

# 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? In other words: is adaptive foraging itself 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

90 relationship holds when both PF and the functional traits of consumers and resources are subject to evolutionary  
 91 dynamics. In this eco-evolutionary context, it is uncertain whether the evolution of PF stabilises communities  
 92 directly, **by altering food-web structure** or indirectly, through its effects on functional diversity.

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

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

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

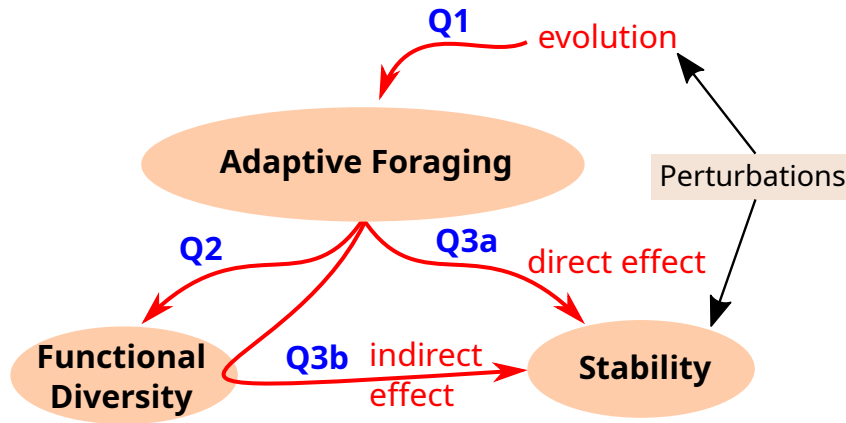


Figure 1: Overview of the main questions: (Q1) Under which ecological conditions does PF evolve? (Q2) Does the evolution of PF increases the diversity of traits involved in the resource-consumer interaction? (Q3) Does the evolution of PF enhances the stability of the resource-consumer system, either 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  $t$ . Although these rates vary with the consumers foraging efforts  $\phi$ , On the other hand, they vary with~~ ~~effectively depend on~~ 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:

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

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

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  $I$ .~~ ~~competition at a rate  $IC$  where  $\mathbf{C}(t) = \iint C(t, x, z) dx dz$  is the total biomass of consumer and  $I$  the intraspecific competition between consumers for other limiting factors than resources.~~

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

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

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

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

## 151 2.2 Foraging strategies and plasticadaptive foraging trait.

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

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

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

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

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

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

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

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

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

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

~~However, the macroscopic characteristics (functional dispersion, total biomass, productivity, niche overlap and average foraging behavior) stabilized around a steady state; these characteristics will therefore be used to assess the effect of PF evolution on the resource-consumer system.~~

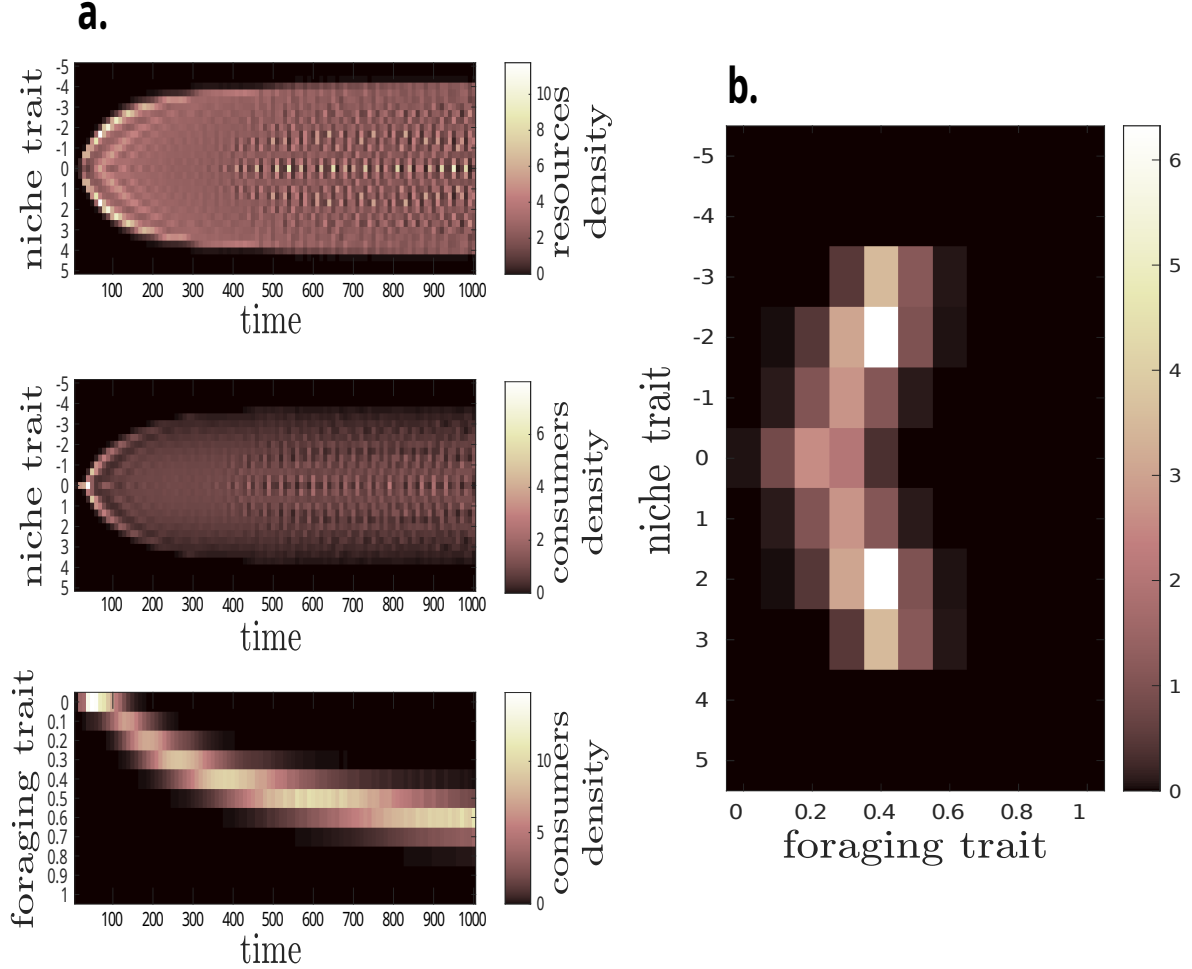


Figure 2: a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer densities  $\int C(t, x, z) dz$ . Bottom panel: foraging trait  $\int C(t, x, z) dx$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

~~The PRCC analysis revealed that the six tested parameters played a significant role in the evolution of PF (Table 1 last column). The conditions favouring the evolution of PF (measured by  $\bar{z}(t)$ ) were essentially the following: a consumers ability to exploit a wide range of resources (large  $\sigma$ , correlation coefficient 0.28), a wide niche for resources (large  $\sigma_K$ , correlation coefficient 0.38), a weak trade-off between PF and searching time (small  $s_{max}$ , correlation coefficient -0.64), a high consumer mortality  $d$  (correlation coefficient 0.13), a strong competition between consumers (large  $I$ , correlation coefficient 0.13) and a high resource growth (large  $g$ ; correlation coefficient 0.11).~~

**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

226 Plessis et al., 2012; Van de Ven et al., 2019) and time budget (Randolph and Cameron, 2001; Fortin et al., 2004).  
227 In the present model the trade-off is only incorporated into the handling time of the type II functional response,  
228 where high handling times reduce resource absorption rates. If the PF strategy had increased mortality  $d$  instead  
229 of handling time, this would have also reduced resource absorption (see Appendix B for a formal derivation of  
230 the model). A trade-off between PF and mortality therefore provided similar results (Fig. SI.4 and SI.5). We are  
231 nevertheless confident that similar results would have been obtained if the trade-off had concerned mortality.

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

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

## 254 4 The effects of PF evolution on community properties

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

### 262 4.1 Effects on biomass

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

268 When the evolution of PF produce consumer populations with a high mean foraging trait  $\bar{z}$ , the resource  
269 biomass is reduced (e.g. -50% when  $\bar{z} = 1$ ) while the consumer biomass increased by 25% on average (Figure  
270 3a). Following the evolution of PF, the functional complementarity and diversity of consumers increase their  
271 biomass at the expense of resources (Figure 3a). This fits with empirical studies showing a relationship between  
272 resource consumption and consumer diversity (Deraison et al., 2015; Lefcheck et al., 2019; Milotić et al., 2019).  
273 However, the variability of the consumer biomass among simulations also increases with  $\bar{z}$ . This pattern has also  
274 been observed when the foraging trait  $z$  of a monomorphic population without PF evolution is increased (Figure  
275 SI.3a).



## 276 4.2 Effects on functional diversity

277 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:

$$278 FDis_R(t) = \int \frac{|y - \bar{y}(t)|R(t, y)}{\int R(t, y)dy} dy \quad \text{and} \quad FDis_C(t) = \int \frac{|x - \bar{x}(t)|\bar{C}(t, x)}{\int \bar{C}(t, x)dx} dx \quad (14)$$

279 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  
280 and  $\bar{C}(t, x) = \int C(t, x, z)dz$  is the biomass of individuals carrying the trait  $x$  in the consumers population.

