

# 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

# 1 Introduction

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

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

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

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

The evolutionary dynamics of phenotypic plasticity has important ecological consequences (Miner et al., 2005; Turcotte and Levine, 2016), which in turn can feed back into the evolutionary dynamics. In the case of PF, behavioural plasticity in diet choice can favour the persistence of consumers in unusual environments and rescue them in the face of environmental changes (e.g. Varner and Dearing, 2014; Kowalczyk et al., 2019). Previous theoretical studies have indeed shown that PF promotes community stability (Křivan and Schmitz, 2003; Abrams and Matsuda, 2004; Kondoh, 2003; Uchida and Drossel, 2007). The third motivation is to test if this positive relationship holds when both PF and the functional traits of consumers and resources are subject to evolutionary

90 dynamics. In this eco-evolutionary context, it is uncertain whether the evolution of PF stabilises communities  
91 directly, by altering food-web structure or indirectly, through its effects on functional diversity.

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

- 93 • Question 1. Under which ecological conditions is PF evolutionary adaptive?
- 94 • Question 2. When PF evolves, what are its effects on the diversity of the traits involved in the resource-  
95 consumer interaction?
- 96 • Question 3. What is the effect of the evolution of PF on the stability of the resource-consumer system, in  
97 response to environmental changes? Are these effects direct (Q3a) or indirect, mediated by the influence  
98 of PF on functional diversity (Q3b)?

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

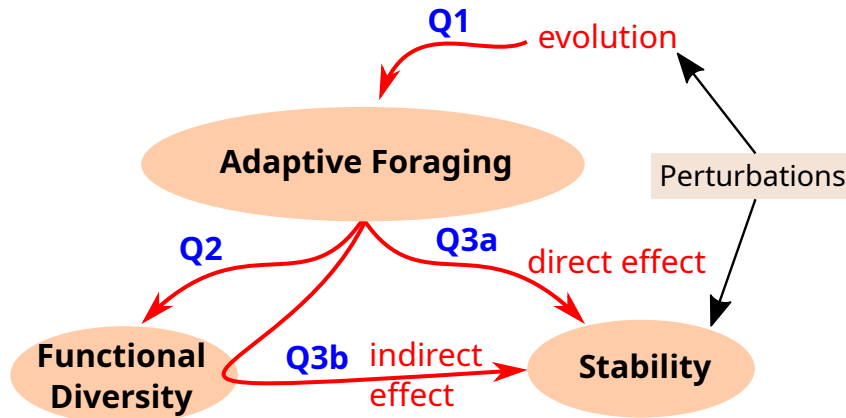


Figure 1: Overview of the main questions: (Q1) Under which ecological conditions does PF evolve? (Q2) Does the evolution of PF increases the diversity of traits involved in the resource-consumer interaction? (Q3) Does the evolution of PF enhances the stability of the resource-consumer system, either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

## 2 Model description

### 2.1 A resource-consumer niche model

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

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

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

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

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

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

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

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

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

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

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

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

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

$$\delta(t) = (d + IC(t)) \quad \text{where} \quad \mathbf{C}(t) = \iint C(t, x, z) dx dz \quad \text{is the total biomass of consumers.} \quad (7)$$

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

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

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

## 149 2.2 Foraging strategies and plastic foraging trait.

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

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

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

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

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

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

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

166 where  $[u(y) - u(y')]_+ = \max\{u(y) - u(y'), 0\}$  is the positive part of the difference between potential resource  
167 uptake. The quantity  $\phi_{PF}$  is analogous to the behavioral trait  $z$  in Abrams and Matsuda (2004). The potential  
168 resource uptake  $u(t, x, y, z)$  of a consumer with traits  $(x, z)$  on a resource with trait  $y$  depends on its foraging  
169 efforts as well as the resource suitability and availability:

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

170 The PF dynamics allow consumers to compare the benefits  $u$  received from different resources. As a result,  
171 consumers increase their efforts on the most beneficial resources and reduce them on sub-optimal resources.  
172 The comparison of resources is assumed time consuming, the efforts are therefore not adjusted instantaneously  
173 but exponentially fast at a rate  $l_\phi$ . When the adjustment rate  $l_\phi$  becomes large, the plastic foraging strategy  
174 becomes closer to the optimal foraging strategy maximizing the potential resource uptake  $u$  (MacArthur and  
175 Pianka, 1966; Loeuille, 2010). Moreover, the searching time  $s(z)$  also increases with the foraging trait:  $s(z) =$   
176  $s_{min} + z(s_{max} - s_{min})$  (Figure SI.1d). This relationship introduces a trade-off between the PF strategy and the  
177 searching time.

### 3 The evolution of plastic foraging

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

#### 3.1 Diversification and emerging foraging strategy

The model is investigated numerically using MATLAB (code available on GitHub <https://github.com/leoledru/Adaptive-Foraging>). The niche traits are discretized into 31 equally distanced values (11 values for the foraging trait). In the simulations, when the density of a resource or a consumer phenotype drops below the critical threshold  $\varepsilon = 10^{-4}$ , the density is set to 0 to save computational time. The simulations start with monomorphic populations at the niche center ( $y = x = 0$ ) and consumers have a purely random foraging strategy ( $z = 0$ ).

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	
$\sigma_C$	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.

