



HAL
open science

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

Léo Ledru, Jimmy Garnier, Océane Guillot, Erwan Faou, Camille Noûs, Sébastien Ibanez

► To cite this version:

Léo Ledru, Jimmy Garnier, Océane Guillot, Erwan Faou, Camille Noûs, et al.. The evolutionary dynamics of plastic foraging and its ecological consequences: a resource-consumer model. Peer Community Journal, 2023, 3, pp.e99. 10.24072/pcjournal.330 . hal-04047341v1

HAL Id: hal-04047341

<https://hal.science/hal-04047341v1>

Submitted on 27 Mar 2023 (v1), last revised 8 Nov 2023 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Is adaptive foraging adaptive? A resource-consumer eco-evolutionary model.

Leo Ledru¹, Jimmy Garnier², Océane Guillot¹, Erwan Faou³, Camille Noûs⁴, Sébastien Ibanez¹

¹Univ. Savoie Mont Blanc, Univ. Grenoble Alpes, CNRS, UMR 5553 LECA, France

²CNRS, Univ. Savoie Mont Blanc, UMR 8050 LAMA, France

³INRIA, Université Rennes 1, UMR CNRS 6625 IRMAR, France

⁴Laboratory Cogitamus

Abstract

Phenotypic plasticity has important ecological and evolutionary consequences. In particular, behavioural phenotypic plasticity such as adaptive foraging (AF) by consumers, may enhance community stability. Yet little is known about the ecological conditions that favor the evolution of AF, and how the evolutionary dynamics of AF 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 adaptatively, as a function of resource abundance, suitability and consumption by competitors. AF 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, AF 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, AF 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 AF behaviour, due to its costs. The causal relationships between AF, 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 AF and stability.

Keywords: phenotypic plasticity, adaptive 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) as it may mitigate environmental changes (Chevin et al., 2013; Vedder et al., 2013; Charmantier et al., 2008). Phenotypic plasticity commonly occurs when a variety of resources are available to consumers investing more or less time on each resource according to its suitability. The resulting *relative foraging efforts* (sensu Abrams, 2010) depend on the (mis)match between the defensive and 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). Relative foraging efforts 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 called *adaptive foraging* (AF, Valdivinos et al., 2013).

Phenotypic plasticity often results from evolution by natural selection (Nussey et al., 2005; Peluc et al., 2008; Van Kleunen and Fischer, 2001), but not always, especially in the context of environmental changes (Merilä and Hendry, 2014). The extent to which phenotypic plasticity is adaptive has been underexplored in the context of AF because previous theoretical works ignored the evolutionary dynamics of AF, 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 AF, 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 AF strategy tends to increase fitness, in some situations AF 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 AF 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 adaptatively is subject to evolution by natural selection. In other words: is adaptive foraging itself adaptive? We define AF as a change in relative foraging efforts that directly increases *energy intake*, but not necessarily *fitness*, in contrast with Loeuille (2010) who defined AF 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 AF. 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 AF. 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 AF 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 AF, 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 AF can alter the evolution of these consumer traits, as well as those of their resources (defenses, nutritional quality). In particular, we expect AF 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 AF, 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 AF 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 AF and the functional traits of consumers and resources are subject to evolutionary dynamics. In this eco-evolutionary context, it is uncertain whether the evolution of AF stabilises communities directly or indirectly, through its effects on functional diversity.

The main questions outlined earlier are sketched in Figure 1:

- 90 • Question 1. Under which ecological conditions is AF evolutionary adaptive? How do environmental
- 91 disturbances alter the evolution of AF?
- 92 • Question 2. When AF evolves, what are its effects on the diversity of the traits involved in the resource-
- 93 consumer interaction?
- 94 • Question 3. What is the effect of the evolution of AF on the stability of the resource-consumer system?
- 95 Are these effects direct (Q3a) or indirect, mediated by the influence of AF on functional diversity (Q3b)?