281 The evolution of PF increases functional dispersion of both resources and consumers (Figure 3b). When the  
282 average foraging trait value is large the consequences on diversity indices becomes heterogeneous, but the effect  
283 of PF is almost always positive. The increase in functional diversity is due to an eco-evolutionary loop between  
284 resources and consumers situated at the niche edge. Following the evolution of PF some consumers forage at  
285 the niche edge, thereby reducing the density of the corresponding resources. This decreases competition among  
286 these resources and promotes the emergence of new resource phenotypes at the niche edge. The diversification  
287 of resources triggered the apparition of consumers standing even further away from the niche centre, and so  
288 on until the resources reached the limits of the exploitable niche. This emphasizes that adaptive phenotypic  
289 plasticity like PF can subsequently fuel evolutionary change (Baldwin, 1896; Crispo, 2007; Laland et al., 2014).  
290 Instead, when no PF evolution is introduced, the few resources standing far away from the niche centre are barely  
291 used by consumers, which can not forage preferentially on them. This prevents the emergence of new resources  
292 further away from the niche centre, due to competition between resources. Since the evolution of PF occurs when  
293 the diversity of resources is initially large enough (large  $\sigma_K$ ), causation is reciprocal: PF both promotes and is  
294 promoted by resource diversity.

## 295 4.3 Effects on productivity

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

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

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

299 The relationship with productivity (i.e the flow of biomass from resources to consumers) is non-linear (Figure  
300 3c). When the system with PF evolution has a rather low mean foraging trait ( $0 < \bar{z} < 0.4$ ) productivity increases  
301 in comparison to the system without PF. This occurs thanks to functional complementarity between consumers  
302 (Poisot et al., 2013). However, when  $\bar{z}$  is above 0.4, the productivity gain does not change on average, because  
303 consumers with high foraging trait impact resources too heavily. ~~However, when  $\bar{z}$  is above 0.4, the productivity gain becomes smaller and even vanishes when  $\bar{z}$  equalled 1, because consumers impact resources too heavily.~~  
304 Strong PF also increases the variability of productivity; among the systems with strong PF some have large gains  
305 of productivity and others ~~small gains or even small deficits. large deficits.~~  
306

## 307 4.4 Effects on niche overlap and functional match

308 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  
309 the correlation coefficient  $\rho_{ij}$  of their resource absorption:

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

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

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

313 The evolution of PF also decreases the niche overlap between consumers by about 30% when the mean foraging  
314 trait is close to 1 (Figure 3d), and increases the functional match between the niche trait of consumers  
315 and the mean niche trait of their resources (Figure SI.9). PF also decreased niche overlap between pollinators in  
316 the model of Valdovinos et al. (2013) and in the empirical studies of Fontaine et al. (2006) and Brosi and Briggs  
317 (2013). At the intraspecific level, niche overlap between individuals of the same species decreased in function of  
318 their abundance (Svanbäck and Bolnick, 2007; Tur et al., 2014). Short-term experimental time scales suggest this

319 pattern was caused by plastic behavior (Svanbäck and Bolnick, 2007), although in the long-term this pattern may  
 320 also be due to genetic diversification. Since abundance favors intraspecific competition, this is consistent with  
 321 our findings that competition between consumers promotes the evolution of PF. The decrease of niche overlap  
 322 between consumers corresponds to niche partitioning, which may favor their coexistence (Behmer and Joern,  
 323 2008; Turcotte and Levine, 2016).  
 324

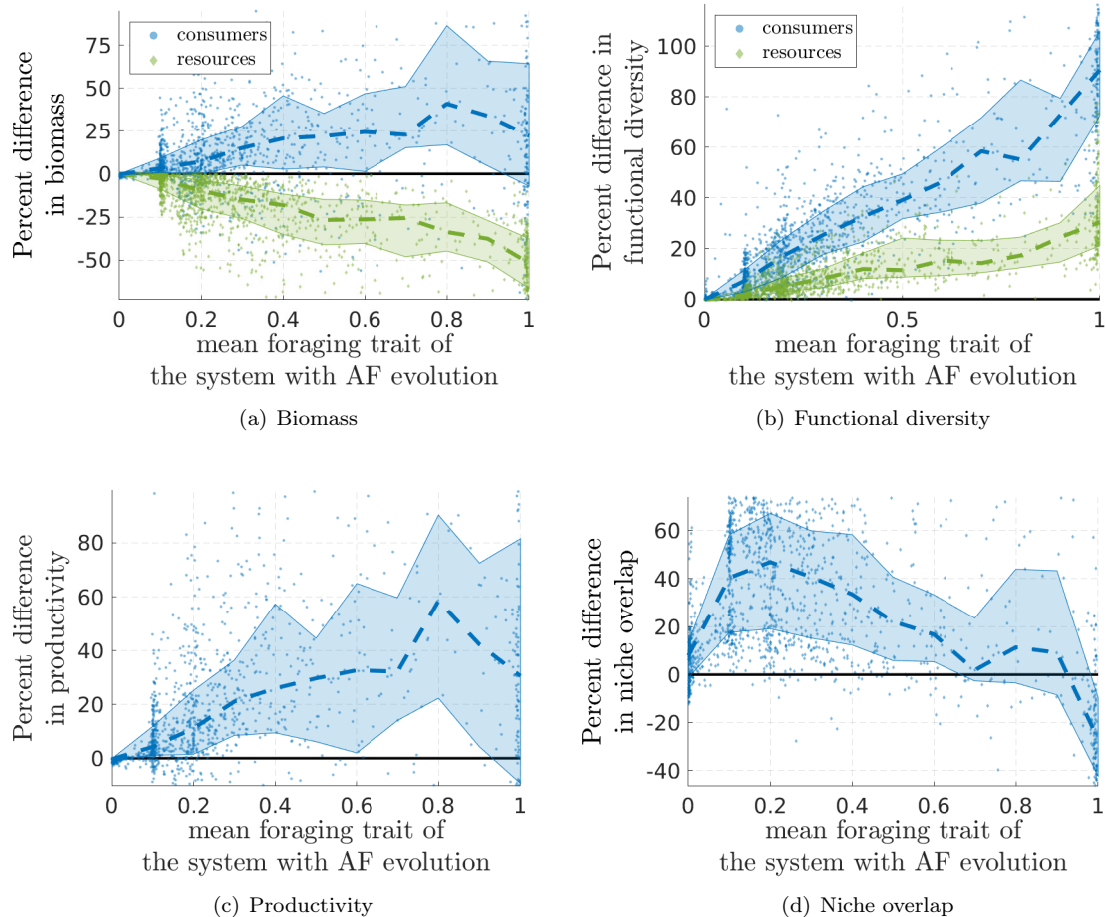


Figure 3: Difference (in %) between systems with PF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly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

## 325 5 The effects of PF on consumer persistence

326 To understand whether the evolution of PF can rescue consumers from environmental changes, three specific  
 327 disturbances are considered: a sudden environmental change where the center of the resource niche is instanta-  
 328 neously shifted at a distance  $\Delta y$  from the initial niche center (e.g. Domínguez-García et al., 2019), an ecosystem  
 329 disturbance where consumer mortality  $d$  increases gradually by  $\Delta d$ , and a constantly changing environment,  
 330 where the niche center is displaced at constant speed  $c$ . The mutation process driving the diversification of  
 331 resources and consumers in the system should help to recover trait diversity after a disturbance. To assess the  
 332 effects of those disturbances on the resource-consumer system, the proportion of consumer biomass lost after the  
 333 disturbance is calculated once a new equilibrium is reached. The difference in the mean foraging trait before and  
 334 after each disturbance is also measured.

335 The resource-consumer system is initialized with consumers carrying a high mean PF trait ( $\bar{z} \approx 0.9$  with  
 336 parameter values set as in Table 1). For each disturbance strength and type, the stability metrics of the system  
 337 with PF evolution is compared to those of the system with RF only, in which the foraging trait of consumers is  
 338 monomorphic ( $z = 0$ ) and fixed ( $\partial_z^2 C = 0$ ). For all disturbance types, the disturbance strength is increased until

339 the consumer population goes to extinction, in order to compute the maximal disturbance level that the system  
340 can tolerate.

## 341 5.1 Ecosystem disturbance and constant environmental change

342 In reaction to increasing levels of consumer mortality, the system with PF evolution behaves as the system with  
343 fixed RF. Indeed, after each increment of mortality the new biomass of consumers is similar; and the consumers  
344 disappears for the same mortality rate (Figure 4a). Moreover, at each mortality increase, consumers in the  
345 system with PF evolution gradually reduce their foraging trait, until PF ultimately disappears (color scale in  
346 Figure 4a). Controlled monomorphic systems having low PF values better tolerate higher mortality rates (Figure  
347 4b), which indicates that when PF is fixed it has a negative effect on the persistence of consumers facing increases  
348 in mortality.

349 Turning to the constant environmental change, the system with PF evolution tolerates niche displacement  
350 better than the system with fixed RF, up to a certain point when it disappears suddenly, earlier than its coun-  
351 terpart (Figure 4c). Moreover, as in the case of ecosystem disturbance, the mean PF value decreases for faster  
352 environmental changes (color scale in Figure 4c). Controlled monomorphic systems having low PF values toler-  
353 ates faster environmental changes (Figure 4d), which indicates that when PF is fixed it has a negative effect on  
354 the persistence of consumers facing constant environmental change.