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

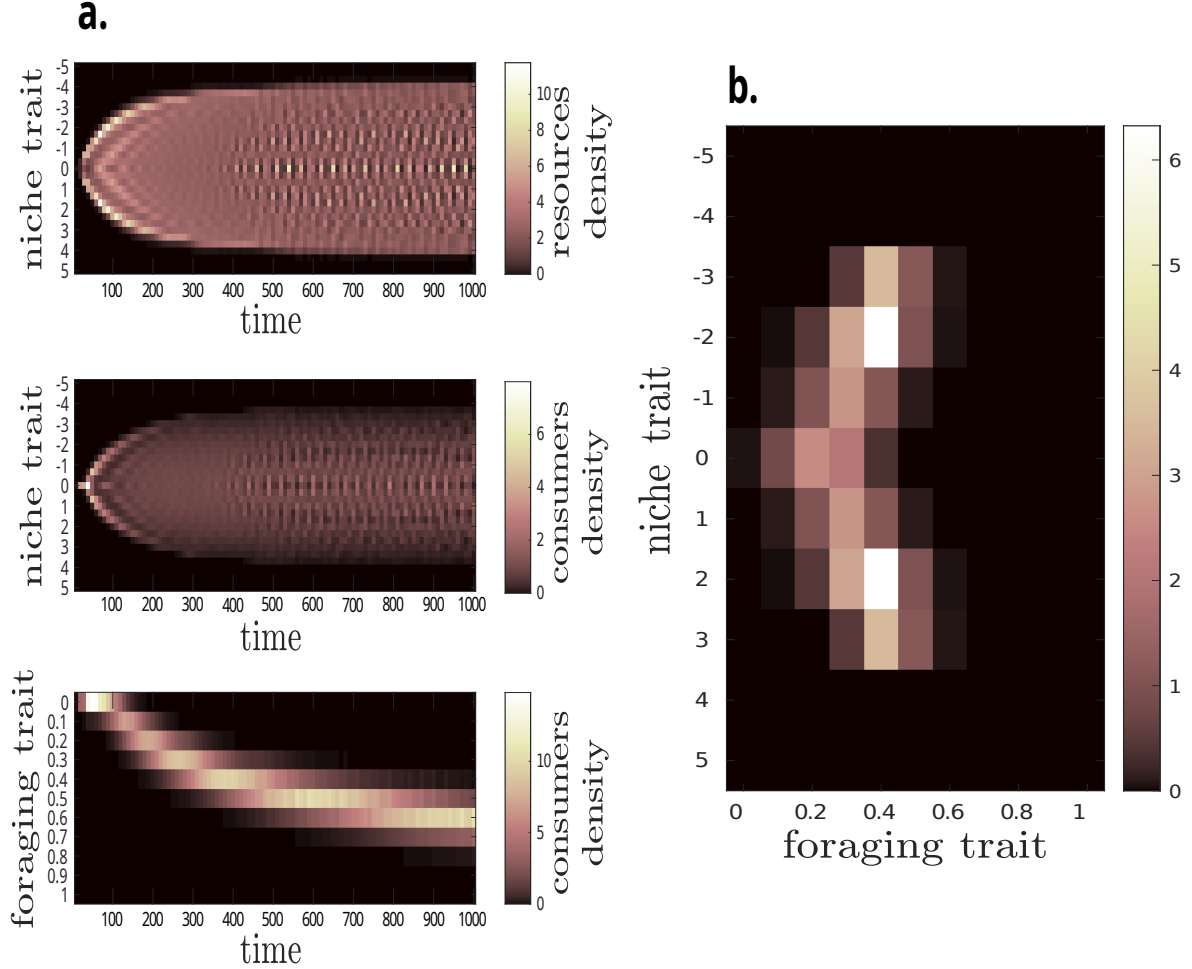


Figure 2: a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer densities  $\int C(t, x, z) dz$ . Bottom panel: foraging trait  $\int C(t, x, z) dx$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

### 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:

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

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).

219 **Consumer niche width** The evolution of PF is instead favored by the niche width of consumers (parameter  
220  $\sigma$ , correlation coefficient 0.28). In nature, a positive correlation between total niche width and inter-individual  
221 niche variation was found for herbivores (Bison et al., 2015) and predators (Bolnick et al., 2007). Inter-individual  
222 niche variation reflects the existence of contrasting foraging strategies, which may be the result of plastic foraging.  
223 Baboons also combine niche breadth with selectivity in resource use (Whiten et al., 1991). Since the evolution  
224 of consumer niche width may itself depend on environmental heterogeneity (Kassen, 2002) (i.e. on resource  
225 diversity in the model), the coevolution of PF, niche width and niche position is a possible avenue for future  
226 research. Niche width foster PF because consumers deplete the whole range of resources when their niche width  
227 is large, therefore competition between consumers is more intense, which leads to the evolution of PF. Empirical  
228 studies have indeed found that generalist consumers competing for resources forage plastically. For instance  
229 generalist bumblebee species visited the larkspur *Delphinium barbeyi* when the most abundant bumblebee species  
230 was experimentally removed, but preferred other plant species otherwise, likely to avoid competition for nectar  
231 (Brosi and Briggs, 2013). A similar behavior has been reported for syrphid flies, which preferentially foraged  
232 on open rather than tubular flowers when competing with bumblebees (Fontaine et al., 2006). In the case  
233 of predators, intraspecific competition between sticklebacks (*Gasterosteus aculeatus*) enhanced the diversity of  
234 foraging behaviors and increased the correlation between diet and morphology (Svanbäck and Bolnick, 2007), as  
235 found here (Figure SI.9).

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

## 241 4 The effects of PF evolution on community properties

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

### 249 4.1 Effects on biomass

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

255 When the evolution of PF produce consumer populations with a high mean foraging trait  $\bar{z}$ , the resource  
256 biomass is reduced (e.g. -50% when  $\bar{z} = 1$ ) while the consumer biomass increased by 25% on average (Figure  
257 3a). Following the evolution of PF, the functional complementarity and diversity of consumers increase their  
258 biomass at the expense of resources (Figure 3a). This fits with empirical studies showing a relationship between  
259 resource consumption and consumer diversity (Deraison et al., 2015; Lefcheck et al., 2019; Milotić et al., 2019).  
260 However, the variability of the consumer biomass among simulations also increases with  $\bar{z}$ . This pattern has also  
261 been observed when the foraging trait  $z$  of a monomorphic population without PF evolution is increased (Figure  
262 SI.3a).

### 263 4.2 Effects on functional diversity

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

$$266 FDis_R(t) = \int \frac{|y - \bar{y}(t)|R(t,y)}{\int R(t,y)dy} dy \quad \text{and} \quad FDis_C(t) = \int \frac{|x - \bar{x}(t)|\bar{C}(t,x)}{\int \bar{C}(t,x)dx} dx \quad (14)$$

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

269 The evolution of PF increases functional dispersion of both resources and consumers (Figure 3b). When the  
270 average foraging trait value is large the consequences on diversity indices becomes heterogeneous, but the effect



270 of PF is almost always positive. The increase in functional diversity is due to an eco-evolutionary loop between  
 271 resources and consumers situated at the niche edge. Following the evolution of PF some consumers forage at  
 272 the niche edge, thereby reducing the density of the corresponding resources. This decreases competition among  
 273 these resources and promotes the emergence of new resource phenotypes at the niche edge. The diversification  
 274 of resources triggered the apparition of consumers standing even further away from the niche centre, and so  
 275 on until the resources reached the limits of the exploitable niche. This emphasizes that adaptive phenotypic  
 276 plasticity like PF can subsequently fuel evolutionary change (Baldwin, 1896; Crispo, 2007; Laland et al., 2014).  
 277 Instead, when no PF evolution is introduced, the few resources standing far away from the niche centre are barely  
 278 used by consumers, which can not forage preferentially on them. This prevents the emergence of new resources  
 279 further away from the niche centre, due to competition between resources. Since the evolution of PF occurs when  
 280 the diversity of resources is initially large enough (large  $\sigma_K$ ), causation is reciprocal: PF both promotes and is  
 281 promoted by resource diversity.