96 To address these issues, we build an eco-evolutionary model in which a consumer species feeds on a resource

97 species. Both species are characterized by an ecological trait; the resource is the most suitable for the consumer

98 when both traits match. In addition, the consumers carry a foraging trait measuring the extent to which they

99 select the resources allowing the largest intake, or instead forage randomly and consume the resources as a

100 function of their abundance. Ecological and foraging traits are subject to evolution; starting from monomorphic

101 initial conditions, they rapidly diversify and reach a stationary regime characterized by a stable diversity of

102 ecological and foraging traits. The stationary regime is then subjected to various environmental disturbances, to

103 test how the evolution of AF responds to environmental changes, and how this cascades down on the ecological

104 properties of the resource-consumer system.

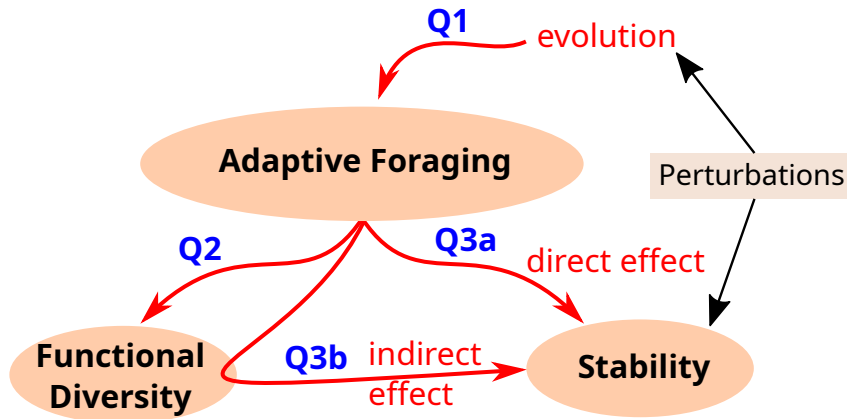


Figure 1: Overview of the main questions: (Q1) Under which ecological conditions does AF evolve? (Q2) Does the evolution of AF increases the diversity of traits involved in the resource-consumer interaction? (Q3) Does the evolution of AF enhances the stability of the resource-consumer system, either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

2 Model and methods

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 adaptive 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 ϕ . 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.

$$\partial_t r(t, y) = r(t, y) \left(\underbrace{g \left(1 - \frac{r_{eff}(t, y)}{K(y)} \right)}_{\text{resource growth}} - \underbrace{F_r[r, c, \phi]}_{\text{resource consumption}} \right) + \underbrace{\mathcal{M}_y(r)(t, y)}_{\text{niche trait mutations}} \quad (1)$$

$$\partial_t c(t, x, z) = c(t, x, z) \left(\underbrace{F_c[r, \phi]}_{\text{resource absorption}} - \underbrace{(d + IC(t))}_{\text{mortality and competition}} \right) + \underbrace{\mathcal{M}_x(c)(t, x, z)}_{\text{niche trait mutations}} + \underbrace{\mathcal{M}_z(r)(t, x, z)}_{\text{AF trait mutations}} \quad (2)$$

Resource-consumer interactions and niche traits. In the absence of consumers, resources grow logistically 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 $r_{eff}(t, y)$, 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 $K_{eff}(y - y')$ exerted by an individual with trait y' on an individual with trait y :

$$r_{eff}(t, y) = \int K_{eff}(y - y') r(t, y') dy' \quad (3)$$

The functions K and K_{eff} are normally distributed around $y = 0$ with variances σ_K and σ_C respectively (Table A1 and Fig. A1). In the presence of consumers, resources are exploited at rate $F_r[r, c, \phi]$, whereas the consumer density increases through resource absorption at a rate $F_c[c, \phi]$. Although these rates vary with the consumers foraging efforts ϕ , they crucially depend on the effective interaction strength $\Delta(x - y)$ between consumer and resource individuals. The function Δ is normally distributed around 0 with a variance σ , which measures the extend to which consumers can deal with a variety of resource types (Table A1). The variance parameter σ 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:

$$F_r[r, c, \phi](t, y) = \iint \frac{b\phi(t, x, y, z)\Delta(x, y)c(t, x, z)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} dx dz \quad (4)$$

$$F_c[r, \phi](t, x, z) = \alpha \int \frac{b\phi(t, x, y, z)\Delta(x, y)r(t, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} dy \quad (5)$$

with α the conversion coefficient, b the extraction coefficient and $s(z)$ the searching time, which depends on the foraging trait z as explained below. Moreover, consumer density is affected by mortality at a constant rate d and by direct competition at a rate IC where $C(t) = \iint c(t, x, z) dx dz$ is the total biomass of consumer and I the intraspecific competition between consumers for other limiting factors than resources.

