 1]	0.28
$\sigma_K$	Resources niche width	2.5	[1; 4]	0.38
$s_{max}$	Cost of PF : maximal increase of searching time due to PF	0.55	[0.1; 2]	- 0.64
$d$	Consumers mortality	0.1	[0.1; 0.6]	0.13
$I$	Competition between consumers (other than for resources)	0.01	[0.01; 0.1]	0.13
$g$	Rate of resource growth	0.8	[0.2; 1.6]	0.11
$K_0$	Maximal carrying capacity	50	Fixed	
$y_0$	resource niche center (mode of carrying capacity function)	0	Fixed	
$\sigma_C$	Width of the competition kernel	$\sigma_K - 1$	Fixed	
$\alpha$	Biomass conversion coefficient from resources to consumers	0.3	Fixed	
$b$	Biomass extraction coefficient	0.5	Fixed	
$l_\phi$	Rate of change in foraging efforts	0.5	Fixed	
$s_{min}$	Cost of PF : minimal increase of searching time due to PF	0.1	Fixed	
$\mu$	Mutation frequency	0.1	Fixed	
$\sigma_m^2$	Mean effect of mutation	0.02	Fixed	
$\varepsilon$	Extinction threshold	$10^{-4}$	Fixed	
$T$	Simulation time	1000	Fixed	

Table 1: Parameters of the model with their reference values used for the analysis of the response to disturbances, and the range used for the 6 parameters tested by the sensitivity analysis. The last column corresponds to the PRCC values, that is the correlation between the mean foraging trait  $\bar{z}(t)$  and the tested parameter.

### 3.2 Parameters influencing the evolution of plastic foraging strategy

To investigate the ecological conditions leading to the evolution of PF, a global sensitivity analysis is performed using Partial Rank Correlations Coefficients (PRCC, Saltelli et al., 2004), on the mean foraging trait value of the consumer population  $\bar{z}(t)$  defined by:

$$\bar{z}(t) = \iint z \frac{C(t, x, z)}{\iint C(t, x', z') dx' dz'} dx dz \quad (13)$$

The analysis focuses on the parameters  $\sigma, \sigma_K, s_{max}, d, I, g$  (Table 1) with 5000 parameter sets sampled in their ranges.

The PRCC analysis revealed that the six tested parameters played a significant role in the evolution of PF (Table 1 last column).

**Handling time** As expected, elevated costs of PF ( $s_{max}$ , Table 1) disfavor its evolution (correlation coefficient  $-0.64$ ), which is in accordance with the existence of a trade-off between PF and other life-history traits like predation (Pangle et al., 2012; Wang et al., 2013; McArthur et al., 2014; Costa et al., 2019), thermoregulation (du Plessis et al., 2012; Van de Ven et al., 2019) and time budget (Randolph and Cameron, 2001; Fortin et al., 2004). In the present model the trade-off is only incorporated into the handling time of the type II functional response, where high handling times reduce resource absorption rates. If the PF strategy had increased mortality  $d$  instead of handling time, this would have also reduced resource absorption (see Appendix B for a formal derivation of the model). A trade-off between PF and mortality therefore provided similar results (Fig. SI.4 and SI.5).



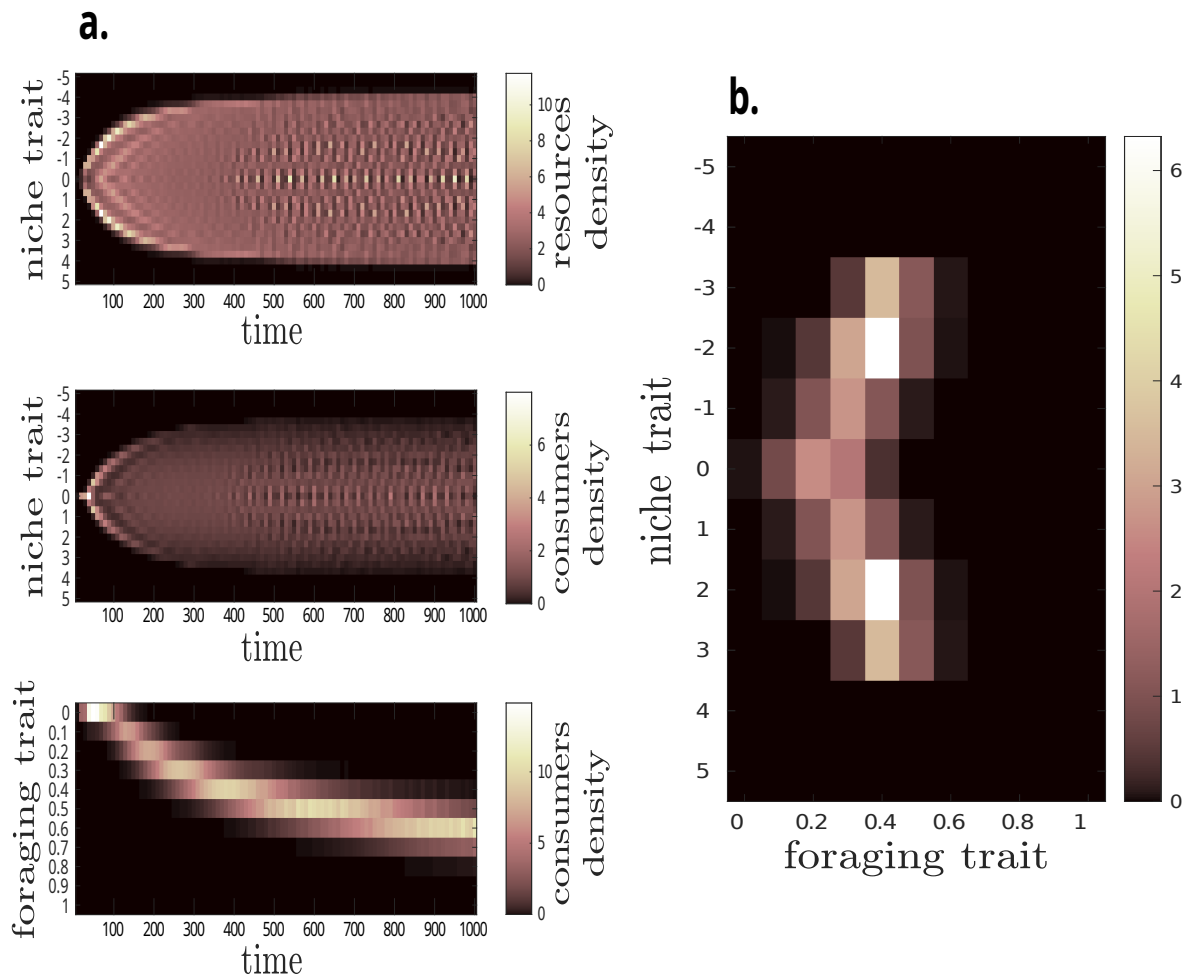


Figure 2: a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer densities  $\int C(t, x, z) dz$ . Bottom panel: foraging trait  $\int C(t, x, z) dx$ . b) The trait distribution of consumers at steady state (1000 time steps).

241 **Consumer niche width** The evolution of PF is instead favored by the niche width of consumers  
 242 (parameter  $\sigma$ , correlation coefficient 0.28). The evolution of plastic foraging may lead to contrasting  
 243 foraging strategies among individuals, which increases inter-individual niche variation. This would  
 244 then fit with the "Niche Variation Hypothesis" (NVH) according to which "populations with wider  
 245 niches are more variable than populations with narrower niches" (Soule and Stewart, 1970). The NVH  
 246 was initially formulated by Leigh van Valen 1965 for morphological traits, although it appears better  
 247 suited to behavioral traits like resource use (Bolnick et al., 2007). Empirical support for the NVH was  
 248 found for herbivores (Bison et al., 2015) and predators (Bolnick et al., 2007), with a positive corre-  
 249 lation between total niche width and inter-individual niche variation. ~~Inter-individual niche variation~~  
 250 ~~reflects the existence of contrasting foraging strategies, which may be the result of plastic foraging.~~  
 251 Baboons also combine niche breadth with selectivity in resource use (Whiten et al., 1991). Since the  
 252 evolution of consumer niche width may itself depend on environmental heterogeneity (Kassen, 2002)  
 253 (i.e. on resource diversity in the model), the coevolution of PF, niche width and niche position is a  
 254 possible avenue for future research. Niche width foster PF because consumers deplete the whole range  
 255 of resources when their niche width is large, therefore competition between consumers is more intense,  
 256 which leads to the evolution of PF. Empirical studies have indeed found that generalist consumers  
 257 competing for resources forage plastically. For instance generalist bumblebee species visited the lark-  
 258 spur *Delphinium barbeyi* when the most abundant bumblebee species was experimentally removed,  
 259 but preferred other plant species otherwise, likely to avoid competition for nectar (Broisi and Briggs,  
 260 2013). A similar behavior has been reported for syrphid flies, which preferentially foraged on open

rather than tubular flowers when competing with bumblebees (Fontaine et al., 2006). In the case of predators, intraspecific competition between sticklebacks (*Gasterosteus aculeatus*) enhanced the diversity of foraging behaviors and increased the correlation between diet and morphology (Svanbäck and Bolnick, 2007), as found here (Figure SI.9).