### 282 4.3 Effects on productivity

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

$$285 \text{Prod} = \iint C(T, x, z) F_C(T, x, z) dx dz \quad (15)$$

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

286 The relationship with productivity (i.e the flow of biomass from resources to consumers) is non-linear (Figure  
 287 3c). When the system with PF evolution has a rather low mean foraging trait ( $0 < \bar{z} < 0.4$ ) productivity  
 288 increases in comparison to the system without PF. This occurs thanks to functional complementarity between  
 289 consumers (Poisot et al., 2013). However, when  $\bar{z}$  is above 0.4, the productivity gain does not change on average,  
 290 because consumers with high foraging trait impact resources too heavily. Strong PF also increases the variability  
 291 of productivity; among the systems with strong PF some have large gains of productivity and others small gains  
 292 or even small deficits.

### 293 4.4 Effects on niche overlap and functional match

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

$$296 \rho_{ij} = \frac{\int \phi(x_i, y, z_i) u(x_i, y, z_i) \phi(x_j, y, z_j) u(x_j, y, z_j) dy}{\sqrt{\int (\phi(x_i, y, z_i) u(x_i, y, z_i))^2 dy + \int (\phi(x_j, y, z_j) u(x_j, y, z_j))^2 dy}} \quad (16)$$

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

$$299 FM(t) = \int |\text{diet}(t, x, z) - x| \frac{C(t, x, z)}{\int C(t, x, z) dx dz} dx dz \quad \text{where} \quad \text{diet}(t, x, z) = \int y \frac{\phi(t, x, y, z) u(t, x, y, z)}{\int \phi u(t, x, y, z) dy} dy \quad (17)$$

300 The evolution of PF also decreases the niche overlap between consumers by about 30% when the mean for-  
 301 aging trait is close to 1 (Figure 3d), and increases the functional match between the niche trait of consumers  
 302 and the mean niche trait of their resources (Figure S1.9). PF also decreased niche overlap between pollinators in  
 303 the model of Valdovinos et al. (2013) and in the empirical studies of Fontaine et al. (2006) and Brosi and Briggs  
 304 (2013). At the intraspecific level, niche overlap between individuals of the same species decreased in function of  
 305 their abundance (Svanbäck and Bolnick, 2007; Tur et al., 2014). Short-term experimental time scales suggest this  
 306 pattern was caused by plastic behavior (Svanbäck and Bolnick, 2007), although in the long-term this pattern may  
 307 also be due to genetic diversification. Since abundance favors intraspecific competition, this is consistent with  
 308 our findings that competition between consumers promotes the evolution of PF. The decrease of niche overlap  
 309 between consumers corresponds to niche partitioning, which may favor their coexistence (Behmer and Joern,  
 310 2008; Turcotte and Levine, 2016).

## 311 5 The effects of PF on consumer persistence

312 To understand whether the evolution of PF can rescue consumers from environmental changes, three specific  
 313 disturbances are considered: a sudden environmental change where the center of the resource niche is instanta-  
 314 neously shifted at a distance  $\Delta y$  from the initial niche center (e.g. Domínguez-García et al., 2019), an ecosystem  
 315 disturbance where consumer mortality  $d$  increases gradually by  $\Delta d$ , and a constantly changing environment,

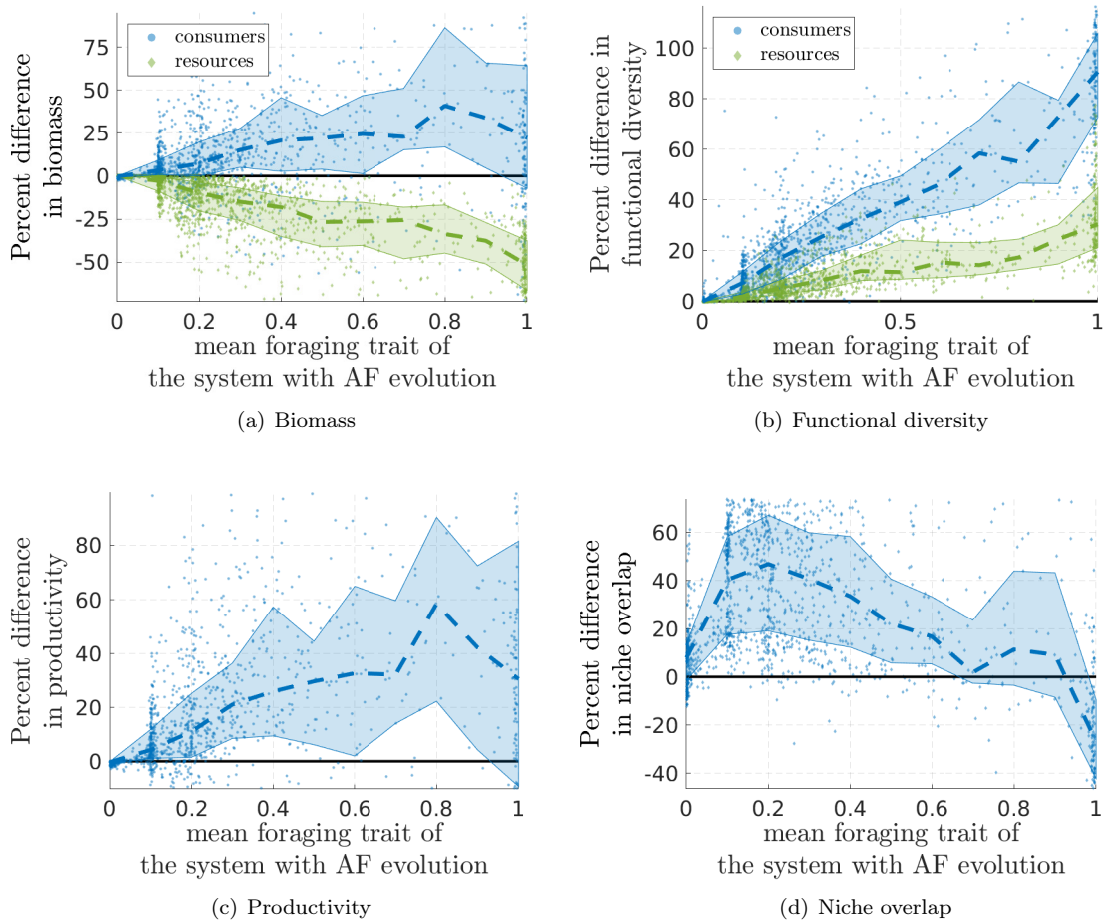


Figure 3: Difference (in %) between systems with PF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly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

316 where the niche center is displaced at constant speed  $c$ . The mutation process driving the diversification of  
 317 resources and consumers in the system should help to recover trait diversity after a disturbance. To assess the  
 318 effects of those disturbances on the resource-consumer system, the proportion of consumer biomass lost after the  
 319 disturbance is calculated once a new equilibrium is reached. The difference in the mean foraging trait before and  
 320 after each disturbance is also measured.