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

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

## 376 5.2 Sudden environmental change

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

388 Previous theoretical studies have shown that PF can stabilize food-webs by favoring **more robust** topologies  
389 able to buffer environmental disturbances (Kondoh, 2003; Heckmann et al., 2012), **but in the present model such**  
390 **inherently robust topologies have not been observed.** Instead, the mechanisms responsible for **the stabilising**  
391 **effect of PF** rely on the dynamical nature of the interaction webs produced by PF, which is caused both by a  
392 direct effect of PF (Question 3a), and by an indirect effect through diversity (Question 3b), as detailed above.  
393 The direct effect of PF on consumer persistence relies on the mitigation of the lag load faced by consumers.  
394 Indeed, resources become adapted to the new niche center more quickly than consumers, which suffer from a  
395 trait mismatch (e.g. Post and Forchhammer, 2008; Miller-Struttman et al., 2015; Damien and Tougeron, 2019).  
396 This indicates that phenotypic plasticity acts as a rapid response mechanism to environmental change (Fox et al.,  
397 2019), in that case. Since random foragers consume the most abundant resources (but not the most suitable),

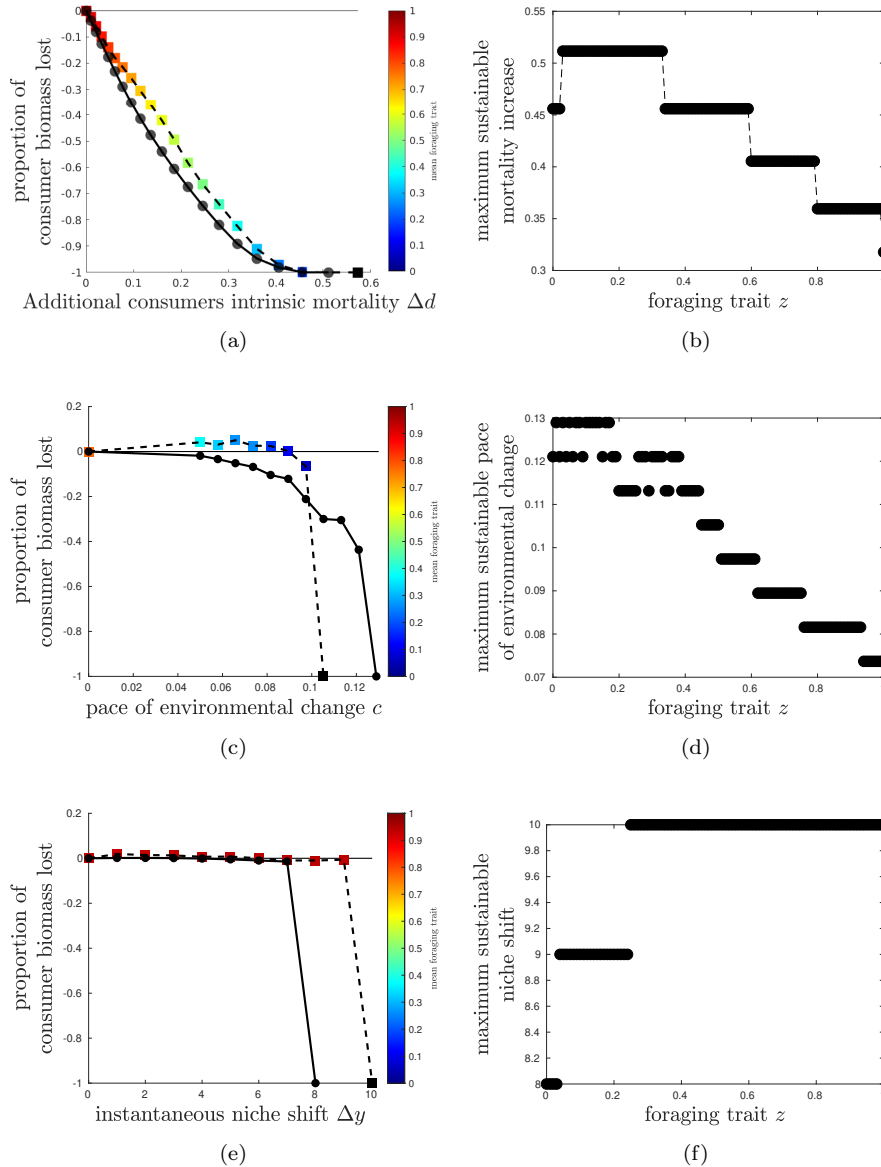


Figure 4: Effect of disturbances: (a, b) increased mortality  $\Delta d$ , (c, d) constant environment change  $c$  and (e, f) instantaneous niche shift  $\Delta y$ . Left column (a, c, e): variations of consumer biomass of systems with and without PF, in function of the intensity of the disturbance.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

398 after a sudden niche shift they feed on sub-optimal resources, which hamper their resilience to environmental  
 399 change. In contrast plastic foragers select less abundant but more suitable resources, which favor their survival.  
 400 In the meantime their traits evolve towards the new niche optimum and ultimately catch up the resources, which  
 401 illustrates that adaptive plasticity can promote persistence in new environmental conditions (Ghalambor et al.,  
 402 2007).

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

410 the niche shift.

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

## 416 6 Assumptions and limitations of the model

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

420 First, in previous works the absence of PF corresponded to a constant interaction matrix between resources  
421 and consumers (e.g. Kondoh, 2003; Valdovinos et al., 2013). Instead, in the present model the alternative to plastic  
422 foraging consists in random foraging, where resources are consumed according to their density. The interaction  
423 matrix is therefore highly dynamic for both foraging strategies, although for different reasons. In the case of  
424 RF the resources exploited by a given consumer change according to their abundance only, whereas in the case  
425 of PF they also change according to their traits, the consumer’s trait, and their degree of exploitation by other  
426 consumers. In previous models allowing the evolutionary diversification of niche traits, the interaction matrices  
427 were dynamic but consumers did not forage plastically adaptively (Loeuille and Loreau, 2005; Allhoff et al.,  
428 2015). In those cases as well as here, new phenotypes constantly appear and need to be incorporated into the  
429 food web, which is therefore inherently dynamic (Appendix A.1). In comparison to RF, a consumer having fixed  
430 interaction coefficients would ignore these new phenotypes even if its favorite resources had gone extinct, which  
431 would make little sense. Besides, PF alone can produce non-equilibrium dynamics even with a fixed community  
432 composition, by triggering consumer-resource cycles (Abrams, 1992; Abrams and Matsuda, 2004).

433 Second, it is assumed that consumers feeding on a single optimal resource have the highest growth rate.  
434 Although this assumption often fits with prey-predator interactions (but see Jensen et al., 2012, for a counter-  
435 example), in the case of plant-herbivore interactions consumers often benefit from resource complementarity  
436 (Abrams, 2010; Unsicker et al., 2008), primarily because of nutrient balancing and toxin dilution (Ibanez et al.,  
437 2012; Behmer and Joern, 2008; Singer et al., 2002). We predict that the inclusion of this feature in the model  
438 would have favored the evolution of PF, since RF strategists mostly consume the most abundant resources,  
439 irrespective of their complementarity.

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

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

## 459 Conclusion

460 The present model illustrates how phenotypic plasticity can be simultaneously a result and a factor of evolution.  
461 On the one hand, plastic foraging (PF) evolves by natural selection acting on consumers. On the other hand, it  
462 stimulates the diversification of ecological characters not only of consumers but also of resources, stressing that  
463 phenotypic plasticity can have far-reaching evolutionary consequences at the community-level (Fordyce, 2006).  
464 Moreover, functional diversity itself promotes the evolution of PF, creating an eco-evolutionary feedback loop  
465 between phenotypic plasticity, natural selection and community composition. This has intricate consequences on  
466 the response of the resource-consumer community to disturbances. In the case of sudden environmental change,  
467 the evolution of PF has a positive effect on community stability, partly via its effects on functional diversity.

468 However for other disturbance types like constant change and increases in mortality, the PF behavior is less  
 469 fit than random foraging and therefore declines. In contrast to previous studies, these results stress that the  
 470 relationship between PF and community stability depends on the type of the disturbance as well as on the  
 471 evolutionary dynamics of PF itself.

## 472 Appendix

### 473 A Model details

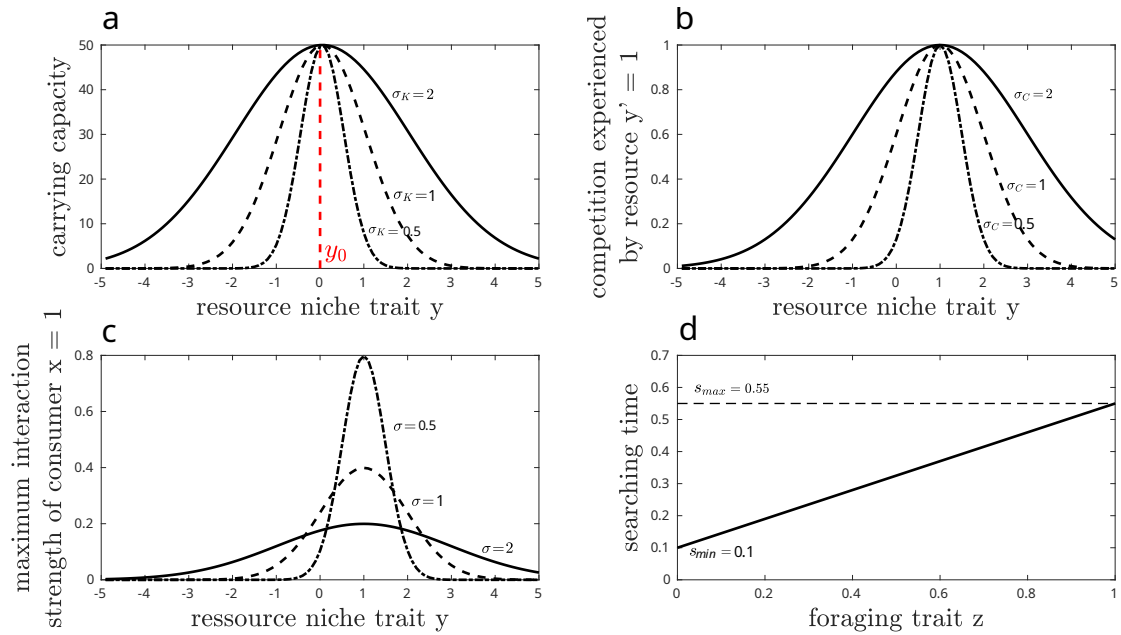


Figure SI.1: a) Carrying capacity  $K(y)$  of resources for various niche width values  $\sigma_K = \{0.5, 1, 2\}$ . The niche centre fixed at  $y_0 = 0$  corresponds to the maximal carrying capacity. b) Competition kernel  $K_{eff}$  for various neighbourhood size  $\sigma_C = \{0.5, 1, 2\}$  between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