**Other parameters** The present model further predicts that PF evolution is favoured by direct competition between consumers  $I$  (correlation coefficient 0.13) as well as by increased consumer mortality  $\delta$  (correlation coefficient 0.13). This is in line with the above results, in the sense that constrained environmental condition for consumers strengthen the need for PF. On the other hand PF becomes useful when resources are diversified enough, hence the positive effect of the resources niche width  $\sigma_K$  (correlation coefficient 0.38).

## 4 The effects of PF evolution on community properties

Starting from a fixed pool of species or phenotypes, most previous theoretical works have shown that PF fosters food web complexity and community stability (Kondoh, 2003; Uchida and Drossel, 2007; Beckerman et al., 2010; Heckmann et al., 2012), although this depended on the way PF was incorporated to the model (Berec et al., 2010). However, had niche traits been also subject to evolution, PF might also have affected stability indirectly, through its effect on functional diversity (Figure 1). The effects of PF on diversity and other community properties (Question 2 in the introduction) are discussed in the present section and the effects on consumer persistence (Question 3) in section 5.

### 4.1 Effects on biomass

To assess the effects of the evolution of PF on biomass, we compare the total biomass  $C$  of consumers in two situations: a freely evolving PF trait  $z$  and a fixed RF strategy ( $z = 0$ ). In both cases, the ecological niche traits  $x$  and  $y$  are subject to evolution. The communities evolve during 1000 time steps, which is enough time for the system to reach a stationary regime with stable community-level characteristics (A.1). The same comparison is done for all the other community properties.

When the evolution of PF produce consumer populations with a high mean foraging trait  $\bar{z}$ , the resource biomass is reduced (e.g. -50% when  $\bar{z} = 1$ ) while the consumer biomass increased by 25% on average (Figure 3a). Following the evolution of PF, the functional complementarity and diversity of consumers increase their biomass at the expense of resources (Figure 3a). This fits with empirical studies showing a relationship between resource consumption and consumer diversity (Deraison et al., 2015; Lefcheck et al., 2019; Milotić et al., 2019). However, the variability of the consumer biomass among simulations also increases with  $\bar{z}$ . This pattern has also been observed when the foraging trait  $z$  of a monomorphic population without PF evolution is increased (Figure SI.3a).

### 4.2 Effects on functional diversity

Resource and consumer functional diversity are measured by the functional dispersion index  $FDis$  (Laliberté and Legendre, 2010), which represents for each population the average absolute deviation from the mean niche trait:

$$FDis_R(t) = \int \frac{|y - \bar{y}(t)|R(t, y)}{\int R(t, y)dy} dy \quad \text{and} \quad FDis_C(t) = \int \frac{|x - \bar{x}(t)| \int C(t, x, z)dz}{\iint C(t, x, z)dx dz} dx \quad (14)$$

where  $\bar{y}(t) = \int \frac{yR(t, y)}{\int R(t, y)dy} dy$  and  $\bar{x}(t) = \int \frac{x \int C(t, x, z)dz}{\iint C(t, x, z)dx dz} dx$  are the mean traits of the resource and consumer. The quantity  $\int C(t, x, z)dz$  corresponds to the biomass of individuals carrying the trait  $x$  in the consumers population.

The evolution of PF increases functional dispersion of both resources and consumers (Figure 3b). When the average foraging trait value is large the consequences on diversity indices becomes heterogeneous, but the effect of PF is almost always positive. The increase in functional diversity is due to

303 an eco-evolutionary loop between resources and consumers situated at the niche edge. Following the  
 304 evolution of PF some consumers forage at the niche edge, thereby reducing the density of the corre-  
 305 sponding resources. This decreases competition among these resources and promotes the emergence  
 306 of new resource phenotypes at the niche edge. The diversification of resources triggered the apparition  
 307 of consumers standing even further away from the niche centre, and so on until the resources reached  
 308 the limits of the exploitable niche. This emphasizes that adaptive phenotypic plasticity like PF can  
 309 subsequently fuel evolutionary change (Baldwin, 1896; Crispo, 2007; Laland et al., 2014). Instead,  
 310 when no PF evolution is introduced, the few resources standing far away from the niche centre are  
 311 barely used by consumers, which can not forage preferentially on them. This prevents the emergence  
 312 of new resources further away from the niche centre, due to competition between resources. Since the  
 313 evolution of PF occurs when the diversity of resources is initially large enough (large  $\sigma_K$ ), causation  
 314 is reciprocal: PF both promotes and is promoted by resource diversity.

### 315 4.3 Effects on productivity

316 Productivity corresponds to the net production of biomass by consumers following resource absorption,  
 317 measured once the system has reached a stationary regime (e.g. Loreau and Hector, 2001; Poisot et al.,  
 318 2013):

$$Prod = \iint C(T, x, z) F_C(T, x, z) dx dz \quad (15)$$

319  $T$  is the time to reach the stationary regime,  $T = 1000$  in the simulations below.

320 The relationship with productivity (i.e the flow of biomass from resources to consumers) is non-  
 321 linear (Figure 3c). When the system with PF evolution has a rather low mean foraging trait ( $0 <$   
 322  $\bar{z} < 0.4$ ) productivity increases in comparison to the system without PF. This occurs thanks to  
 323 functional complementarity between consumers (Poisot et al., 2013). However, when  $\bar{z}$  is above 0.4,  
 324 the productivity gain does not change on average, because consumers with high foraging trait impact  
 325 resources too heavily. Strong PF also increases the variability of productivity; among the systems with  
 326 strong PF some have large gains of productivity and others small gains or even small deficits.

### 327 4.4 Effects on niche overlap and functional match

328 The niche overlap between two consumers with niche traits  $x_i$  and  $x_j$  and foraging traits  $z_i$  and  $z_j$  is  
 329 defined by the correlation coefficient  $\rho_{ij}$  of their resource absorption:

$$\rho_{ij} = \frac{\int U(x_i, y, z_i) U(x_j, y, z_j) dy}{\sqrt{\int U^2(x_i, y, z_i) dy \int U^2(x_j, y, z_j) dy}} \quad (16)$$

330 The overall niche overlap between consumers  $\rho$  is the average of this correlation coefficient of all  
 331 consumers (Chesson and Kuang, 2008). The functional match  $FM$  corresponds to the mean difference  
 332 between the niche trait of the consumer and the mean niche trait of its diet, that is the resources  
 333 absorbed by the consumer:

$$FM(t) = \int \int |diet(t, x, z) - x| \frac{C(t, x, z)}{\int \int C(t, x, z) dx dz} dx dz$$

$$\text{where } diet(t, x, z) = \int y \frac{\phi(t, x, y, z) u(t, x, y, z)}{\int \phi u(t, x, y, z) dy} dy \quad (17)$$

334 The evolution of PF also decreases the niche overlap between consumers by about 90% as soon as  
 335 the mean foraging trait exceeds 0.230% ~~when the mean foraging trait is close to 1~~ (Figure 3d), and  
 336 increases the functional match between the niche trait of consumers and the mean niche trait of their  
 337 resources (Figure SI.9). PF also decreased niche overlap between pollinators in the model of Valdovinos  
 338 et al. (2013) and in the empirical studies of Fontaine et al. (2006) and Brosi and Briggs (2013). At

339 the intraspecific level, niche overlap between individuals of the same species decreased in function of  
 340 their abundance (Svanbäck and Bolnick, 2007; Tur et al., 2014). Short-term experimental time scales  
 341 suggest this pattern was caused by plastic behavior (Svanbäck and Bolnick, 2007), although in the  
 342 long-term this pattern may also be due to genetic diversification. Since abundance favors intraspecific  
 343 competition, this is consistent with our findings that competition between consumers promotes the  
 344 evolution of PF. The decrease of niche overlap between consumers corresponds to niche partitioning,  
 345 which may favor their coexistence (Behmer and Joern, 2008; Turcotte and Levine, 2016).