Foraging strategies and adaptive foraging trait. Consumers can use two different foraging strategies during their foraging time: Random Foraging (RF) or Adaptive Foraging (AF). When using RF, the consumer randomly forages its environment without selecting resources. The resulting efforts ϕ_{RF} is proportional to the density of the resources:

$$\phi_{RF}(t, y) = \frac{r(t, y)}{\int r(t, y') dy'} \quad (6)$$

Conversely, when using AF, consumers actively search for resources, that maximize their energy intake, that depends on the resource availability and suitability (e.g. Sundell et al., 2003). The resulting relative foraging efforts ϕ_{AF} may change over time as follows:

$$\partial_t \phi_{AF}(t, x, y, z) = l_\phi c(t, x, z) \left(\int r(t, y') \phi_{AF}(t, x, y', z) [u(t, x, y, z) - u(t, x, y', z)]_+ dy' - \int r(t, y') \phi_{AF}(t, x, y, z) [u(t, x, y', z) - u(t, x, y, z)]_+ dy' \right) \quad (7)$$

141 The quantity ϕ_{AF} is analogous to the behavioral trait z in [Abrams and Matsuda \(2004\)](#). The potential gain
 142 $u(t, x, y, z)$ of a consumer with traits (x, z) on a resource with trait y depends on its foraging efforts as well as
 143 the resource suitability and availability:

$$u(t, x, y, z) = \frac{b\Delta(x, y)r(t, y)}{1 + s(z)b \int \phi(t, x, y, z)\Delta(x, y)r(t, y)dy} \quad (8)$$

144 The AF dynamics allow consumers to compare the benefits received from different resources. As a result,
 145 consumers increase their efforts on the most beneficial resources and reduce them on sub-optimal resources. The
 146 comparison of resources is assumed time consuming, the efforts are therefore not adjusted instantaneously but
 147 exponentially fast at a rate l_ϕ . When the adjustment rate l_ϕ becomes large, the adaptive foraging strategy becomes
 148 closer to the optimal foraging strategy maximizing the potential gain u ([MacArthur and Pianka, 1966](#); [Loeuille,
 149 2010](#)). Moreover, the searching time $s(z)$ also increases with the foraging trait: $s(z) = s_{min} + z(s_{max} - s_{min})$
 150 (Figure A1d). This relationship introduces a trade-off between the AF strategy and the searching time.

151 Finally, the effective consumer foraging strategy depends on its foraging trait $z \in [0, 1]$, which corresponds to
 152 the proportion of its general foraging effort spent using the AF strategy. The effective consumer efforts is thus:

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

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

$$\mathcal{M}_x(c)(t, x, z) = \frac{U\sigma_m^2}{2}\partial_x^2 c(t, x, z), \quad \mathcal{M}_y(r)(t, y) = \frac{U\sigma_m^2}{2}\partial_y^2 r(t, y) \quad \text{and} \quad \mathcal{M}_z(c)(t, x, z) = \frac{U\sigma_m^2}{2}\partial_z^2 c(t, x, z), \quad (10)$$

157 where U is the mutation frequency and σ_m^2 is the variance of the mutational effects. This approach contrasts
 158 with the adaptive dynamic framework, in which a mutant phenotype is introduced sequentially and persists only
 159 if its invasive fitness is positive ([Geritz et al., 1998](#)).

160 2.2 Analysis of the model

161 **Sensitivity analysis on the mean foraging trait.** The model is investigated numerically using
 162 MATLAB (code available on GitHub <https://github.com/leoledru/Adaptive-Foraging>). The niche traits are
 163 discretized into 31 equally distanced values (11 values for the foraging trait). In the simulations, when the density
 164 of a resource or a consumer phenotype drops below the critical threshold $\varepsilon = 10^{-4}$, the density is set to 0 to
 165 save computational time. The simulations start with monomorphic populations at the niche center ($y = x = 0$)
 166 and consumers have a purely random foraging strategy ($z = 0$). To investigate the ecological conditions leading
 167 to the evolution of AF, a global sensitivity analysis is performed using Partial Rank Correlations Coefficients
 168 (PRCC, [Saltelli et al., 2004](#)), on the mean foraging trait value of the consumer population $\bar{z}(t)$ defined by:

$$\bar{z}(t) = \frac{\iint z \frac{c(t, x, z) dx dz}{\iint c(t, x', z') dx' dz'}}{\iint c(t, x, z) dx dz} \quad (11)$$