## 474 A.1 Stationary regime

475 The stationary regime is visible in this simulation of the emergence of a community in which plastic foraging  
 476 evolves: <https://drive.google.com/file/d/1c1nNXJl9aR76FrwFcrJppJbk-Rg7o9tn/view>. The system follows  
 477 a perpetual turnover of resources and consumers densities in function of their niche and foraging traits, but  
 478 the macroscopic criteria of the community (exemplified here by the functional diversity  $FD_{is}$ ) reach a quasi  
 479 equilibrium. Top panels: distribution of resources and consumers in function of their niche trait. Middle panels:  
 480 distribution of consumers in function of their foraging trait (left) and community-level mean foraging trait in  
 481 function of time (right). Bottom panels: functional diversity  $FD_{is}$  of resources and consumers. The other  
 482 community-level characteristics are also stabilized once the stationary regime is reached.

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

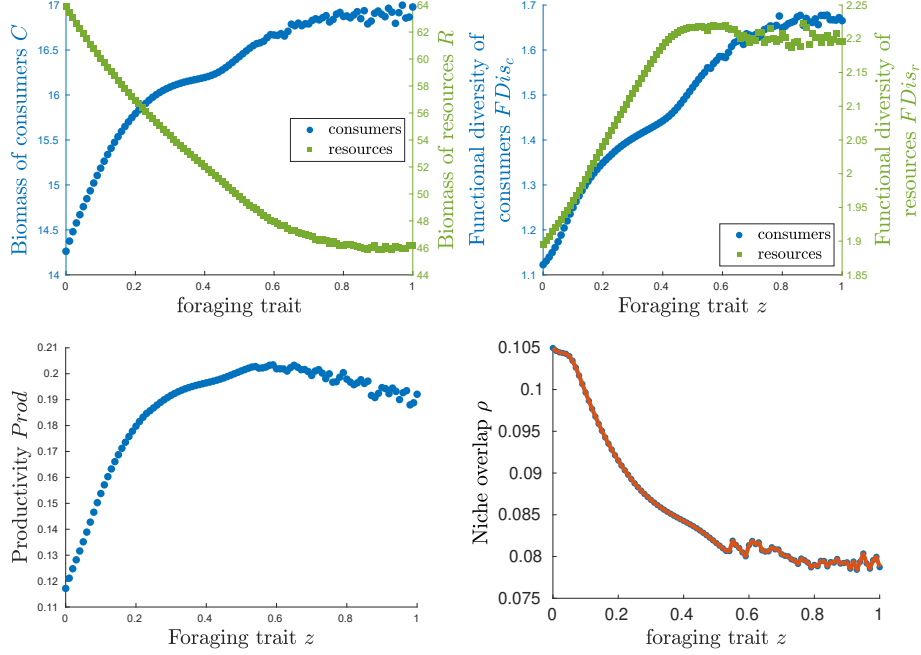


Figure SI.3: Effect of a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

## 484 B Trade-off on mortality

485 Our model assumes a trade-off between PF and handling time. In this case, an increase of the foraging trait  
 486 induces an increases of searching handling time, which eventually induces a reduction of the resource absorption  
 487 rate. More precisely, for a given foraging trait  $z$ , an increase  $\delta z$  of the trait reduces the absorption rate as follows  
 488

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

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

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

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

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

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

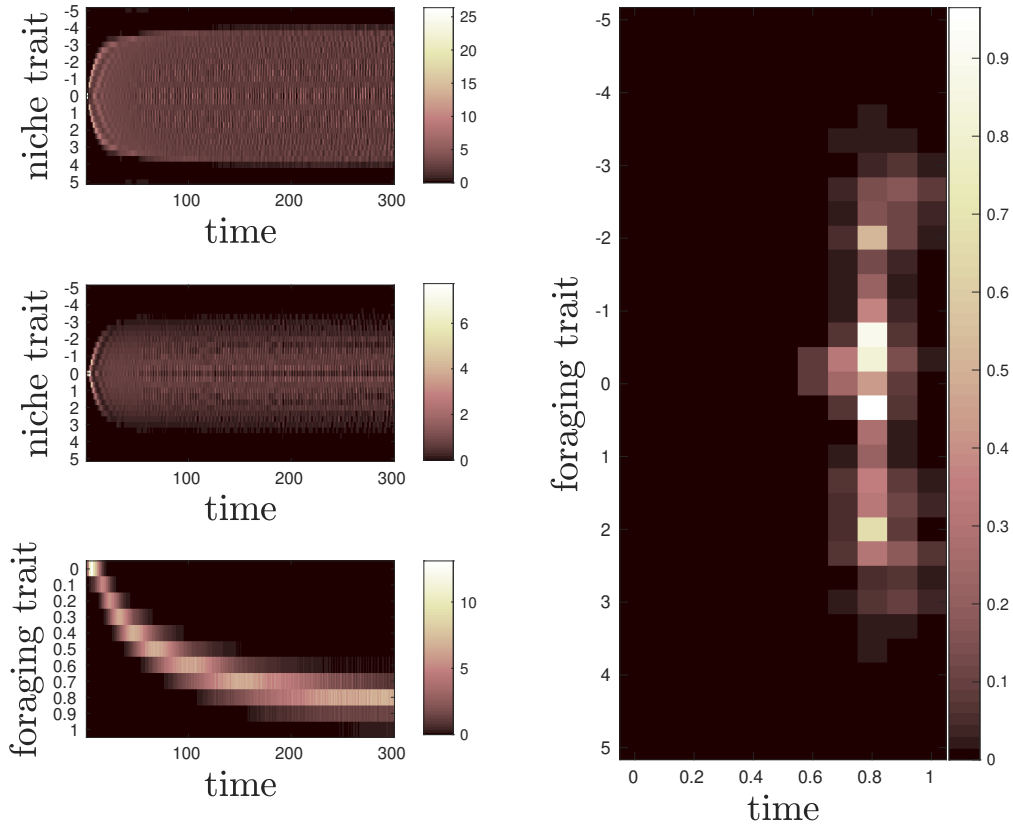


Figure SI.4: Distribution of resources and consumers over time with a trade-off on mortality. a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities  $R(t, y)$ . Middle panel: consumer 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).



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

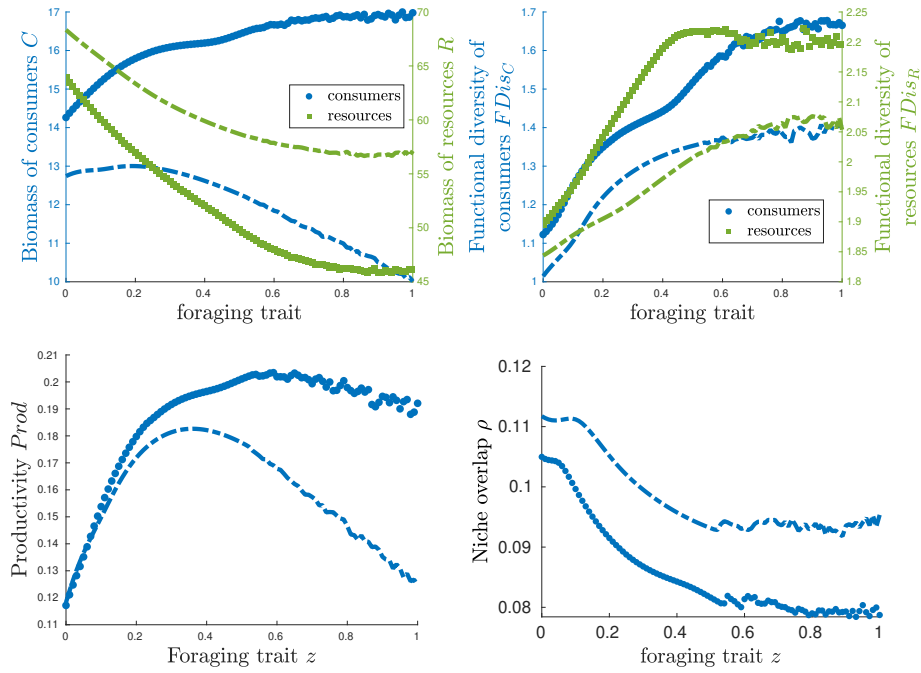


Figure SI.5: Effect of the competition kernel  $K_{eff}$  with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two competition kernel: Gaussian kernel  $K_{eff}(y) = K_0 \exp(-y^2/(2\sigma_K^2))$  (dotted markers) 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.