346

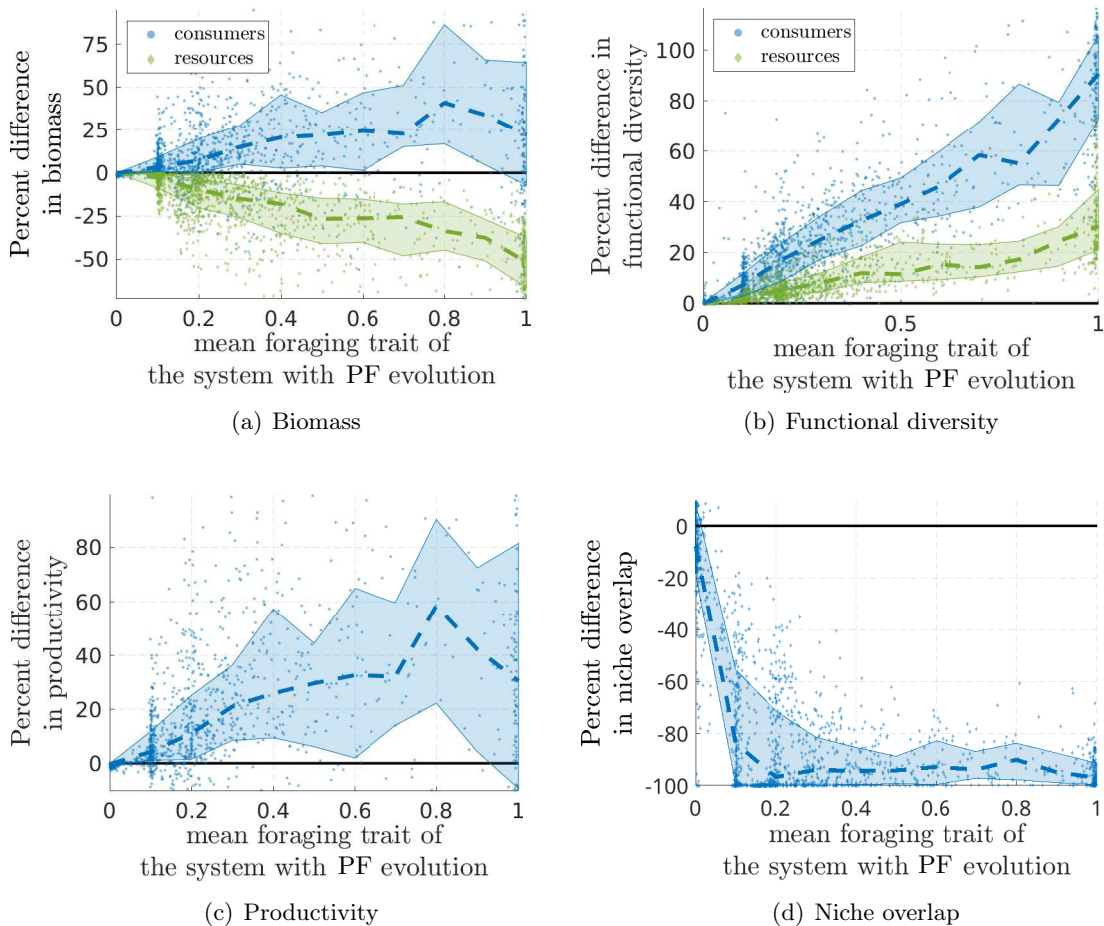


Figure 3: Difference (in %) between systems with PF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

## 347 5 The effects of PF on consumer persistence

348 To understand whether the evolution of PF can rescue consumers from environmental changes, three  
 349 specific disturbances are considered: a sudden environmental change where the `mode`  $y_0$  center of the  
 350 resource niche is instantaneously shifted at a distance  $\Delta y$  from the initial niche center,  $y_0 + \Delta y$  (e.g.  
 351 Domínguez-García et al., 2019), an ecosystem disturbance where consumer mortality  $d$  increases grad-  
 352 ually by  $\Delta d$ , and a constantly changing environment, where the `mode`  $y_0$  of the niche is displaced at  
 353 constant speed  $c$ ,  $y_0 + ct$ . The mutation process driving the diversification of resources and consumers  
 354 in the system should help to recover trait diversity after a disturbance. To assess the effects of those  
 355 disturbances on the resource-consumer system, the proportion of consumer biomass lost after the dis-

356 turbance is calculated once a new equilibrium is reached. The difference in the mean foraging trait  
357 before and after each disturbance is also measured.

358 Before the perturbation, we start with a resource-consumer system at equilibrium for each system:  
359 with PF evolution and with fixed RF, that is the foraging trait of consumers is monomorphic ( $z = 0$ )  
360 and does not evolve ( $\partial_z^2 C = 0$ ). In the system with PF evolution, the mean PF trait is stabilized  
361 around a high value,  $\bar{z} \approx 0.9$ , with the parameters set in Table 1. ~~The resource-consumer system  
362 is initialized with consumers carrying a high mean PF trait ( $\bar{z} \approx 0.9$  with parameter values set as  
363 in Table 1).~~ For each disturbance strength and type, we wait until a new equilibrium is reached.  
364 The stability metrics of the system with PF evolution is compared to those of the system with fixed  
365 RF at this new equilibrium. ~~, in which the foraging trait of consumers is monomorphic ( $z = 0$ ) and  
366 fixed ( $\partial_z^2 C = 0$ ).~~ For all disturbance types, the disturbance strength is increased until the consumer  
367 population goes to extinction, in order to compute the maximal disturbance level that the system  
368 can tolerate. Monomorphic systems for different foraging trait values are also initialized to test their  
369 response to disturbances.

## 370 5.1 Ecosystem disturbance and constant environmental change

371 In reaction to increasing levels of consumer mortality, the system with PF evolution behaves as the  
372 system with fixed RF. Indeed, after each increment of mortality the new biomass of consumers is  
373 similar; and the consumers disappear for the same mortality rate (Figure 4a). Moreover, at each  
374 mortality increase, consumers in the system with PF evolution gradually reduce their foraging trait,  
375 until PF ultimately disappears (color scale in Figure 4a). ~~Indeed, increased mortality leads to reduced  
376 competition between consumers via their reduced density, and to the non-viability of the niche edge  
377 for consumers, both leading to a reduction in PF trait.~~ Controlled monomorphic systems having low  
378 PF values better tolerate higher mortality rates (Figure 4b), which indicates that when PF is fixed it  
379 has a negative effect on the persistence of consumers facing increases in mortality.

380 Turning to the constant environmental change, the system with PF evolution tolerates niche dis-  
381 placement better than the system with fixed RF, up to a certain point when it disappears suddenly,  
382 earlier than its counterpart (Figure 4c). Moreover, as in the case of ecosystem disturbance, the mean  
383 PF value decreases for faster environmental changes (color scale in Figure 4c). Controlled monomor-  
384 phic systems having low PF values tolerate faster environmental changes (Figure 4d), which indicates  
385 that when PF is fixed it has a negative effect on the persistence of consumers facing constant environ-  
386 mental change.

387 For both disturbances the cost of PF becomes larger than the benefits, and choosy consumers  
388 go extinct earlier than random consumers. In particular, constant environmental changes weathers  
389 resource diversity to such a point that RF and PF consumers have a similar diet, which annihilates the  
390 benefits of PF. It has been stressed that phenotypic plasticity can retard adaptation to environmental  
391 change, shielding suboptimal phenotypes from natural selection (Fox et al., 2019), but in the present  
392 model phenotypic plasticity is limited to the foraging strategy of consumers. Instead, niche traits  
393 are not plastic and are therefore entirely sensitive to selection; the negative effect of PF on consumer  
394 persistence is therefore only due to its cost. In nature however, niche trait can also be plastic (e.g.  
395 Rossiter, 1987), but this was ignored by the model.