321 The resource-consumer system is initialized with consumers carrying a high mean PF trait ( $\bar{z} \approx 0.9$  with  
 322 parameter values set as in Table 1). For each disturbance strength and type, the stability metrics of the system  
 323 with PF evolution is compared to those of the system with RF only, in which the foraging trait of consumers is  
 324 monomorphic ( $z = 0$ ) and fixed ( $\partial_z^2 C = 0$ ). For all disturbance types, the disturbance strength is increased until  
 325 the consumer population goes to extinction, in order to compute the maximal disturbance level that the system  
 326 can tolerate.

## 327 5.1 Ecosystem disturbance and constant environmental change

328 In reaction to increasing levels of consumer mortality, the system with PF evolution behaves as the system with  
 329 fixed RF. Indeed, after each increment of mortality the new biomass of consumers is similar; and the consumers  
 330 disappears for the same mortality rate (Figure 4a). Moreover, at each mortality increase, consumers in the  
 331 system with PF evolution gradually reduce their foraging trait, until PF ultimately disappears (color scale in  
 332 Figure 4a). Controlled monomorphic systems having low PF values better tolerate higher mortality rates (Figure  
 333 4b), which indicates that when PF is fixed it has a negative effect on the persistence of consumers facing increases  
 334 in mortality.

335 Turning to the constant environmental change, the system with PF evolution tolerates niche displacement  
 336 better than the system with fixed RF, up to a certain point when it disappears suddenly, earlier than its coun-

337 terpart (Figure 4c). Moreover, as in the case of ecosystem disturbance, the mean PF value decreases for faster  
 338 environmental changes (color scale in Figure 4c). Controlled monomorphic systems having low PF values toler-  
 339 ates faster environmental changes (Figure 4d), which indicates that when PF is fixed it has a negative effect on  
 340 the persistence of consumers facing constant environmental change.

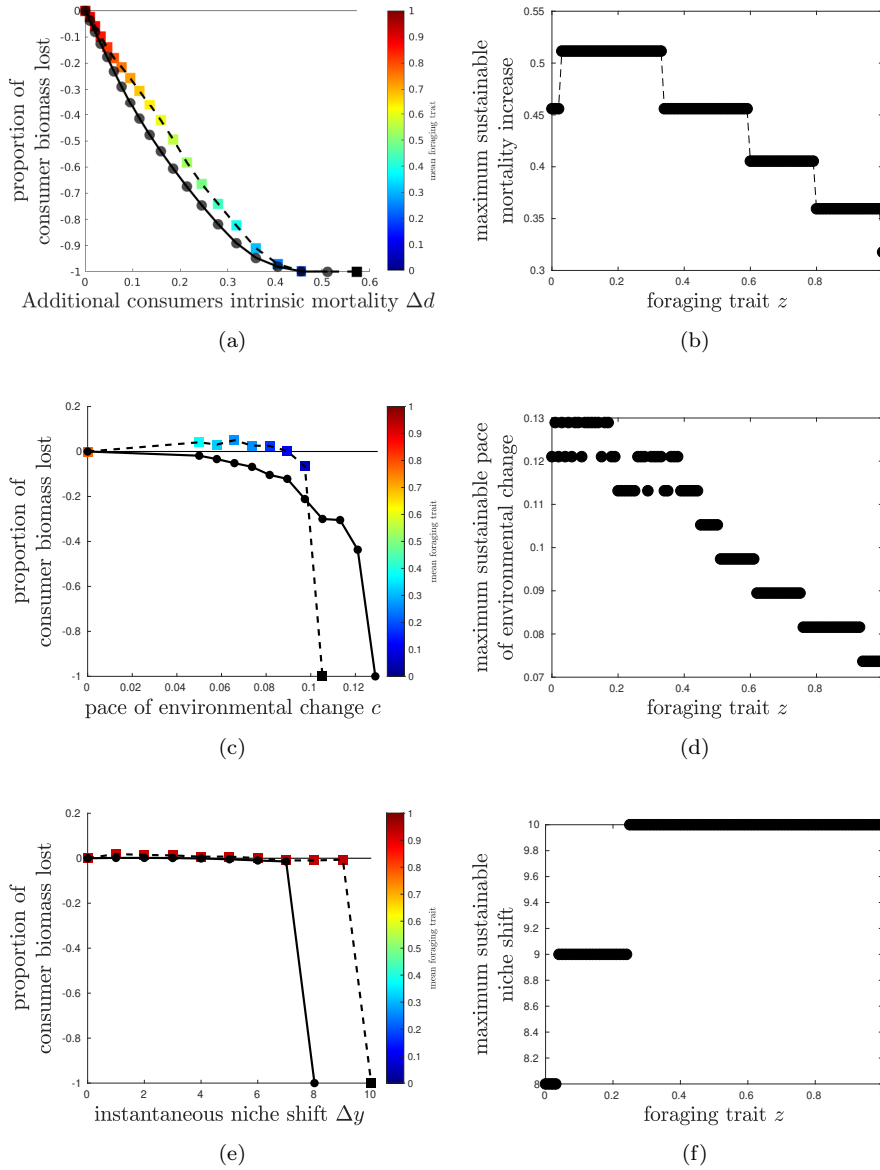


Figure 4: Effect of disturbances: (a, b) increased mortality  $\Delta d$ , (c, d) constant environment change  $c$  and (e, f) instantaneous niche shift  $\Delta y$ . Left column (a, c, e): variations of consumer biomass of systems with and without PF, in function of the intensity of the disturbance. 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 the consumer species. Right column (b, d, f): maximal sustainable mortality for monomorphic consumers, in function of their controlled foraging trait  $z$ .

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

349 In figures 4b and d PF is fixed, but when PF can evolve, it gradually decreases in function of the intensity  
350 of the disturbances (see color scales in Figures 4 a and c). In the case of a particularly fast environmental  
351 change, consumers do not have enough time to reduce their PF searching behaviour and become extinct slightly  
352 earlier (Figure 4c). The constant environmental change creates a lag load to consumers, whose niche traits run  
353 after those of resources; in addition PF imposes a second lag load, corresponding to the time needed for the  
354 evolutionary regression of PF. In the case of ecosystem disturbance, however, since optimal foragers quickly turn  
355 into random foragers, both types of foraging strategies respond in a similar way (Figure 4a). A purely ecological  
356 model ignoring the evolutionary dynamics of PF would have missed the possibility of its evolutionary regression,  
357 and would have therefore overestimated the negative effect of PF on consumer persistence. In the simulations, the  
358 various disturbance types have been applied independently, but in nature they can be combined. In such cases,  
359 ecosystem disturbance and/or constant environmental change might first lead to the evolutionary regression of  
360 the PF behaviour, and a sudden shift might then facilitate the extinction of consumers, since they would not be  
361 protected by PF any more.