499 C Effect of a quartic carrying capacity functions

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

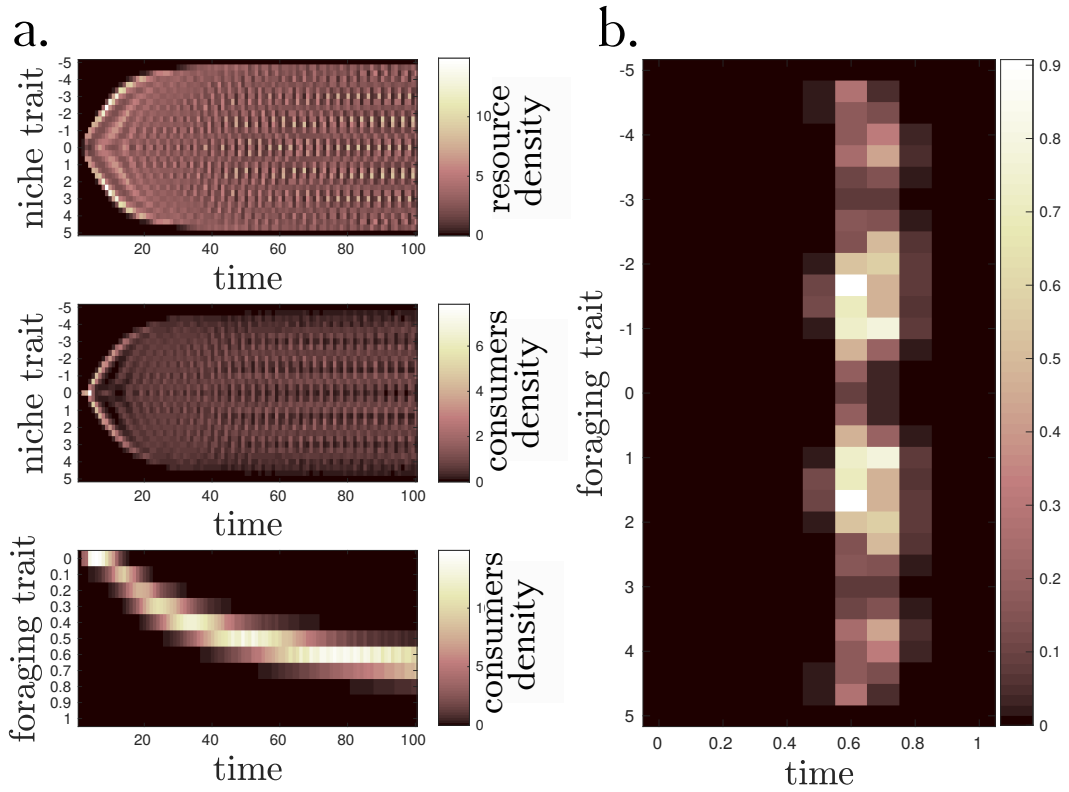


Figure SI.6: Distribution of resources and consumers over time with a quartic competition kernel between resources  $K_{\epsilon(y)} = K_0 \exp(-y^4/(12\sigma_K^4))$ . a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy.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

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

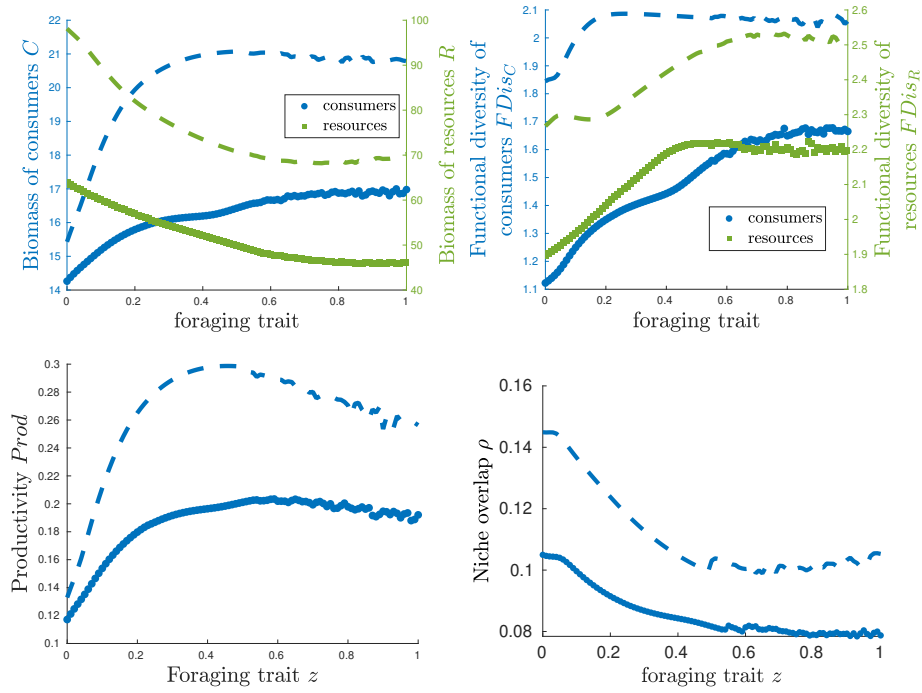


Figure SI.7: Effect of the competition kernel  $K_{eff}$  with a fixed foraging trait value  $z$  on systems where only the niche traits  $x$  and  $y$  of resources and consumers can evolve. We compare two competition kernel: Gaussian kernel  $K_{eff}(y) = K_0 \exp(-y^2/(2\sigma_K^2))$  (dotted markers) 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

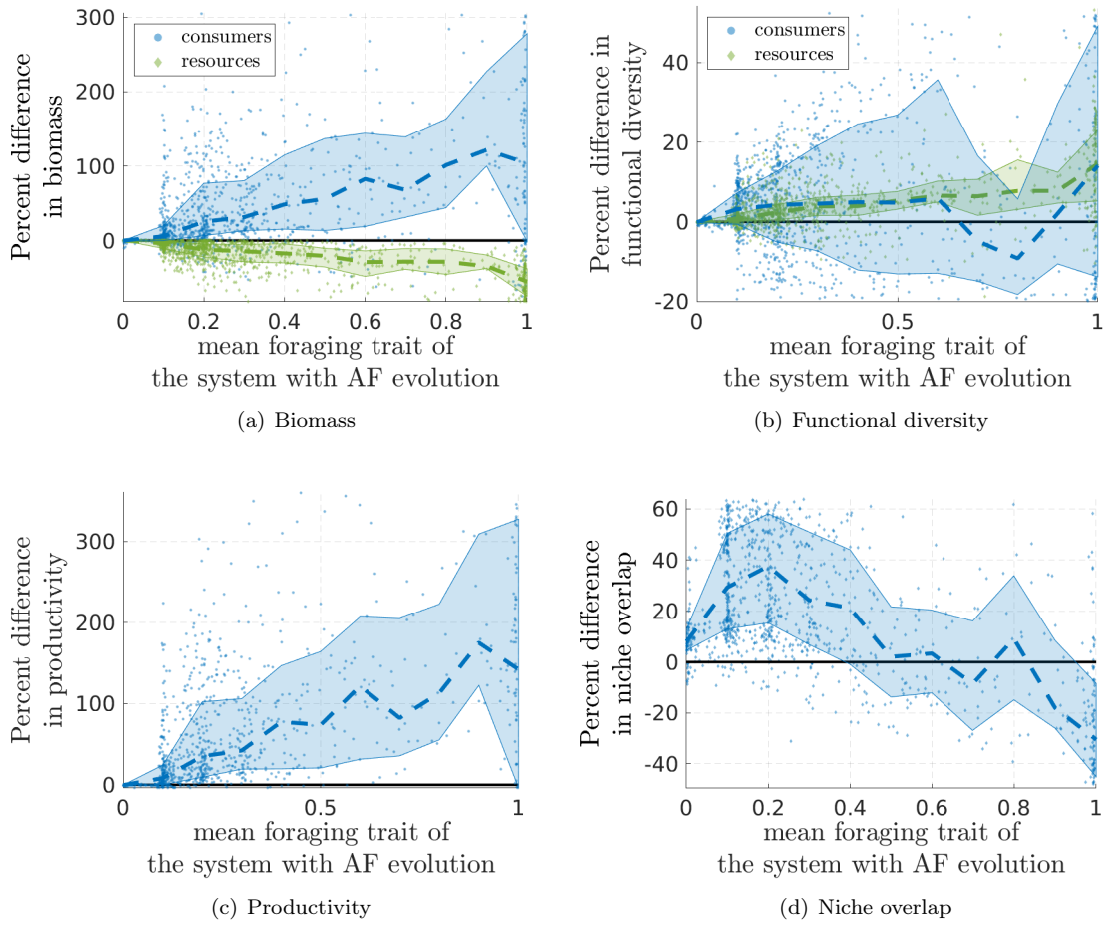


Figure SI.8: Difference (in %) between systems with PF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with PF evolution were compared to simulations with fixed RF, the parameters being randomly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

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

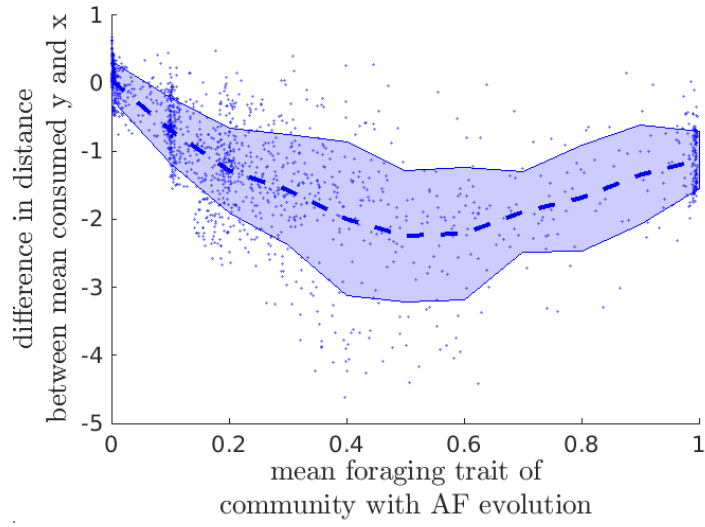


Figure SI.9: Difference in functional matching between systems with PF evolution and systems with fixed RF. 500 pairs of systems were compared, each pair having the same parameter set randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

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 <a href="#">resource uptake gain</a> 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.