396 In figures 4b and d PF is fixed, but when PF can evolve, it gradually decreases in function of the  
397 intensity of the disturbances (see color scales in Figures 4 a and c), ~~although for different reasons. In  
398 the case of ecosystem disturbance, plastic foragers located at the edge of the niche trait distribution  
399 (Figure 2b) disappear progressively due to increases in mortality. The average PF trait therefore  
400 decreases (Figure 4a) due to demographic changes of a pre-existing trait diversity. In the case of a  
401 constant environmental change, however, the typical trait distribution depicted in Figure 2b no longer  
402 exists because niche traits constantly run after those of resources, which corresponds to an evolutionary  
403 lag load. In that case, consumers do not have enough time to reduce their PF searching behaviour  
404 and become extinct slightly earlier (Figure 4c); PF therefore imposes a second lag load, corresponding  
405 to the time needed for the evolutionary regression of PF.~~

406 A purely ecological model ignoring the evolutionary dynamics of PF would have missed the pos-  
407 sibility of its evolutionary regression, and would have therefore overestimated the negative effect of

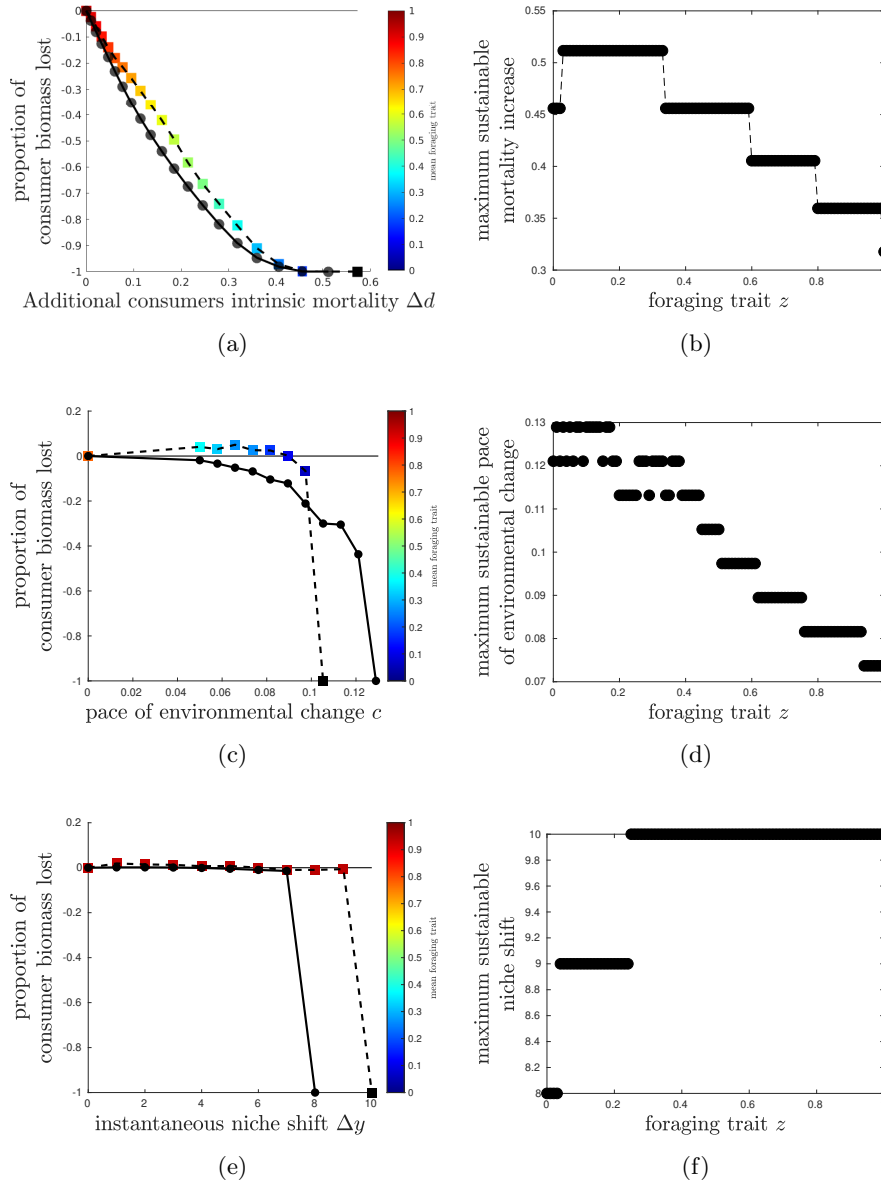


Figure 4: Effect of disturbances: (a, b) increased mortality  $\Delta d$ , (c, d) constant environment change  $c$  and (e, f) instantaneous niche shift  $\Delta y$ . Left column (a, c, e): variations of consumer biomass of systems with and without PF, in function of the intensity of the disturbance. A negative variation indicates a decrease in biomass, for instance  $-0.2$  indicates that 20% of the biomass is lost. The value  $-1$  corresponds to the extinction of all consumers. The coloured gradient indicates the average PF trait of consumers. Right column (b, d, f): maximal sustainable mortality for monomorphic consumers, in function of their controlled foraging trait  $z$ .

408 PF on consumer persistence. In the simulations, the various disturbance types have been applied  
 409 independently, but in nature they can be combined. In such cases, ecosystem disturbance and/or  
 410 constant environmental change might first lead to the evolutionary regression of the PF behaviour,  
 411 and a sudden shift might then facilitate the extinction of consumers, since they would not be protected  
 412 by PF any more.

## 413 5.2 Sudden environmental change

414 After a sudden environmental change, either consumers disappear or they persist in a new state close  
 415 to the original one. In that case their niche traits shift towards the new optimum and their foraging  
 416 traits remain unchanged, which is an indication of resilience. The variation of biomass before and

417 after disturbance is therefore uninformative; instead the maximal sudden environmental change that  
418 the consumer can tolerate is used to quantify its stability (Figure 4e). The system with PF evolution  
419 resists to a larger sudden change ( $\delta_y = 10$ ) compared with the system with fixed RF ( $\delta_y = 8$ ). In  
420 order to disentangle the direct effect of PF on stability from its indirect effect through diversity, the  
421 PF values of the consumers with PF are set to 0, while retaining the original diversity of the niche  
422 traits  $x$  and  $y$  of both guilds. The resulting hybrid system tolerates a large environmental change  
423 ( $\delta_y = 10$ ), which indicates that the positive effect of PF on the persistence of consumers is mainly due  
424 to its effects on diversity. In line with the above results, controlled monomorphic systems having high  
425 PF values tolerates larger sudden environmental changes (Figure 4d).

426 Previous theoretical studies have shown that PF can stabilize food-webs by favoring topologies  
427 able to buffer environmental disturbances (Kondoh, 2003; Heckmann et al., 2012), but in the present  
428 model such inherently robust topologies have not been observed. Instead, the mechanisms responsible  
429 for the stabilising effect of PF rely on the dynamical nature of the interaction webs produced by  
430 PF, which is caused both by a direct effect of PF (Question 3a), and by an indirect effect through  
431 diversity (Question 3b), as detailed above. The direct effect of PF on consumer persistence relies on  
432 the mitigation of the lag load faced by consumers. Indeed, resources become adapted to the new niche  
433 center more quickly than consumers, which suffer from a trait mismatch (e.g. Post and Forchhammer,  
434 2008; Miller-Struttman et al., 2015; Damien and Tougeron, 2019). This indicates that phenotypic  
435 plasticity acts as a rapid response mechanism to environmental change (Fox et al., 2019), in that  
436 case. Since random foragers consume the most abundant resources (but not the most suitable), after a  
437 sudden niche shift they feed on sub-optimal resources, which hamper their resilience to environmental  
438 change. In contrast plastic foragers select less abundant but more suitable resources, which favor their  
439 survival. In the meantime their traits evolve towards the new niche optimum and ultimately catch up  
440 the resources, which illustrates that adaptive plasticity can promote persistence in new environmental  
441 conditions (Ghalambor et al., 2007).

442 Turning to the indirect effect of PF on consumer persistence (Question 3b), when PF increases  
443 the diversity of both resources and consumers this favors the emergence of extreme phenotypes far  
444 away from the niche center. The extreme phenotypes are pre-adapted to the niche shift and therefore  
445 persist, unlike the central species. The positive effect of biodiversity on ecosystem functioning can  
446 be caused by complementarity and selection effects (e.g. Loreau and Hector, 2001). In the present  
447 case, a few well-adapted phenotypes determine the resilience to the niche shift : this corresponds to  
448 a selection effect. Although PF also increases complementarity between species as discussed earlier,  
449 this do not create any synergy between phenotypes, at least with respect to the resilience to the niche  
450 shift.