## 362 5.2 Sudden environmental change

363 After a sudden environmental change, either consumers disappear or they persist in a new state close to the  
364 original one. In that case their niche traits shift towards the new optimum and their foraging traits remain  
365 unchanged, which is an indication of resilience. The variation of biomass before and after disturbance is therefore  
366 uninformative; instead the maximal sudden environmental change that the consumer can tolerate is used to  
367 quantify its stability (Figure 4e). The system with PF evolution resists to a larger sudden change ( $\delta_y = 10$ )  
368 compared with the system with fixed RF ( $\delta_y = 8$ ). In order to disentangle the direct effect of PF on stability  
369 from its indirect effect through diversity, the PF values of the consumers with PF are set to 0, while retaining  
370 the original diversity of the niche traits  $x$  and  $y$  of both guilds. The resulting hybrid system tolerates a large  
371 environmental change ( $\delta_y = 10$ ), which indicates that the positive effect of PF on the persistence of consumers  
372 is mainly due to its effects on diversity. In line with the above results, controlled monomorphic systems having  
373 high PF values tolerates larger sudden environmental changes (Figure 4d).

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

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

396 In summary, consumer persistence is fostered either by the evolution of PF in the case of a sudden environ-  
397 mental change or by its regression in the cases of ecosystem disturbance and constant environmental change.  
398 This corresponds to a combination of evolutionary rescue (Gonzalez et al., 2013; Kopp and Matuszewski, 2014),  
399 because PF is subject to evolution, and of plastic rescue (Kovach-Orr and Fussmann, 2013), since PF is a type  
400 of phenotypic plasticity.

## 401 6 Assumptions and limitations of the model

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

405 First, in previous works the absence of PF corresponded to a constant interaction matrix between resources  
406 and consumers (e.g. Kondoh, 2003; Valdovinos et al., 2013). Instead, in the present model the alternative to  
407 plastic foraging consists in random foraging, where resources are consumed according to their density. The

408 interaction matrix is therefore highly dynamic for both foraging strategies, although for different reasons. In the  
409 case of RF the resources exploited by a given consumer change according to their abundance only, whereas in  
410 the case of PF they also change according to their traits, the consumer's trait, and their degree of exploitation  
411 by other consumers. In previous models allowing the evolutionary diversification of niche traits, the interaction  
412 matrices were dynamic but consumers did not forage plastically (Loeuille and Loreau, 2005; Allhoff et al., 2015).  
413 In those cases as well as here, new phenotypes constantly appear and need to be incorporated into the food web,  
414 which is therefore inherently dynamic (Appendix A.1). In comparison to RF, a consumer having fixed interaction  
415 coefficients would ignore these new phenotypes even if its favorite resources had gone extinct, which would make  
416 little sense. Besides, PF alone can produce non-equilibrium dynamics even with a fixed community composition,  
417 by triggering consumer-resource cycles (Abrams, 1992; Abrams and Matsuda, 2004).

418 Second, it is assumed that consumers feeding on a single optimal resource have the highest growth rate.  
419 Although this assumption often fits with prey-predator interactions (but see Jensen et al., 2012, for a counter-  
420 example), in the case of plant-herbivore interactions consumers often benefit from resource complementarity  
421 (Abrams, 2010; Unsicker et al., 2008), primarily because of nutrient balancing and toxin dilution (Ibanez et al.,  
422 2012; Behmer and Joern, 2008; Singer et al., 2002). We predict that the inclusion of this feature in the model  
423 would have favored the evolution of PF, since RF strategists mostly consume the most abundant resources,  
424 irrespective of their complementarity.

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

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

## 444 Conclusion

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

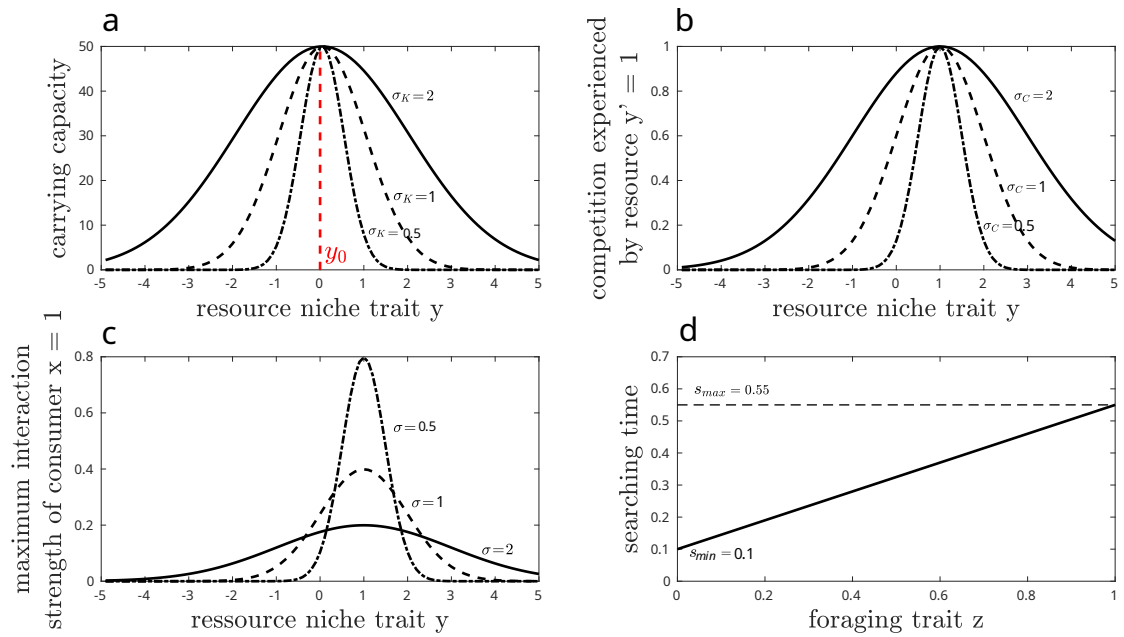


Figure SI.1: a) Carrying capacity  $K(y)$  of resources for various niche width values  $\sigma_K = \{0.5, 1, 2\}$ . The niche centre fixed at  $y_0 = 0$  corresponds to the maximal carrying capacity. b) Competition kernel  $K_{eff}$  for various neighbourhood size  $\sigma_C = \{0.5, 1, 2\}$  between 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.

## 459 A.1 Stationary regime

460 The stationary regime is visible in this simulation of the emergence of a community in which plastic foraging  
 461 evolves: <https://drive.google.com/file/d/1c1nNXJl9aR76FrwFcrJppJbk-Rg7o9tn/view>. The system follows  
 462 a perpetual turnover of resources and consumers densities in function of their niche and foraging traits, but  
 463 the macroscopic criteria of the community (exemplified here by the functional diversity  $FDis$ ) reach a quasi  
 464 equilibrium. Top panels: distribution of resources and consumers in function of their niche trait. Middle panels:  
 465 distribution of consumers in function of their foraging trait (left) and community-level mean foraging trait in  
 466 function of time (right). Bottom panels: functional diversity  $FDis$  of resources and consumers. The other  
 467 community-level characteristics are also stabilized once the stationary regime is reached.