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

171 **Effect of AF evolution on biomass, functional diversity, productivity and niche overlap.** To
 172 assess the effect of AF on the resource-consumer system, several characteristics were measured: the biomass of
 173 resources and consumers, their functional dispersion $FDis$ ([Laliberté and Legendre, 2010](#)), the productivity $Prod$,
 174 the niche overlap between consumers ρ ([Chesson and Kuang, 2008](#)) and the functional match between consumers
 175 and their resources. The biomass of resources R and consumers C are given respectively by $R(t) = \int r(t, y) dy$
 176 and $C(t) = \iint c(t, x, z) dx dz$. The functional dispersion $FDis$ represents for each population the average absolute
 177 deviation from the mean niche trait:

$$FDis_r(t) = \int \frac{|y - \bar{y}(t)| r(t, y)}{\int r(t, y) dy} dy \quad \text{and} \quad FDis_c(t) = \int \frac{|x - \bar{x}(t)| c(t, x)}{\int c(t, x) dx} dx \quad (12)$$

178 where $\bar{y}(t) = \int \frac{y r(t, y)}{\int r(t, y) dy} dy$ and $\bar{x}(t) = \int \frac{x c(t, x)}{\int c(t, x) dx} dx$ are the mean traits of the resource and consumer and
 179 $c(t, x) = \int c(t, x, z) dz$ is the biomass of individuals carrying the trait x in the consumers population. Productivity
 180 corresponds to the net production of biomass by consumers following resource absorption, measured once the
 181 system has reached a stationary regime (e.g. [Loreau and Hector, 2001](#); [Poisot et al., 2013](#)):

$$Prod = \iint c(T, x, z) F_c[r, \phi](T, x, z) dx dz \quad (13)$$

| Parameters | | Values for the response to disturbances | Ranges for the sensitivity analysis | PRCC values |
|---------------|--|---|-------------------------------------|-------------|
| σ | Consumers niche width | 0.9 | [0; 1] | 0.28 |
| σ_K | Resources niche width | 2.5 | [1; 4] | 0.38 |
| s_{max} | Cost of AF : maximal increase of searching time due to AF | 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 | |
| σ_C | Width of the competition kernel | $\sigma_K - 1$ | Fixed | |
| α | Biomass conversion coefficient from resources to consumers | 0.3 | Fixed | |
| b | Biomass extraction coefficient | 0.5 | Fixed | |
| l_ϕ | Rate of change in foraging efforts | 0.5 | Fixed | |
| s_{min} | Cost of AF : minimal increase of searching time due to AF | 0.1 | Fixed | |
| U | Mutation frequency | 0.1 | Fixed | |
| σ_m^2 | Mean effect of mutation | 0.02 | Fixed | |
| ε | 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.

182 T is the time to reach the stationary regime, $T = 1000$ in the simulations below. The niche overlap between two
183 consumers with niche traits x_i and x_j and foraging traits z_i and z_j is defined by the correlation coefficient ρ_{ij} of
184 their resource absorption:

$$\rho_{ij} = \frac{\int \phi(x_i, y, z_i)u(x_i, y, z_i) \phi(x_j, y, z_j)u(x_j, y, z_j)dy}{\sqrt{\int (\phi(x_i, y, z_i)u(x_i, y, z_i))^2 dy + \int (\phi(x_j, y, z_j)u(x_j, y, z_j))^2 dy}} \quad (14)$$

185 The overall niche overlap between consumers ρ is the average of this correlation coefficient of all consumers. The
186 functional match FM corresponds to the mean difference between the niche trait of the consumer and the mean
187 niche trait of its diet, that is the resources absorbed by the consumer:

$$FM(t) = \int |diet(t, x, z) - x| \frac{c(t, x, z)}{\int c(t, x, z)dx dz} dx dz \quad \text{where} \quad diet(t, x, z) = \int y \frac{\phi(t, x, y, z)u(t, x, y, z)}{\int \phi u(t, x, y, z)dy} dy \quad (15)$$

188 To assess the effects of the evolution of AF on the system, we compare the total biomass C of consumers in two
189 situations: a freely evolving AF trait z and a fixed RF strategy ($z = 0$). In both cases, the ecological niche traits
190 x and y are subject to evolution. The communities evolved during 1000 time steps, which is enough time for
191 the system to reach a stationary regime with stable community-level characteristics (A.2). The same comparison
192 was done for all the other system-level characteristics.