451 In summary, consumer persistence is fostered either by the evolution of PF in the case of a sudden  
452 environmental change or by its regression in the cases of ecosystem disturbance and constant envi-  
453 ronmental change. This corresponds to a combination of evolutionary rescue (Gonzalez et al., 2013;  
454 Kopp and Matuszewski, 2014), because PF is subject to evolution, and of plastic rescue (Kovach-Orr  
455 and Fussmann, 2013), since PF is a type of phenotypic plasticity.

## 456 6 Assumptions and limitations of the model

457 As outlined earlier, compared with other existing models exploring the influence of PF on community  
458 stability, the main novelty of the model is to study the evolution of the propensity to forage plastically,  
459 together with the evolution of niche traits of resources and consumers. Several other specificities also  
460 require some consideration.

461 First, in previous works the absence of PF corresponded to a constant interaction matrix between  
462 resources and consumers (e.g. Kondoh, 2003; Valdovinos et al., 2013). Instead, in the present model the  
463 alternative to plastic foraging consists in random foraging, where resources are consumed according  
464 to their density. The interaction matrix is therefore highly dynamic for both foraging strategies,  
465 although for different reasons. In the case of RF the resources exploited by a given consumer change  
466 according to their abundance only, whereas in the case of PF they also change according to their  
467 traits, the consumer's trait, and their degree of exploitation by other consumers. In previous models

468 allowing the evolutionary diversification of niche traits, the interaction matrices were dynamic but  
469 consumers did not forage plastically (Loeuille and Loreau, 2005; Allhoff et al., 2015). In those cases  
470 as well as here, new phenotypes constantly appear and need to be incorporated into the food web,  
471 which is therefore inherently dynamic (Appendix A.1). In comparison to RF, a consumer having  
472 fixed interaction coefficients would ignore these new phenotypes even if its favorite resources had gone  
473 extinct, which would make little sense. Besides, PF alone can produce non-equilibrium dynamics even  
474 with a fixed community composition, by triggering consumer-resource cycles (Abrams, 1992; Abrams  
475 and Matsuda, 2004).

476 Second, it is assumed that consumers feeding on a single optimal resource have the highest growth  
477 rate. Although this assumption often fits with prey-predator interactions (but see Jensen et al., 2012,  
478 for a counter-example), in the case of plant-herbivore interactions consumers often benefit from resource  
479 complementarity (Abrams, 2010; Unsicker et al., 2008), primarily because of nutrient balancing and  
480 toxin dilution (Ibanez et al., 2012; Behmer and Joern, 2008; Singer et al., 2002). We predict that the  
481 inclusion of this feature in the model would have favored the evolution of PF, since RF strategists  
482 mostly consume the most abundant resources, irrespective of their complementarity.

483 Third, foraging costs (quantified by the searching time  $s(z)$ ) were assumed independent of resource  
484 abundance, although the searching time may be larger for rare than for abundant resources. Moreover,  
485 the spatial distribution of resources is ignored, although travel time is costly (WallisDeVries, 1996;  
486 Hassell and Southwood, 1978). For instance, the random distribution of low preferred plant species  
487 can disfavor herbivore foraging selectivity (Wang et al., 2010). These two factors may hamper the  
488 evolution of PF.

489 Finally, the competition kernel modelling the strength of competition between resources and the  
490 carrying capacity functions were both assumed Gaussian. Under this hypothesis and in the absence of  
491 consumers, the evolutionary dynamics produce a continuum of resources (MacArthur, 1970; Slatkin and  
492 Lande, 1976). There are however many deviations from this special case, by choosing for instance non  
493 Gaussian competition kernels or carrying capacity functions, which leads to a discrete distribution of  
494 resources (Sasaki and Ellner, 1995; Szabó and Meszéna, 2006; Pigolotti et al., 2010; Hernández-García  
495 et al., 2009; Sasaki and Dieckmann, 2011). The presence of consumers using PF also results in a  
496 discrete distribution of resources, either with Gaussian functions (Fig.2) or with a quartic function,  
497 which was instead used in Appendix C. Platykurtic functions like the quartic function tend to broaden  
498 the resource distribution (Sasaki and Dieckmann, 2011). Under the quartic scenario, the resource  
499 distribution is indeed enlarged and the mean foraging trait is larger (compare Fig. 2 to Fig. SI.6).  
500 Moreover, the gain in consumer biomass and productivity due to PF is larger in the quartic case  
501 (compare Fig. 3a-c to Fig. SI.8a-c). However, the quartic carrying capacity function tends to reduce  
502 the effect of PF on the functional diversity (Fig.SI.8b). Although functional diversity is higher with a  
503 platykurtic than with a Gaussian carrying capacity function, the gain due to PF is small (Fig. SI.7).

## 504 Conclusion

505 The present model illustrates how phenotypic plasticity can be simultaneously a result and a factor of  
506 evolution. On the one hand, plastic foraging (PF) evolves by natural selection acting on consumers.  
507 On the other hand, it stimulates the diversification of ecological characters not only of consumers but  
508 also of resources, stressing that phenotypic plasticity can have far-reaching evolutionary consequences  
509 at the community-level (Fordyce, 2006). Moreover, functional diversity itself promotes the evolution  
510 of PF, creating an eco-evolutionary feedback loop between phenotypic plasticity, natural selection and  
511 community composition. This has intricate consequences on the response of the resource-consumer  
512 community to disturbances. In the case of sudden environmental change, the evolution of PF has a  
513 positive effect on community stability, partly via its effects on functional diversity. However for other  
514 disturbance types like constant change and increases in mortality, the PF behavior is less fit than  
515 random foraging and therefore declines. In contrast to previous studies, these results stress that the  
516 relationship between PF and community stability depends on the type of the disturbance as well as  
517 on the evolutionary dynamics of PF itself.



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## 520 Conflict of interest disclosure

521 The authors of this article declare that they have no financial conflict of interest with the content of  
522 this article.

## 523 Data, script and code availability

524 All the codes used to compute the outcomes of our model and the figures of the paper are available  
525 online: <https://zenodo.org/badge/latestdoi/481122645>.

## 526 Appendix

### 527 A Model details

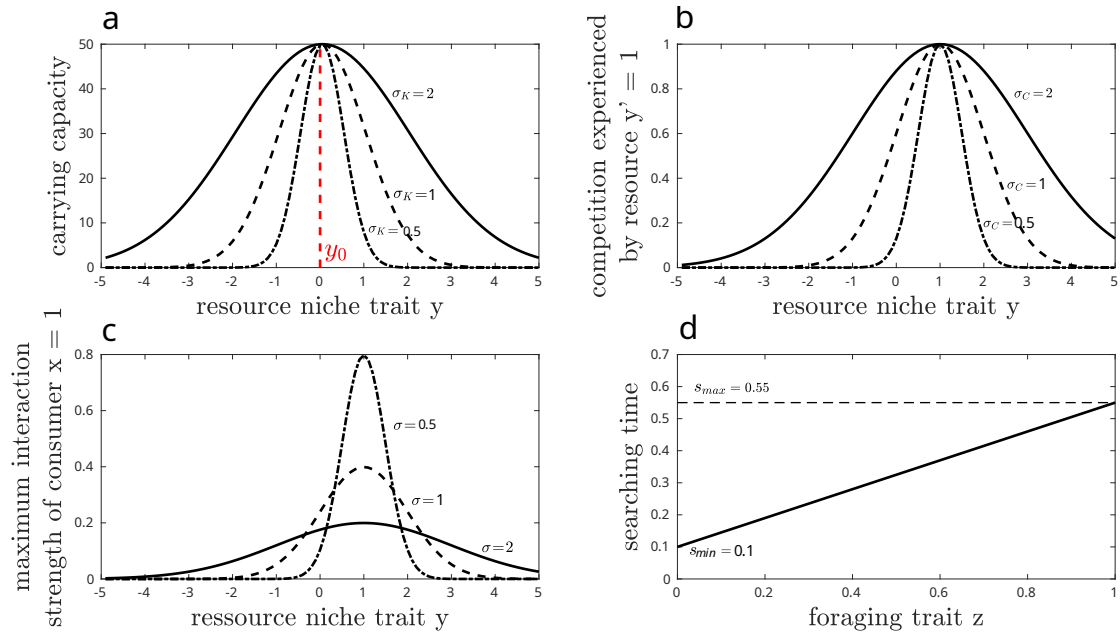


Figure SI.1: a) Carrying capacity  $K(y)$  of resources for various niche width values  $\sigma_K = \{0.5, 1, 2\}$ . The niche centre fixed at  $y_0 = 0$  corresponds to the maximal carrying capacity. b) Competition kernel  $K_e$  for various neighbourhood size  $\sigma_C = \{0.5, 1, 2\}$  between a focal resource  $y' = 1$  and all resources in function of their niche trait  $y$ . c) Interactions kernel  $\Delta$  for various generalization levels ( $\sigma = \{0.5, 1, 2\}$ ) between a focal consumer ( $x = 1$ ) and all the resources in function of their niche trait  $y$ . d) Searching time  $s$  in function of the foraging trait  $z$ . Parameter values as in Table 1.