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

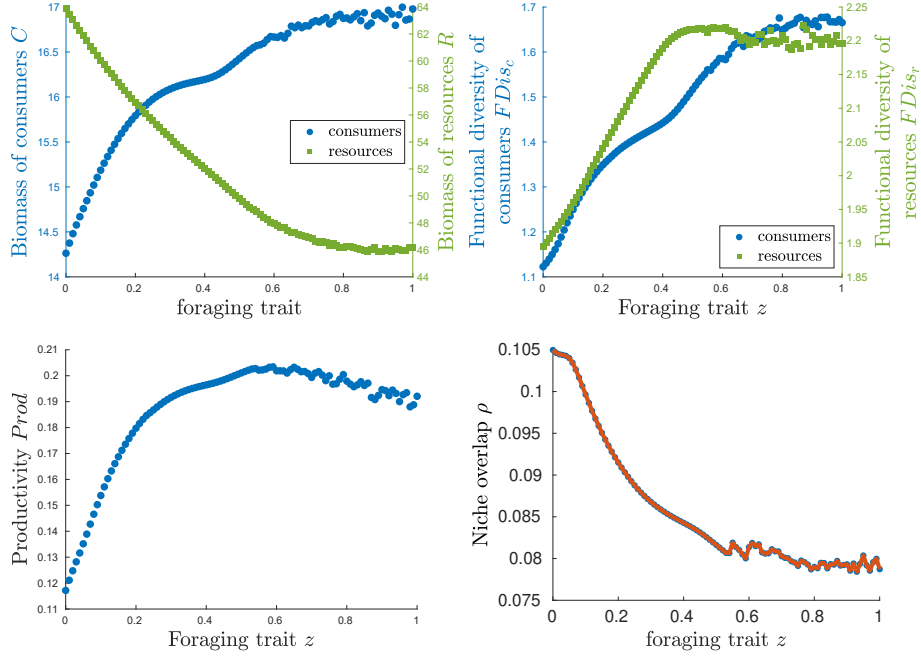


Figure SI.3: Effect of a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

## 469 B Trade-off on mortality

470 Our model assumes a trade-off between PF and handling time. In this case, an increase of the foraging trait  
 471 induces an increases of searching handling time, which eventually induces a reduction of the resource absorption  
 472 rate. More precisely, for a given foraging trait  $z$ , an increase  $\delta z$  of the trait reduces the absorption rate as follows  
 473

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

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

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

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

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

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

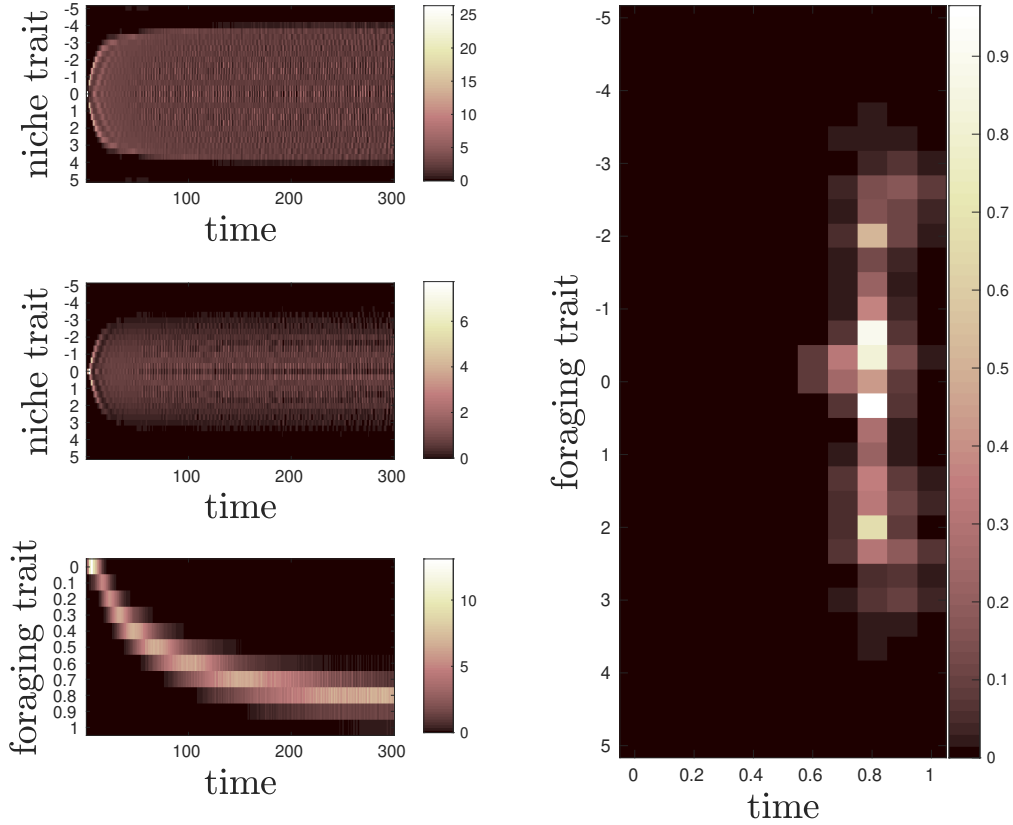


Figure SI.4: Distribution of resources and consumers over time with a quartic competition kernel between resources  $K_{eff}(y) = K_0 \exp(-y^4/(12\sigma_K^4))$ . a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. 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).