## References

- 504  
505 P.A. Abrams. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology*, 6(1):  
506 56–72, 1992. doi: 10.1007/BF02285334.
- 507 P.A. Abrams. Can adaptive evolution or behaviour lead to diversification of traits determining a trade-off between  
508 foraging gain and predation risk? *Evolutionary Ecology Research*, 5(5):653–670, 2003.
- 509 P.A. Abrams. Implications of flexible foraging for interspecific interactions: Lessons from simple models. *Func-*  
510 *tional Ecology*, 24(1):7–17, 2010. doi: 10.1111/j.1365-2435.2009.01621.x.
- 511 P.A. Abrams and H. Matsuda. Consequences of behavioral dynamics for the population dynamics of predator-prey  
512 systems with switching. *Population Ecology*, 46(1):13–25, 2004. doi: 10.1007/s10144-003-0168-2.
- 513 K.T. Allhoff, D. Ritterskamp, B.C. Rall, B. Drossel, and C. Guill. Evolutionary food web model based on body  
514 masses gives realistic networks with permanent species turnover. *Scientific Reports*, 5(1):10955, 2015. doi:  
515 10.1038/srep10955.
- 516 F. Altermatt. Tell me what you eat and I’ll tell you when you fly: Diet can predict phenological changes in  
517 response to climate change: Phenological change and diet breadth. *Ecology Letters*, 13(12):1475–1484, 2010.  
518 doi: 10.1111/j.1461-0248.2010.01534.x.
- 519 J.M. Baldwin. A new factor in evolution. *The american naturalist*, 30(354):441–451, 1896.
- 520 J.S. Bale, G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse,  
521 J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press,  
522 I. Symrnioudis, A.D. Watt, and J.B. Whittaker. Herbivory in global climate change research: Direct effects  
523 of rising temperature on insect herbivores. *Global Change Biology*, 8(1):1–16, 2002. doi: 10.1046/j.1365-2486.  
524 2002.00451.x.
- 525 A. Beckerman, O.L. Petchey, and P.J. Morin. Adaptive foragers and community ecology: Linking individuals to  
526 communities and ecosystems. *Functional Ecology*, 24(1):1–6, 2010. doi: 10.1111/j.1365-2435.2009.01673.x.
- 527 A.P. Beckerman, O.L. Petchey, and P.H. Warren. Foraging biology predicts food web complexity. *Proceedings of*  
528 *the National Academy of Sciences*, 103(37):13745–13749, 2006. doi: 10.1073/pnas.0603039103.
- 529 S.T. Behmer and A. Joern. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings*  
530 *of the National Academy of Sciences*, 105(6):1977–1982, 2008. doi: 10.1073/pnas.0711870105.
- 531 L. Berec, J. Eisner, and V. Křivan. Adaptive foraging does not always lead to more complex food webs. *Journal*  
532 *of Theoretical Biology*, 266(2):211–218, 2010. doi: 10.1016/j.jtbi.2010.06.034.
- 533 C.M. Bergman, J.M. Fryxell, C.C. Gates, and D. Fortin. Ungulate foraging strategies: Energy maximizing or  
534 time minimizing? *Journal of Animal Ecology*, 70(2):289–300, 2001. doi: 10.1111/j.1365-2656.2001.00496.x.
- 535 M.G. Bidart-Bouzat and A. Imeh-Nathaniel. Global change effects on plant chemical defenses against insect  
536 herbivores. *Journal of Integrative Plant Biology*, 50(11):1339–1354, 2008. doi: 10.1111/j.1744-7909.2008.  
537 00751.x.
- 538 M. Bison, S. Ibanez, C. Redjadj, F. Boyer, E. Coissac, C. Miquel, D. Rioux, S. Said, D. Maillard, P. Taberlet,  
539 N.G. Yoccoz, and A. Loison. Upscaling the niche variation hypothesis from the intra- to the inter-specific level.  
540 *Oecologia*, 179(3):835–842, 2015. doi: 10.1007/s00442-015-3390-7.
- 541 M. Boersma, K.A. Mathew, B. Niehoff, K.L. Schoo, R.M. Franco-Santos, and C.L. Meunier. Temperature driven  
542 changes in the diet preference of omnivorous copepods: No more meat when it’s hot? *Ecology Letters*, 19(1):  
543 45–53, 2016. doi: 10.1111/ele.12541.
- 544 D.I. Bolnick, R. Svanbäck, M.S. Araújo, and L. Persson. Comparative support for the niche variation hypothesis  
545 that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of*  
546 *Sciences*, 104(24):10075–10079, 2007. doi: 10.1073/pnas.0703743104.
- 547 B.J. Brosi and H.M. Briggs. Single pollinator species losses reduce floral fidelity and plant reproductive function.  
548 *Proceedings of the National Academy of Sciences*, 110(32):13044–13048, 2013. doi: 10.1073/pnas.1307438110.
- 549 L. Buisson, G. Grenouillet, S. Villéger, J. Canal, and P. Laffaille. Toward a loss of functional diversity in stream  
550 fish assemblages under climate change. *Global change biology*, 19(2):387–400, 2013. doi: 10.1111/gcb.12056.
- 551 A. Charmantier, R.H. McCleery, L.R. Cole, C. Perrins, L.E.B. Kruuk, and Ben C. Sheldon. Adaptive phenotypic  
552 plasticity in response to climate change in a wild bird population. *science*, 320(5877):800–803, 2008. doi:  
553 10.1126/science.1157174.
- 554 P. Chesson and J.J. Kuang. The interaction between predation and competition. *Nature*, 456(7219):235–238,  
555 2008. doi: 10.1038/nature07248.
- 556 L-M. Chevin, S. Collins, and F. Lefèvre. Phenotypic plasticity and evolutionary demographic responses to climate  
557 change: Taking theory out to the field. *Functional Ecology*, 27(4):967–979, 2013. doi: 10.1111/j.1365-2435.  
558 2012.02043.x.
- 559 F.J. Clissold, G.D. Sanson, J. Read, and S.J. Simpson. Gross vs. net income: How plant toughness affects

560 performance of an insect herbivore. *Ecology*, 90(12):3393–3405, 2009. doi: 10.1890/09-0130.1.

561 A.N. Costa, H.L. Vasconcelos, E.H.M. Vieira-Neto, and E.M. Bruna. Adaptive foraging of leaf-cutter ants to  
562 spatiotemporal changes in resource availability in Neotropical savannas. *Ecological Entomology*, 44(2):227–238,  
563 2019. doi: 10.1111/een.12697.

564 E. Crispo. The Baldwin effect and genetic assimilation: Revisiting two mechanisms of evolutionary change  
565 mediated by phenotypic plasticity. *Evolution: International Journal of Organic Evolution*, 61(11):2469–2479,  
566 2007. doi: 10.1111/j.1558-5646.2007.00203.x.

567 M. Damien and K. Tougeron. Prey–predator phenological mismatch under climate change. *Current opinion in  
568 insect science*, 35:60–68, 2019. doi: 10.1016/j.cois.2019.07.002.

569 H. Deraison, I. Badenhauer, N. Loeuille, C. Scherber, and N. Gross. Functional trait diversity across trophic  
570 levels determines herbivore impact on plant community biomass. *Ecology letters*, 18(12):1346–1355, 2015. doi:  
571 10.1111/ele.12529.

572 U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400(6742):354, 1999.  
573 doi: 10.1038/22521.

574 L.M. Dill. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic  
575 Sciences*, 40(4):398–408, 1983. doi: 10.1139/f83-058.

576 V. Domínguez-García, V. Dakos, and S. Kéfi. Unveiling dimensions of stability in complex ecological networks.  
577 *Proceedings of the National Academy of Sciences*, page 201904470, 2019. doi: 10.1073/pnas.1904470116.

578 K.L. du Plessis, R.O. Martin, P.A.R. Hockey, S.J. Cunningham, and A.R. Ridley. The costs of keeping cool in  
579 a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an  
580 arid-zone bird. *Global Change Biology*, 18(10):3063–3070, 2012. doi: 10.1111/j.1365-2486.2012.02778.x.