Quantitative traits		Ranges
$x$	Consumers niche trait	$[-5; 5]$
$y$	Resources niche trait	$[-5; 5]$
$z$	Consumers foraging trait	$[0; 1]$
State variables		Shapes
$R(t, y)$	Resource density	see Eq. (1)
$\bar{y}(t)$	Mean resource trait	$\bar{y}(t) = \int y \frac{R(t, y)}{\int R(t, y) dy} dy$
$C(t, x, z)$	Consumer density with foraging trait $z$	see Eq. (2)
$\bar{x}(t)$	Mean consumer niche trait	$\bar{x}(t) = \int x \frac{\int C(t, x, z) dz}{\iint C(t, x, z) dx dz} dx$
$\bar{z}(t)$	Mean foraging trait	$\bar{z}(t) = \iint z \frac{C(t, x, z)}{\iint C(t, x, z) dx dz} dx dz$
$\phi_{RF}(t, y)$	Random Foraging efforts	$\phi_{RF}(t, y) = \frac{R(t, y)}{\int R(t, y) dy}$
$\phi_{PF}(t, x, y, z)$	Relative Foraging efforts	see Eq. (11)
$\phi(t, x, y, z)$	Effective Foraging efforts	$\phi = z\phi_{PF} + (1 - z)\phi_{RF}$
Functional responses		Shapes
$F_R(t, y)$	Resource consumption	$\iint U(t, x, y, z) C(t, x, z) dx dz$
$F_C(t, x, z)$	Resource absorption	$\alpha \int U(t, x, y, z) R(t, y) dy$
$U(t, x, y, z)$	resource uptake per consumer	see Eq. (6)
$K(y)$	Carrying capacity	$K(y) = K_0 e^{-\frac{y^2}{2\sigma_K^2}}$
$K_e(y)$	Competition strength	$K_e(y) = e^{-\frac{y^2}{2\sigma_e^2}}$
$r_e(t, y)$	Effective resource density	see Eq. (4)
$\Delta(x, y)$	Interaction strength between resources and consumers	$\Delta(x, y) = \frac{e^{-\frac{(x-y)^2}{2\sigma^2}}}{\sqrt{2\pi\sigma^2}}$
$u(t, x, y, z)$	Potential resource uptake of a consumer	see Eq. (12)
$s(z)$	Searching time	$s(z) = s_{min} + z(s_{max} - s_{min})$
$\mathcal{M}_R(t, y)$	Resource niche trait mutations	see Eq. (8)
$\mathcal{M}_C(t, x, z)$	Consumer trait mutations	see Eq. (8)
Aggregate properties		Shapes
$FDiS_R(t)$	Functional dispersion of resources	$FDiS_R(t) = \int \frac{ y - \bar{y}(t)  R(t, y)}{\int R(t, y) dy} dy$
$FDiS_C(t)$	Functional dispersion of consumers	$FDiS_C(t) = \int \frac{ x - \bar{x}(t)  \int C(t, x, z) dz}{\iint C(t, x, z) dx dz} dx$
$Prod$	Productivity	$Prod = \iint C(T, x, z) F_C(T, x, z) dx dz$
$\rho_{ij}$	Niche overlap between foraging traits	see Eq. (16)
$FM(t)$	Functional match	see Eq. (17)

Table SI.1: List of the quantitative traits subject to evolutionary change, the state variables, the functions and the aggregate system-level properties involved the model.

## 528 A.1 Stationary regime

529 The stationary regime is visible in this simulation of the emergence of a community in which plastic  
530 foraging evolves: <https://drive.google.com/file/d/1c1nNXJl9aR76FrwFcrJppJbk-Rg7o9tn/view>.  
531 The system follows a perpetual turnover of resources and consumers densities in function of their niche

532 and foraging traits, but the macroscopic criteria of the community (exemplified here by the functional  
533 diversity  $FDis$ ) reach a quasi equilibrium. Top panels: distribution of resources and consumers in  
534 function of their niche trait. Middle panels: distribution of consumers in function of their foraging  
535 trait (left) and community-level mean foraging trait in function of time (right). Bottom panels:  
536 functional diversity  $FDis$  of resources and consumers. The other community-level characteristics are  
537 also stabilized once the stationary regime is reached.

## 538 A.2 Effect of a fixed PF trait

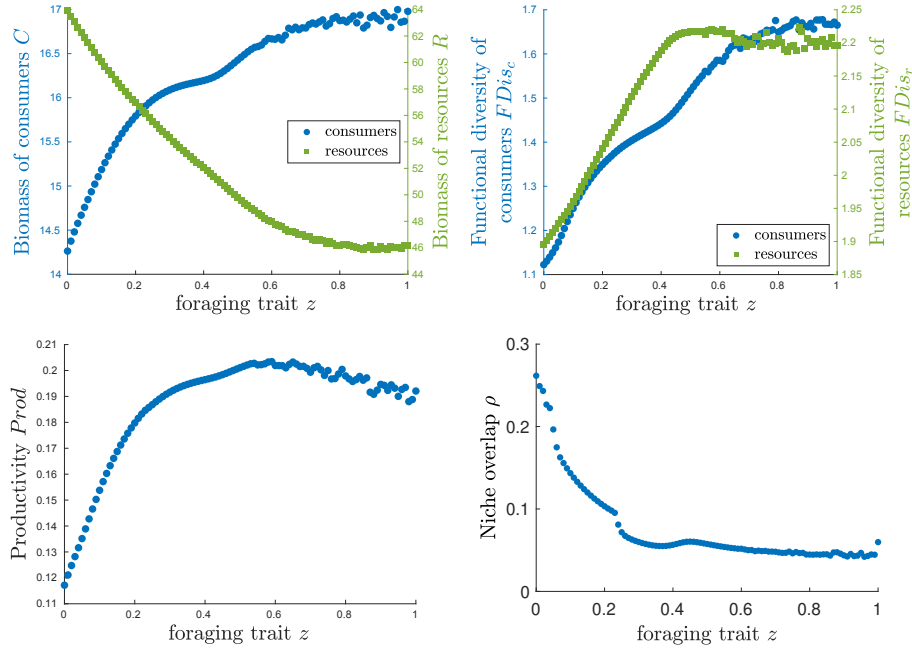


Figure SI.3: Effect of a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

## 539 B Trade-off on mortality

540 Our model assumes a trade-off between PF and handling time. In this case, an increase of the foraging  
541 trait induces an increases of searching handling time, which eventually induces a reduction of the  
542 resource absorption rate. More precisely, for a given foraging trait  $z$ , an increase  $\delta z$  of the trait  
543 reduces the absorption rate as follows

$$\begin{aligned}
F_C(z + \delta z) &= \alpha \frac{b \int \phi(y) \Delta(x, y) R(y) dy}{1 + s(z + \delta z) b \int \phi(y) \Delta(x, y) R(y)} \\
&= \alpha \frac{b \int \phi(y) \Delta(x, y) R(y) dy}{1 + s(z) b \int \phi(y) \Delta(x, y) R(y) + \delta z (s_{max} - s_{min}) b \int \phi(y) \Delta(x, y) R(y)} \\
&\approx \alpha \frac{b \int \phi(y) \Delta(x, y) R(y) dy}{1 + s(z) b \int \phi(y) \Delta(x, y) R(y)} - \delta z (s_{max} - s_{min}) \alpha \left( \frac{b \int \phi(y) \Delta(x, y) R(y)}{1 + s(z) b \int \phi(y) \Delta(x, y) R(y)} \right)^2 \\
&\approx F_C(z) - \delta z (s_{max} - s_{min}) \alpha
\end{aligned} \tag{18}$$

544 Thus an increase of foraging trait will reduce the growth rate of the consumers ( $F_C - d - I \iint C$ )  
 545 proportionally to the difference of the PF cost ( $s_{max} - s_{min}$ ).