193 **Effects of environmental disturbance** To understand whether the evolution of AF can rescue consumers
194 from environmental changes, three specific disturbances are considered: (a) an ecosystem disturbance where
195 consumer mortality d increases gradually by Δd , (b) a constantly changing environment, where the niche center
196 is shifted at constant speed c and (c) an sudden environmental change where the center of the resource niche is
197 instantaneously shifted at a distance Δy from the initial niche center (e.g. Domínguez-García et al., 2019). The
198 mutation process driving the diversification of resources and consumers in the system should help to recover trait
199 diversity after a disturbance. To assess the effects of those disturbances on the resource-consumer system, the
200 proportion of consumer biomass lost after the disturbance is calculated once a new equilibrium is reached. The
201 difference in the mean foraging trait before and after each disturbance is also measured.

202 The resource-consumer system is initialized with consumers carrying a high mean AF trait ($\bar{z} \approx 0.9$ with
203 parameter values set as in Table 1). For each disturbance strength and type, the stability metrics of the system

204 with AF evolution is compared to those of the system with RF only, in which the foraging trait of consumers was
 205 monomorphic ($z = 0$) and fixed ($\mathcal{M}_z(c) = 0$). For all disturbance types, the disturbance strength is increased
 206 until the consumer population goes to extinction, in order to compute the maximal disturbance level that the
 207 system can tolerate.

208 3 Results

209 3.1 The evolution of adaptive foraging

210 A typical outcome of the model was the diversification of the resources and consumers along the ecological
 211 gradient (Figure 2a). Although the distribution of the consumer foraging trait reached a unimodal distribution
 212 (Figure 2a), the consumers positioned at the niche center foraged randomly, while those at the niche edges foraged
 213 adaptatively (Figure 2b). In addition, the distributions of the niche traits reached a stationary regime that varied
 214 over time due to the AF strategy (Appendix A.2). However, the macroscopic characteristics (functional dispersion,
 215 total biomass, productivity, niche overlap and average foraging behavior) stabilized around a steady state; these
 216 characteristics will therefore be used to assess the effect of AF evolution on the resource-consumer system.