483 B.2 Effect of mortality trade-off with a fixed PF trait

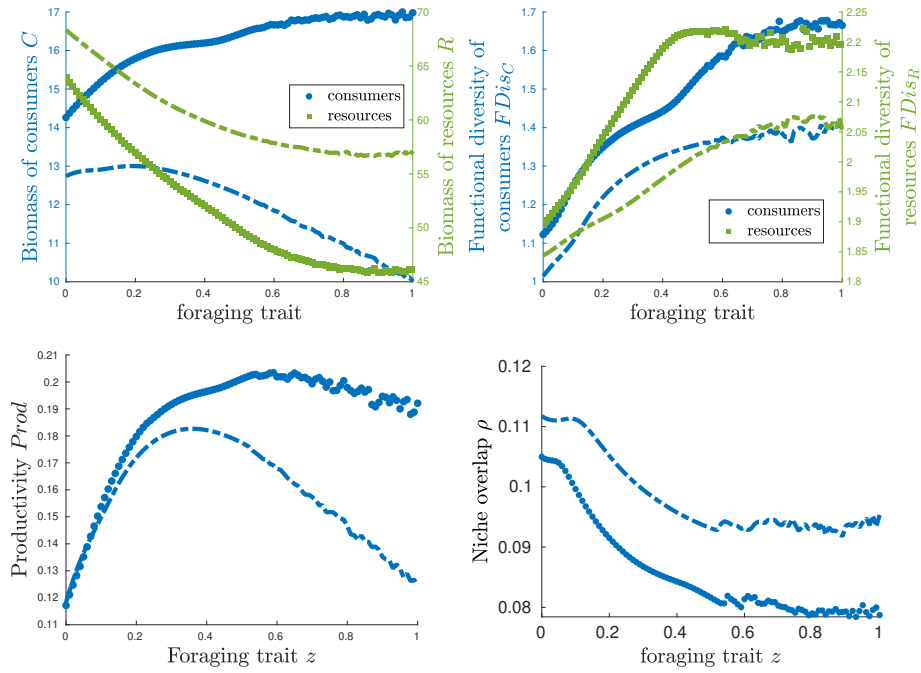


Figure SI.5: Effect of the competition kernel  $K_{eff}$  with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two competition kernel: Gaussian kernel  $K_{eff}(y) = K_0 \exp(-y^2/(2\sigma_K^2))$  (dotted markers) and Quartic kernel  $K_{eff}(y) = K_0 \exp(-y^4/(12\sigma_K^4))$  (dashed curves). The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

484 C Effect of a quartic carrying capacity functions

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

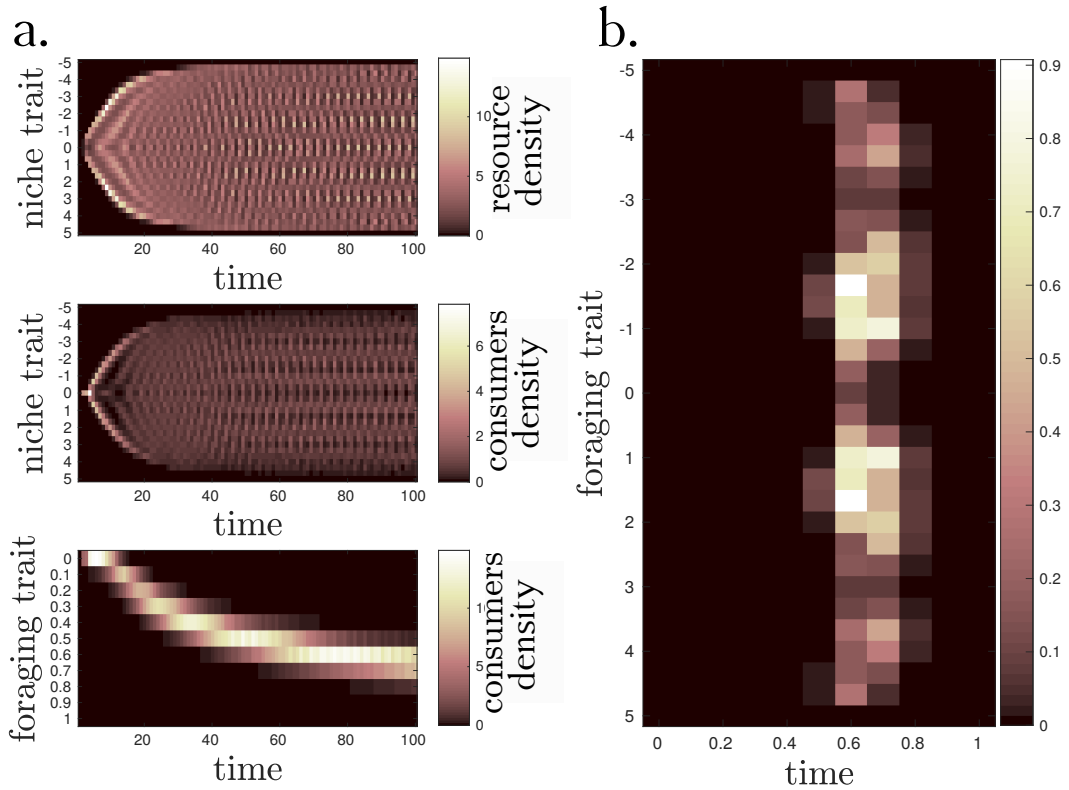


Figure SI.6: Distribution of resources and consumers over time with a quartic competition kernel between resources  $K_{eff}(y) = K_0 \exp(-y^4/(12\sigma_K^4))$ . a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. 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).

486 C.2 Effect of a quartic carrying capacity function with a fixed PF trait

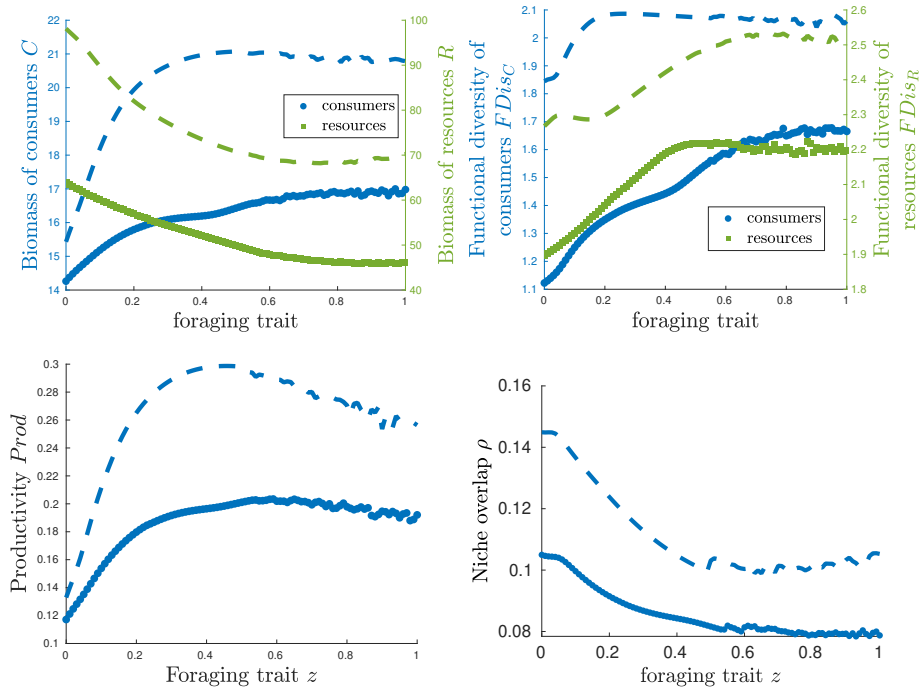


Figure SI.7: Effect of the competition kernel  $K_{eff}$  with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two competition kernel: Gaussian kernel  $K_{eff}(y) = K_0 \exp(-y^2/(2\sigma_K^2))$  (dotted markers)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