546 As mentioned in the main text, the model may have assumed different trade-off such as a positive  
 547 dependence between mortality rate and foraging trait. In this case the mortality rate may take the  
 548 following form

$$d(z) = d_{min} + z(d_{max} - d_{min}), \quad (19)$$

549 where  $d_{min}$  is the basal mortality rate while  $d_{max}$  is the maximal increase of mortality due to PF.  
 550 In this case, an increase of the foraging trait will increase the mortality rate proportionally to the  
 551 maximal increment of mortality ( $d_{max} - d_{min}$ ). The growth rate will reduce proportionally to this  
 552 quantity. We thus see that the effect of the trade-off will have similar consequences on the evolution  
 553 of the foraging trait.

### 554 B.1 Effect of mortality trade-off on community emergence

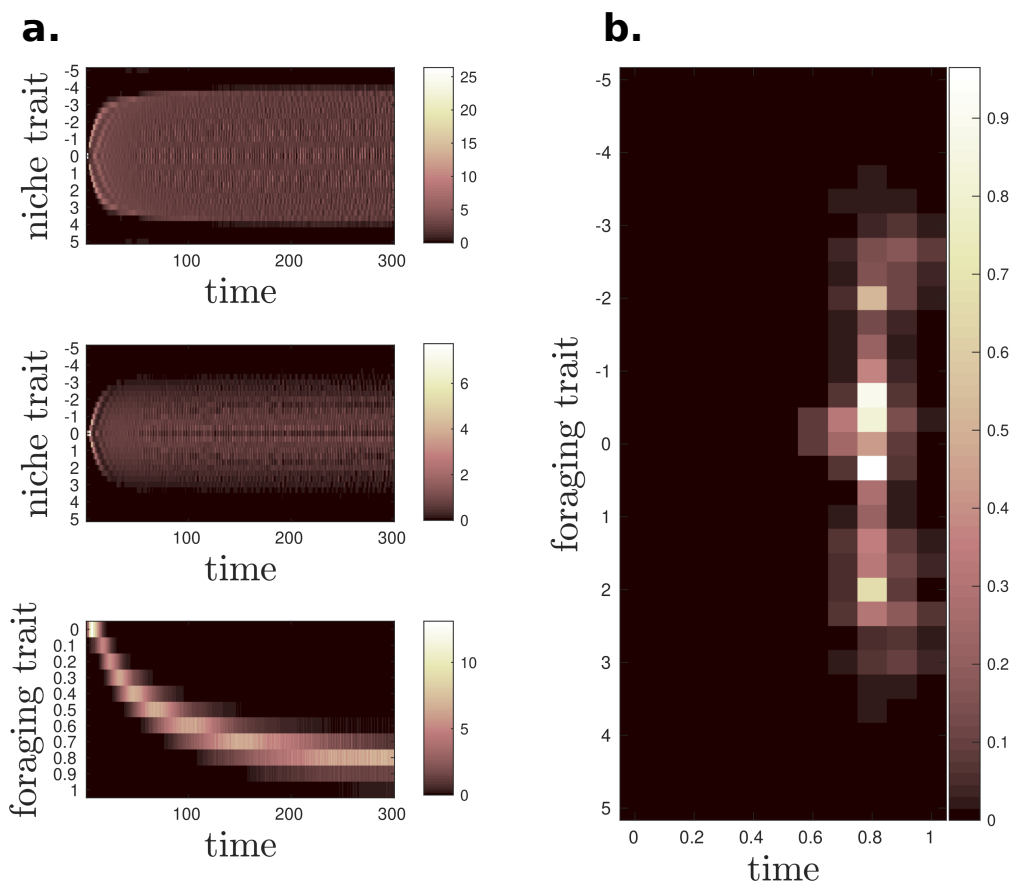


Figure SI.4: Distribution of resources and consumers over time with a trade-off on mortality. a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer densities  $\int C(t, x, z) dz$ . Bottom panel: foraging trait  $\int C(t, x, z) dx$ . b) The trait distribution of consumers at steady state (1000 time steps).

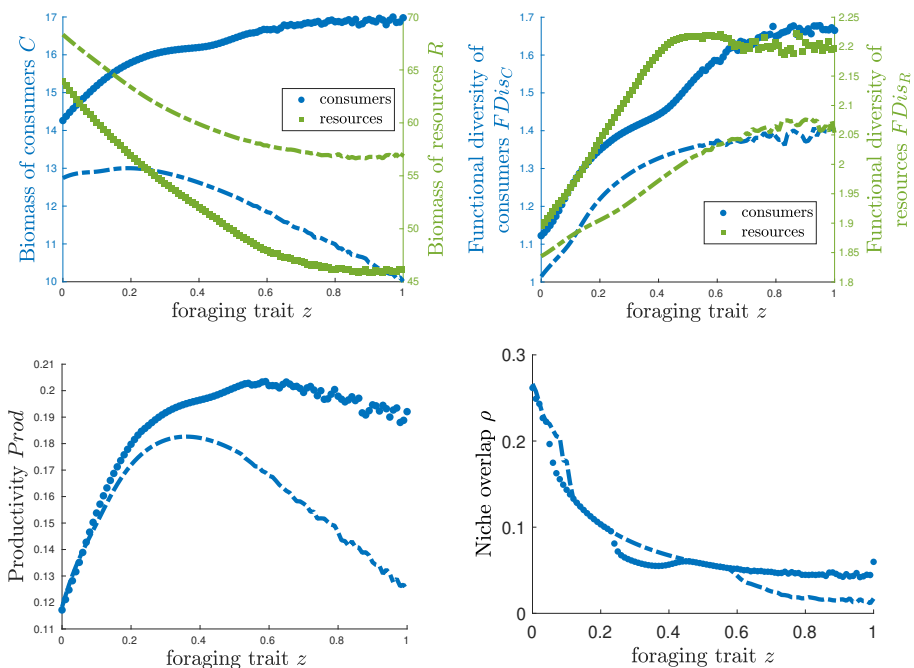


Figure SI.5: Effect of different mortality trade-off with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two mortality trade-off, between PF and: handling time (dotted markers), and mortality rate (dashed curves). The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

556 C Effect of a quartic carrying capacity functions

557 C.1 Effect of a quartic carrying capacity function on community emergence

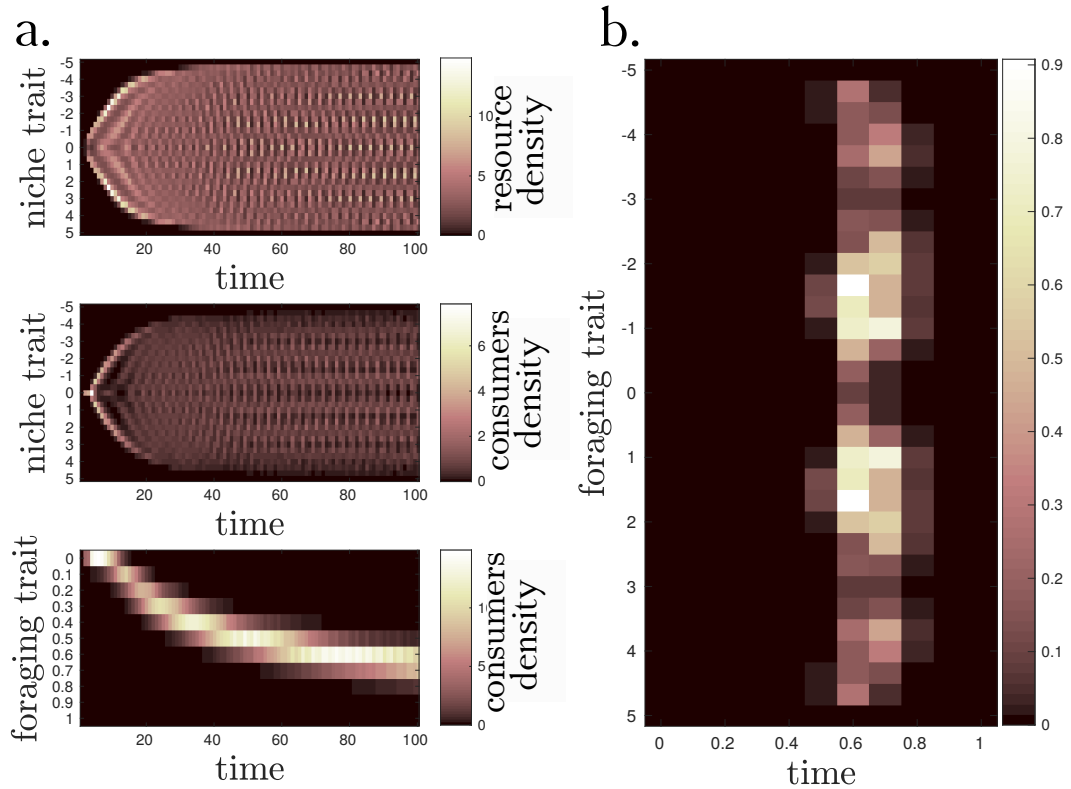


Figure SI.6: Distribution of resources and consumers over time with a quartic carrying capacity function  $K(y) = K_0 \exp(-y^4/(12\sigma_K^4))$ . a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer densities  $\int C(t, x, z) dz$ . Bottom panel: foraging trait  $\int C(t, x, z) dx$ . b) The trait distribution of consumers at steady state (1000 time steps).