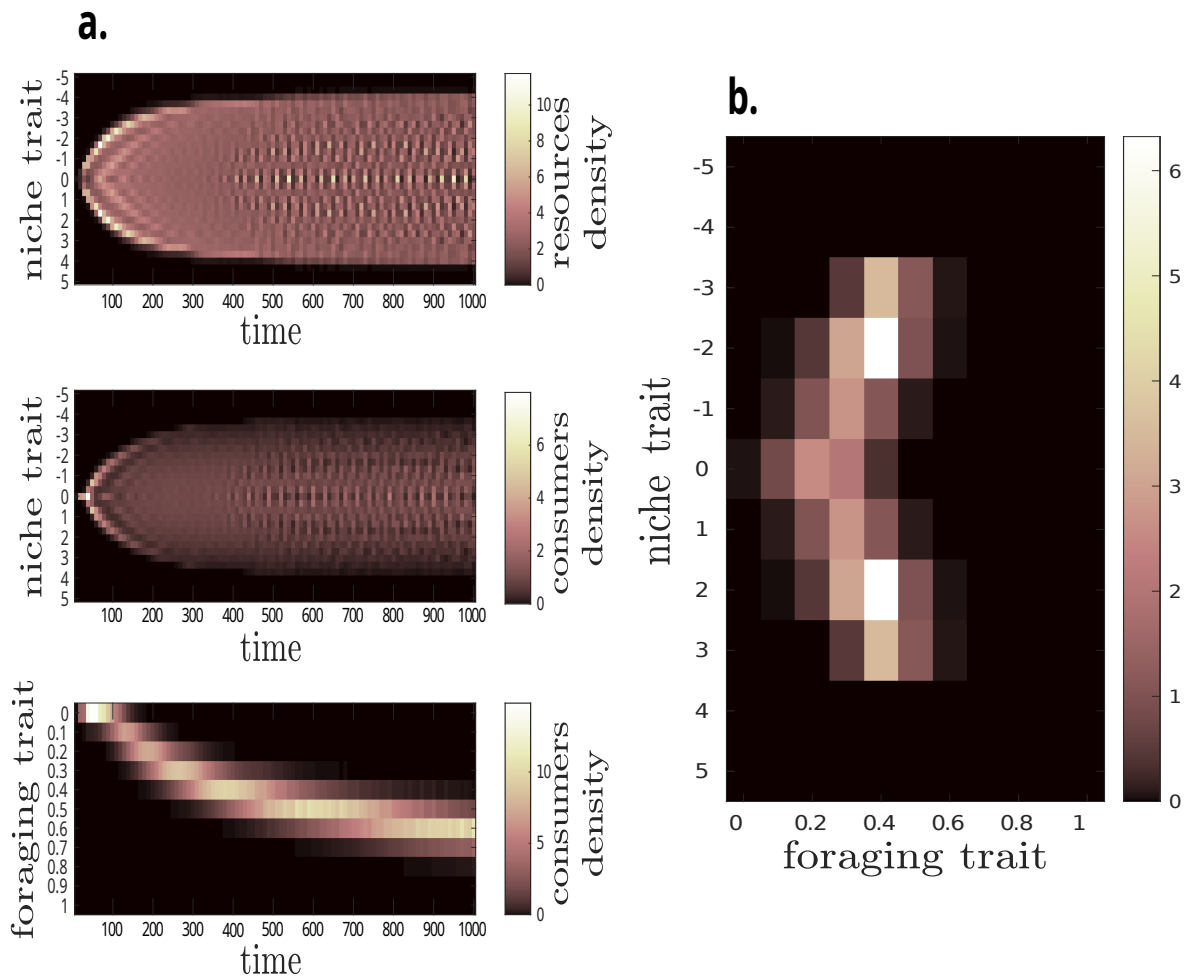


Figure 2: a) Diversification of niche and foraging traits starting from a single resource and consumer at the niche centre, and a RF consumer strategy. Top panel: resource densities $r(t, y)$. Middle panel: consumer densities $\int c(t, x, z) dz$. Bottom panel: foraging trait $\int c(t, x, z) dx$. b)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

217 The PRCC analysis revealed that the six tested parameters played a significant role in the evolution of
 218 AF (Table 1 last column). The conditions favouring the evolution of AF (measured by $\bar{z}(t)$) were essentially
 219 the following: a consumers ability to exploit a wide range of resources (large σ , correlation coefficient 0.28),
 220 a wide niche for resources (large σ_K , correlation coefficient 0.38), a weak trade-off between AF and searching
 221 time (small s_{max} , correlation coefficient -0.64), a high consumer mortality d (correlation coefficient 0.13), a

222 strong competition between consumers (large I , correlation coefficient 0.13) and a high resource growth (large g ,
 223 correlation coefficient 0.11).

224 3.2 The effects of AF on functional diversity and other macroscopic charac- 225 teristics

226 When the evolution of AF produces consumer populations with a high mean foraging trait \bar{z} , the resource biomass
 227 is reduced (e.g. -50% when $\bar{z} = 1$) while the consumer biomass increases by 25% on average (Figure 3a). How-
 228 ever, the variability of the consumer biomass among simulations also increases with \bar{z} . This pattern has also
 229 been observed when the foraging trait z of a monomorphic population without AF evolution is increased (Figure
 230 A3a). Turning to diversity, the evolution of AF increases functional dispersion of both resources and consumers
 231 (Figure 3b). Again, when the average foraging trait value was large the consequences on diversity indices become
 232 heterogeneous, but this time the effect of AF was almost always positive. The relationship with productivity
 233 (i.e the flow of biomass from resources to consumers) was non-linear (Figure 3c). When the system with AF
 234 evolution had a rather low mean foraging trait ($0 < \bar{z} < 0.4$) productivity increased in comparison to the system
 235 without AF. However, when \bar{z} was above 0.4, the productivity gain became smaller and even vanished when \bar{z}
 236 equalled 1. Strong AF also increased the variability of productivity; among the systems with strong AF some
 237 had large gains of productivity and others large deficits. Finally, the evolution of AF also decreased the niche
 238 overlap between consumers by about 40% when the mean foraging trait was close to 1 (Figure 3d), and increased
 239 the functional match between the niche trait of consumers and the mean niche trait of their resources (Figure A4).
 240