581 M. Egas, M.W. Sabelis, and U. Dieckmann. Evolution of specialization and ecological character displacement of  
582 herbivores along a gradient of plant quality. *Evolution*, 59(3):507–520, 2005. doi: 10.1111/j.0014-3820.2005.  
583 tb01011.x.

584 C. Fontaine, I. Dajoz, J. Meriguet, and M. Loreau. Functional Diversity of Plant–Pollinator Interaction Webs  
585 Enhances the Persistence of Plant Communities. *PLoS Biol*, 4(1):e1, 2006. doi: 10.1371/journal.pbio.0040001.

586 J.A. Fordyce. The evolutionary consequences of ecological interactions mediated through phenotypic plasticity.  
587 *Journal of Experimental Biology*, 209(12):2377–2383, 2006. doi: 10.1242/jeb.02271.

588 D. Fortin, M.S. Boyce, E.H. Merrill, and J.M. Fryxell. Foraging costs of vigilance in large mammalian herbivores.  
589 *Oikos*, 107(1):172–180, 2004. doi: 10.1111/j.0030-1299.2004.12976.x.

590 R.J. Fox, J.M. Donelson, C. Schunter, T. Ravasi, and J.D. Gaitán-Espitia. Beyond buying time: The role of  
591 plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal  
592 Society B: Biological Sciences*, 374(1768):20180174, 2019. doi: 10.1098/rstb.2018.0174.

593 S.A.H. Geritz, E. Kisdi, G. Meszéna, and J.A.J. Metz. Evolutionarily singular strategies and the adaptive growth  
594 and branching of the evolutionary tree. *Evolutionary ecology*, 12(1):35–57, 1998. doi: 10.1023/A:1006554906681.

595 C.K. Ghahambor, J.K. McKay, S.P. Carroll, and D.N. Reznick. Adaptive versus non-adaptive phenotypic plasticity  
596 and the potential for contemporary adaptation in new environments. *Functional ecology*, 21(3):394–407, 2007.  
597 doi: 10.1111/j.1365-2435.2007.01283.x.

598 A. Gonzalez, O. Ronce, R. Ferriere, and M.E. Hochberg. Evolutionary rescue: An emerging focus at the inter-  
599 section between ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
600 368(1610):20120404, 2013. doi: 10.1098/rstb.2012.0404.

601 M.P. Hassell and T.R.E. Southwood. Foraging strategies of insects. *Annual review of ecology and systematics*, 9  
602 (1):75–98, 1978. doi: 10.1146/annurev.es.09.110178.000451.

603 L. Heckmann, B. Drossel, U. Brose, and C. Guill. Interactive effects of body-size structure and adaptive foraging  
604 on food-web stability. *Ecology letters*, 15(3):243–250, 2012. doi: 10.1111/j.1461-0248.2011.01733.x.

605 Emilio Hernández-García, Cristóbal López, Simone Pigolotti, and Ken H. Andersen. Species competition: coex-  
606 istence, exclusion and clustering. *Philosophical Transactions of the Royal Society A: Mathematical, Physical  
607 and Engineering Sciences*, 367(1901):3183–3195, 2009. doi: 10.1098/rsta.2009.0086.

608 S. Ibanez, C. Gallet, and L. Després. Plant insecticidal toxins in ecological networks. *Toxins*, 4(4):228–243, 2012.  
609 doi: 10.3390/toxins4040228.

610 K. Jensen, D. Mayntz, S. Toft, F.J. Clissold, J. Hunt, D. Raubenheimer, and S.J. Simpson. Optimal foraging for  
611 specific nutrients in predatory beetles. *Proceedings of the Royal Society of London B: Biological Sciences*, 279  
612 (1736):2212–2218, 2012. doi: 10.1098/rspb.2011.2410.

613 R. Kassen. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of  
614 evolutionary biology*, 15(2):173–190, 2002. doi: 10.1046/j.1420-9101.2002.00377.x.

615 J.T. Kerby, C.C. Wilmers, and E. Post. Climate change, phenology, and the nature of consumer–resource  
616 interactions: Advancing the match/mismatch hypothesis. In *Trait-Mediated Indirect Interactions: Ecological*



- 617 *and Evolutionary Perspectives*, pages 508–25. 2012.
- 618 M. Kondoh. Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. *Science*,  
619 299(5611):1388–1391, 2003. doi: 10.1126/science.1079154.
- 620 M. Kopp and S. Matuszewski. Rapid evolution of quantitative traits: Theoretical perspectives. *Evolutionary*  
621 *Applications*, 7(1):169–191, 2014. doi: 10.1111/eva.12127.
- 622 C. Kovach-Orr and G.F. Fussmann. Evolutionary and plastic rescue in multitrophic model communities.  
623 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1610):20120084, 2013. doi:  
624 10.1098/rstb.2012.0084.
- 625 R. Kowalczyk, J.M. Wójcik, P. Taberlet, T. Kamiński, C. Miquel, A. Valentini, J.M. Craine, and E. Coissac.  
626 Foraging plasticity allows a large herbivore to persist in a sheltering forest habitat: DNA metabarcoding diet  
627 analysis of the European bison. *Forest Ecology and Management*, 449:117474, October 2019. doi: 10.1016/j.  
628 foreco.2019.117474.
- 629 V. Křivan and O.J. Schmitz. Adaptive foraging and flexible food web topology. *Evolutionary Ecology Research*,  
630 5(5):623–652, 2003.
- 631 K. Laland, T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, J. Odling-Smee, G.A.  
632 Wray, H.E. Hoekstra, D.J. Futuyma, R.E. Lenski, T.F.C. Mackay, D. Schluter, and J.E. Strassmann. Does  
633 evolutionary theory need a rethink? *Nature News*, 514(7521):161, 2014. doi: 10.1038/514161a.
- 634 E. Laliberté and P. Legendre. A distance-based framework for measuring functional diversity from multiple traits.  
635 *Ecology*, 91(1):299–305, 2010. doi: 10.1890/08-2244.1.
- 636 J.S. Lefcheck, A.A. Innes-Gold, S.J. Brandl, R.S. Steneck, R.E. Torres, and D.B. Rasher. Tropical fish diversity  
637 enhances coral reef functioning across multiple scales. *Science Advances*, 5(3):eaav6420, March 2019. doi:  
638 10.1126/sciadv.aav6420.
- 639 W.C. Lemon. Heritability of selectively advantageous foraging behaviour in a small passerine. *Evolutionary*  
640 *Ecology*, 7(4):421–428, July 1993. doi: 10.1007/BF01237873.
- 641 N. Loeuille. Consequences of adaptive foraging in diverse communities. *Functional Ecology*, 24(1):18–27, February  
642 2010. doi: 10.1111/j.1365-2435.2009.01617.x.
- 643 N. Loeuille and M. Loreau. Evolutionary emergence of size-structured food webs. *Proceedings of the National*  
644 *Academy of Sciences*, 102(16):5761–5766, 2005. doi: 10.1073/pnas.0408424102.
- 645 M. Loreau and A. Hector. Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412  
646 (6842):72–76, July 2001. doi: 10.1038/35083573.
- 647 R. MacArthur. Species packing and competitive equilibrium for many species. *Theoretical Population Biology*, 1  
648 (1):1–11, 1970. ISSN 0040-5809. doi: 10.1016/0040-5809(70)90039-0.
- 649 R.H. MacArthur and E.R. Pianka. On optimal use of a patchy environment. *The American Naturalist*, 100(916):  
650 603–609, 1966.
- 651 C. McArthur, P.B. Banks, R. Boonstra, and J.S. Forbey. The dilemma of foraging herbivores: Dealing with food  
652 and fear. *Oecologia*, 176(3):677–689, 2014. doi: 10.1007/s00442-014-3076-6.
- 653 J. Merilä and A.P. Hendry. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence.  
654 *Evolutionary applications*, 7(1):1–14, 2014. doi: 10.1111/eva.12137.
- 655 N.E. Miller-Struttman, J.C. Geib, J.D. Franklin, P.G. Kevan, R.M. Holdo, D. Ebert-May, A.M. Lynn, J.A.  
656 Kettenbach, E. Hedrick, and C. Galen. Functional mismatch in a bumble bee pollination mutualism under  
657 climate change. *Science*, 349(6255):1541–1544, 2015. doi: 10.1126/science.aab0868.
- 658 T. Milotić, C. Baltzinger, C. Eichberg, A.E. Eycott, M. Heurich, J. Müller, J.A. Noriega, R. Menendez, J. Stadler,  
659 and R. Ádám. Functionally richer communities improve ecosystem functioning: Dung removal and secondary  
660 seed dispersal by dung beetles in the Western Palaearctic. *Journal of Biogeography*, 46(1):70–82, 2019. doi:  
661 10.1111/jbi.13452.
- 662 B.G. Miner, S.E. Sultan, S.G. Morgan, D.K. Padilla, and R.A. Relyea. Ecological consequences of phenotypic  
663 plasticity. *Trends in ecology & evolution*, 20(12):685–692, 2005. doi: 10.1016/j.tree.2005.08.002.
- 664 D.H. Nussey, E. Postma, P. Gienapp, and M.E. Visser. Selection on heritable phenotypic plasticity in a wild bird  
665 population. *Science*, 310(5746):304–306, 2005. doi: 10.1126/science.1117004.
- 666 K.L. Pangle, T.D. Malinich, D.B. Bunnell, D.R. DeVries, and S.A. Ludsin. Context-dependent planktivory:  
667 Interacting effects of turbidity and predation risk on adaptive foraging. *Ecosphere*, 3(12):1–18, 2012. doi:  
668 10.1890/ES12-00224.1.
- 669 S.I. Peluc, T.S. Sillett, J.T. Rotenberry, and C.K. Ghalambor. Adaptive phenotypic plasticity in an island songbird  
670 exposed to a novel predation risk. *Behavioral Ecology*, 19(4):830–835, 2008. doi: 10.1093/beheco/arn033.
- 671 D.W. Pfennig. *Phenotypic Plasticity & Evolution: Causes, Consequences, Controversies*. Taylor & Francis, 2021.
- 672 Simone Pigolotti, Cristóbal López, Emilio Hernández-García, and Ken Haste Andersen. How gaussian com-  
673 petition leads to lumpy or uniform species distributions. *Theoretical Ecology*, 3:89–96, 2010. doi: 10.1007/

674 s12080-009-0056-2.