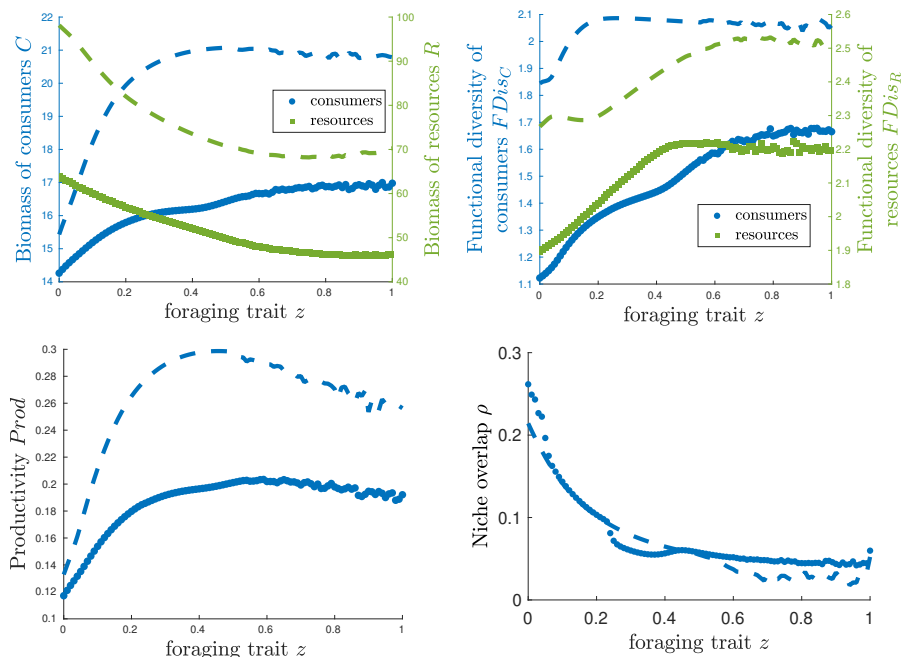


Figure SI.7: Effect of the carrying capacity kernel  $K$  with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two carrying capacity function: Gaussian function  $K(y) = K_0 \exp(-y^2/(2\sigma_K^2))$  (dotted markers) and Quartic function  $K(y) = K_0 \exp(-y^4/(12\sigma_K^4))$  (dashed curves). The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

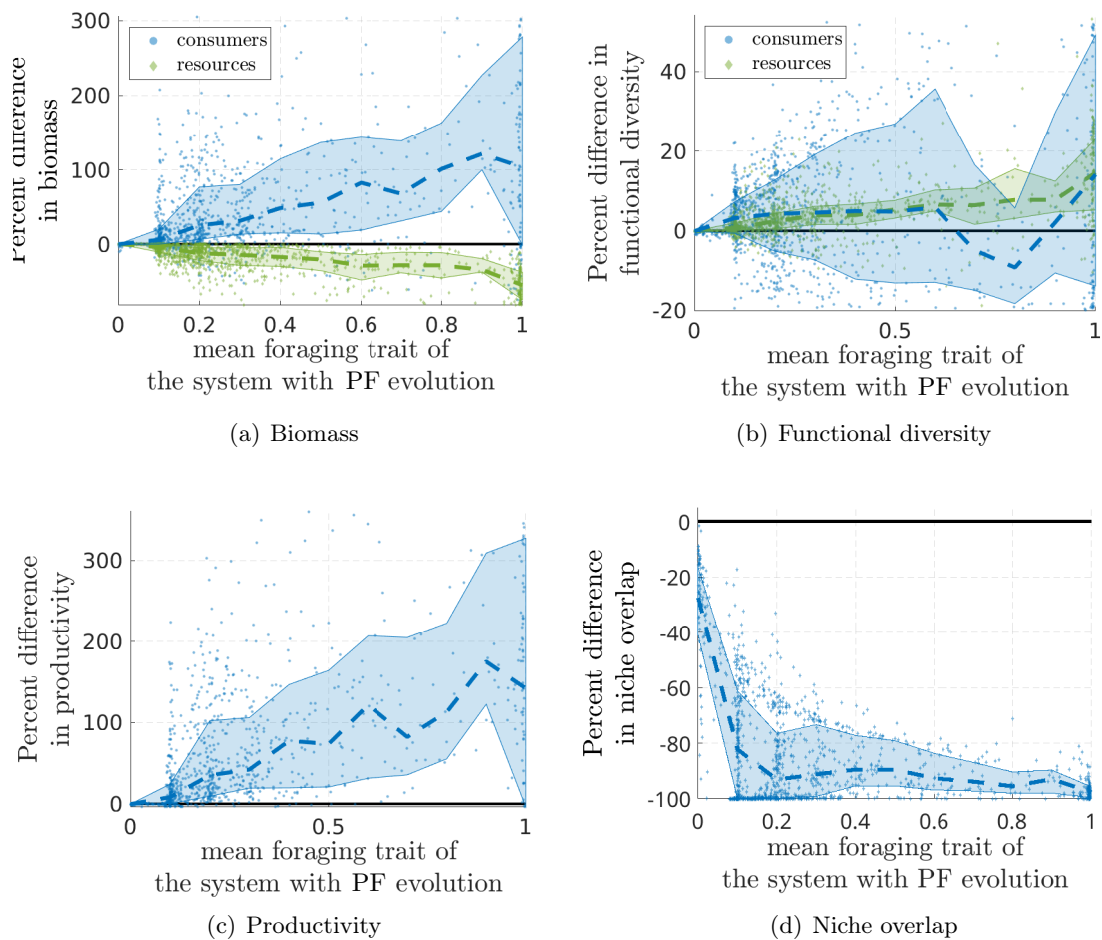


Figure SI.8: Difference (in %) between systems with PF evolution and fixed RF with a quartic carrying capacity function  $K(y) = K_0 \exp(-y^4/(12\sigma_K^4))$ , for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.



560 **D** Functional match between resources and consumers

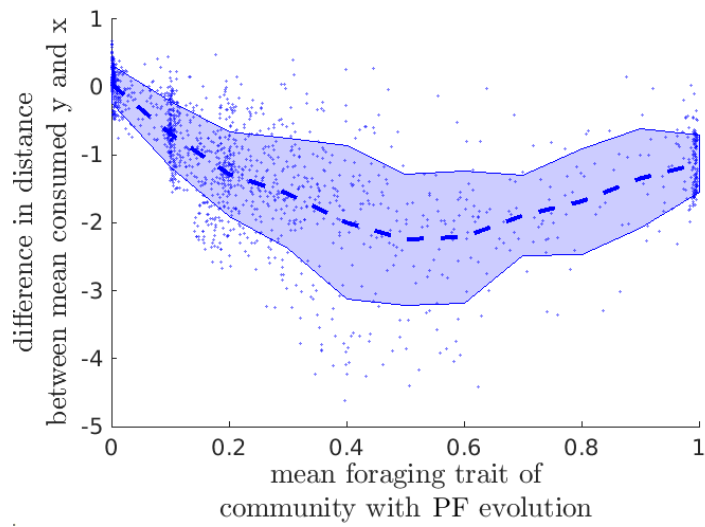


Figure SI.9: Difference in functional matching between systems with PF evolution and systems with fixed RF. 500 pairs of systems were compared, each pair having the same parameter set randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

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