### C.3 Effect of a quartic carrying capacity function with an evolving PF trait

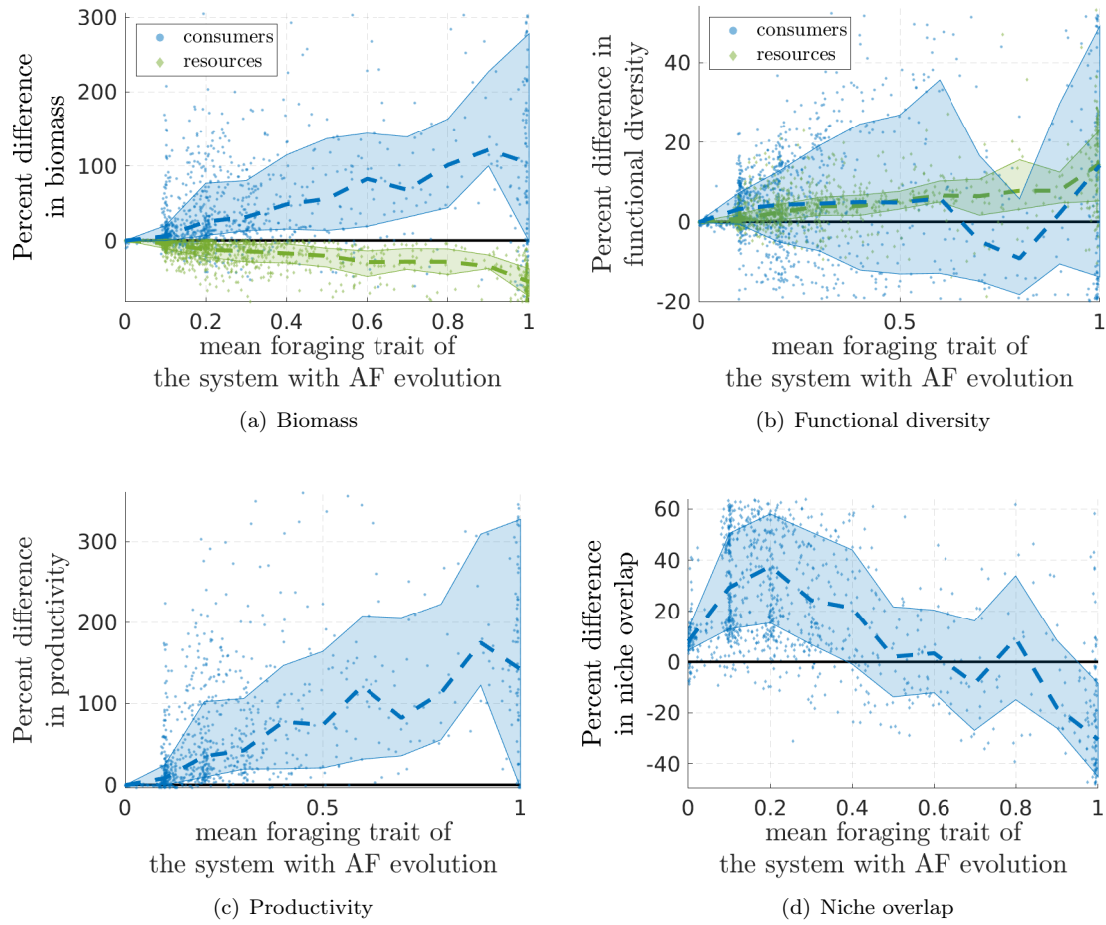


Figure SI.8: Difference (in %) between systems with PF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

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

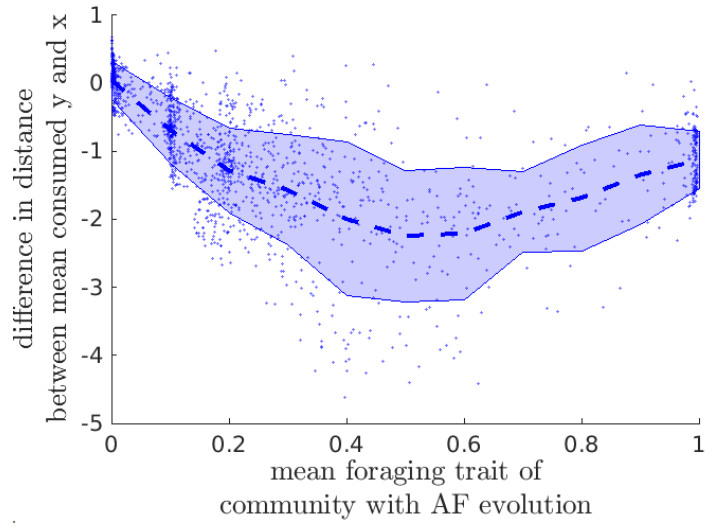


Figure SI.9: Difference in functional matching between systems with PF evolution and systems with fixed RF. 500 pairs of systems were compared, each pair having the same parameter set randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

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)
$\mathbf{R}(t)$	Total resource biomass	$\mathbf{R}(t) = \int R(t, y) dy$
$\bar{y}(t)$	Mean resource trait	$\bar{y}(t) = \int y \frac{R(t, y)}{\mathbf{R}(t)} dy$
$C(t, x, z)$	Consumer density with foraging trait $z$	see Eq. (2)
$\bar{C}(t, x)$	Consumer biomass with trait $x$	$\bar{C}(t, x) = \int C(t, x, z) dz$
$\mathbf{C}(t)$	Total consumer biomass	$\mathbf{C}(t) = \iint C(t, x, z) dx dz$
$\bar{x}(t)$	Mean consumer niche trait	$\bar{x}(t) = \int x \frac{\bar{C}(t, x)}{\mathbf{C}(t)} dx$
$\bar{z}(t)$	Mean foraging trait	$\bar{z}(t) = \iiint z \frac{C(t, x, z)}{\mathbf{C}(t)} dx dz$
$\phi_{RF}(t, y)$	Random Foraging efforts	$\phi_{RF}(t, y) = \frac{R(t, y)}{\mathbf{R}(t)}$
$\phi_{PF}(t, x, y, z)$	Relative Foraging efforts	see Eq. (??)
$\phi(t, x, y, z)$	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	$K(y) = K_0 \frac{e^{-\frac{y^2}{2\sigma_K^2}}}{\sqrt{2\pi\sigma_K^2}}$
$K_{eff}(y)$	Competition strength	$K_{eff}(y) = \frac{e^{-\frac{y^2}{2\sigma_C^2}}}{\sqrt{2\pi\sigma_C^2}}$
$r_{eff}(t, y)$	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	$FDis_C(t) = \int \frac{ x - \bar{x}(t)  \bar{C}(t, x)}{\int \bar{C}(t, x) dx} dx$
$Prod$	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.

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