675 T. Poisot, N. Mouquet, and D. Gravel. Trophic complementarity drives the biodiversity–ecosystem functioning  
676 relationship in food webs. *Ecology Letters*, 16(7):853–861, 2013. doi: 10.1111/ele.12118.

677 S.M.J. Portalier, J. Candau, and F. Lutscher. A temperature-driven model of phenological mismatch provides  
678 insights into the potential impacts of climate change on consumer–resource interactions. *Ecography*, n/a(n/a):  
679 e06259. doi: 10.1111/ecog.06259.

680 E. Post and M.C. Forchhammer. Climate change reduces reproductive success of an Arctic herbivore through  
681 trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1501):2367–2373,  
682 2008. doi: 10.1098/rstb.2007.2207.

683 J.C. Randolph and G.N. Cameron. Consequences of diet choice by a small generalist herbivore. *Ecological  
684 Monographs*, 71(1):117–136, 2001. doi: 10.1890/0012-9615(2001)071[0117:CODCBA]2.0.CO;2.

685 S. Rasmann and L. Pellissier. Adaptive responses of plants to insect herbivores under climate change. In *Climate  
686 Change and Insect Pests*, pages 38–53. 2015.

687 S. Rasmann, L. Pellissier, E. Defosse, H. Jactel, and G. Kunstler. Climate-driven change in plant–insect inter-  
688 actions along elevation gradients. *Functional Ecology*, 28(1):46–54, 2014. doi: 10.1111/1365-2435.12135.

689 A.E. Rosenblatt and O.J. Schmitz. Climate Change, Nutrition, and Bottom-Up and Top-Down Food Web  
690 Processes. *Trends in Ecology & Evolution*, 31(12):965–975, 2016. doi: 10.1016/j.tree.2016.09.009.

691 M.C. Rossiter. Genetic and phenotypic variation in diet breadth in a generalist herbivore. *Evolutionary Ecology*,  
692 1(3):272–282, 1987. doi: 10.1007/BF02067557.

693 A. Saltelli, S. Tarantola, F. Campolongo, and M. Ratto. *Sensitivity Analysis in Practice: A Guide to Assessing  
694 Scientific Models*. Chichester, England, 2004. doi: 10.1111/j.1467-985X.2005.358\_13.x.

695 Akira Sasaki and U Dieckmann. Oligomorphic dynamics for analyzing the quantitative genetics of adaptive  
696 speciation. *J. Math. Biol.*, 63:601–635, 2011. doi: 10.1007/s00285-010-0380-6.

697 Akira Sasaki and Stephen Ellner. The evolutionarily stable phenotype distribution in a random environment.  
698 *Evolution*, 49(2):337–350, 1995. doi: 10.1111/j.1558-5646.1995.tb02246.x.

699 C. Scherber, D.J. Gladbach, K. Stevnbak, R.J. Karsten, I.K. Schmidt, A. Michelsen, K.R. Albert, K.S. Larsen,  
700 T.N. Mikkelsen, and C. Beier. Multi-factor climate change effects on insect herbivore performance. *Ecology  
701 and evolution*, 3(6):1449–1460, 2013. doi: 10.1002/ece3.564.

702 G.G. Simpson. The baldwin effect. *Evolution*, 7(2):110–117, 1953. doi: 10.2307/2405746.

703 M.S. Singer, E.A. Bernays, and Y. Carriere. The interplay between nutrient balancing and toxin dilution in  
704 foraging by a generalist insect herbivore. *Animal Behaviour*, 64(4):629–643, 2002. doi: 10.1006/anbe.2002.3082.

705 M Slatkin and R Lande. Niche width in a fluctuating environment-density independent model. *Am Nat*, 110  
706 (971):31–55, 1976. doi: 10.1086/283047.

707 J.T. Staley and S.N. Johnson. Climate change impacts on root herbivores. In *Root Feeders: An Ecosystem  
708 Perspective*, pages 192–215. 2008. doi: 10.1079/9781845934613.019.

709 J. Sundell, J.A. Eccard, R. Tiilikainen, and H. Ylönen. Predation rate, prey preference and predator switching:  
710 Experiments on voles and weasels. *Oikos*, 101(3):615–623, 2003. doi: 10.1034/j.1600-0706.2003.12264.x.

711 R. Svanbäck and D.I. Bolnick. Intraspecific competition drives increased resource use diversity within a natural  
712 population. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611):839–844, 2007. doi: 10.1098/  
713 rspb.2006.0198.

714 Péter Szabó and Géza Meszéna. Limiting similarity revisited. *Oikos*, 112(3):612–619, 2006. doi: 10.1111/j.  
715 0030-1299.2006.14128.x.

716 W. Thuiller, S. Lavorel, M.T. Sykes, and M.B. Araújo. Using niche-based modelling to assess the impact of  
717 climate change on tree functional diversity in Europe. *Diversity and Distributions*, 12(1):49–60, 2006. doi:  
718 10.1111/j.1366-9516.2006.00216.x.

719 C; Tur, J.M. Olesen, and A. Traveset. Increasing modularity when downscaling networks from species to indi-  
720 viduals. *Oikos*, 2014. doi: 10.5061/dryad.63fp5.

721 M.M. Turcotte and J.M. Levine. Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*,  
722 31(10):803–813, 2016. doi: 10.1016/j.tree.2016.07.013.

723 S. Uchida and B. Drossel. Relation between complexity and stability in food webs with adaptive behavior. *Journal  
724 of theoretical biology*, 247(4):713–722, 2007. doi: 10.1016/j.jtbi.2007.04.019.

725 S.B. Unsicker, A. Oswald, G. Köhler, and W.W. Weisser. Complementarity effects through dietary mixing  
726 enhance the performance of a generalist insect herbivore. *Oecologia*, 156(2):313–324, 2008. doi: 10.1007/  
727 s00442-008-0973-6.

728 F.S. Valdovinos, P. Moisset de Espanés, J.D. Flores, and R. Ramos-Jiliberto. Adaptive foraging allows the  
729 maintenance of biodiversity of pollination networks. *Oikos*, 122(6):907–917, 2013. doi: 10.1111/j.1600-0706.

730 2012.20830.x.

731 T.M. Van de Ven, A.E. McKechnie, and S. Cunningham. The costs of keeping cool: Behavioural trade-offs between  
732 foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, 191  
733 (1):205–215, 2019. doi: 10.1007/s00442-019-04486-x.

734 M. Van Kleunen and M. Fischer. Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology*, 82  
735 (12):3309–3319, 2001. doi: 10.1890/0012-9658(2001)082[3309:AEOPFR]2.0.CO;2.

736 J. Varner and M.D. Dearing. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal*  
737 *of Mammalogy*, 95(1):72–81, 2014. doi: 10.1644/13-MAMM-A-099.1.

738 O. Vedder, S. Bouwhuis, and B.C. Sheldon. Quantitative Assessment of the Importance of Phenotypic Plasticity  
739 in Adaptation to Climate Change in Wild Bird Populations. *PLOS Biology*, 11(7):e1001605, 2013. doi:  
740 10.1371/journal.pbio.1001605.

741 A. Wallin. The genetics of foraging behaviour: Artificial selection for food choice in larvae of the fruitfly,  
742 *Drosophila melanogaster*. *Animal Behaviour*, 36(1):106–114, 1988. doi: 10.1016/S0003-3472(88)80253-7.

743 M.F. WallisDeVries. Effects of resource distribution patterns on ungulate foraging behaviour: A modelling  
744 approach. *Forest Ecology and Management*, 88(1):167–177, 1996. doi: 10.1016/S0378-1127(96)03822-4.

745 L. Wang, D. Wang, Y. Bai, G. Jiang, J. Liu, Y. Huang, and Y. Li. Spatial distributions of multiple plant species  
746 affect herbivore foraging selectivity. *Oikos*, 119(2):401–408, 2010. doi: 10.1111/j.1600-0706.2009.17774.x.

747 M-Y. Wang, T.C. Ings, M.J. Proulx, and L. Chittka. Can bees simultaneously engage in adaptive foraging  
748 behaviour and attend to cryptic predators? *Animal Behaviour*, 86(4):859–866, 2013. doi: 10.1016/j.anbehav.  
749 2013.07.029.

750 M.J. West-Eberhard. *Developmental Plasticity and Evolution*. Oxford University Press, 2003.

751 A. Whiten, R.W. Byrne, R.A. Barton, P.G. Waterman, and S.P. Henzi. Dietary and foraging strategies of  
752 baboons. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 334(1270):  
753 187–197, 1991. doi: 10.1098/rstb.1991.0108.