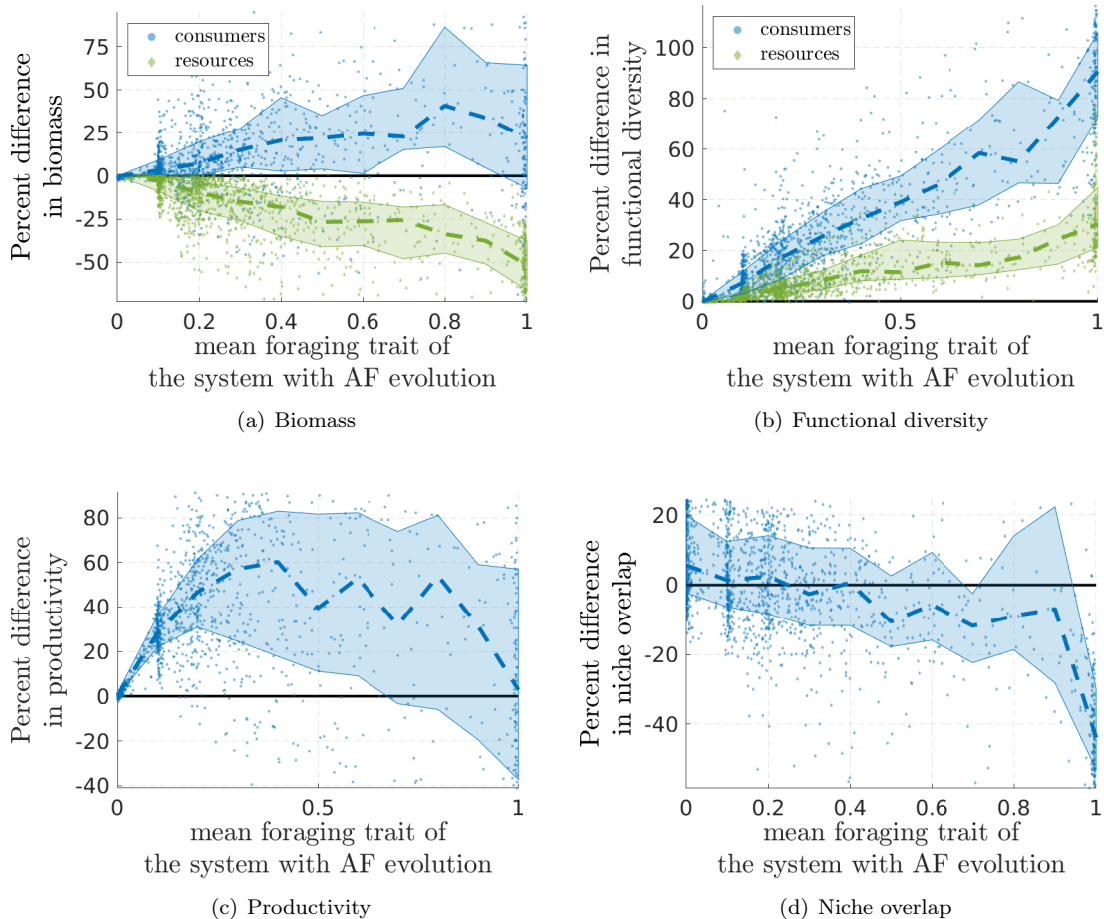


Figure 3: Difference (in %) between systems with AF evolution and fixed RF, for (a) biomass, (b) functional dispersion, (c) productivity, and (d) niche overlap. For each panel, 1500 simulations of 1000 time steps with AF evolution were compared to simulations with fixed RF, the parameters being randomly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

241 **3.3 The effects of disturbances**

242 **Ecosystem disturbance**

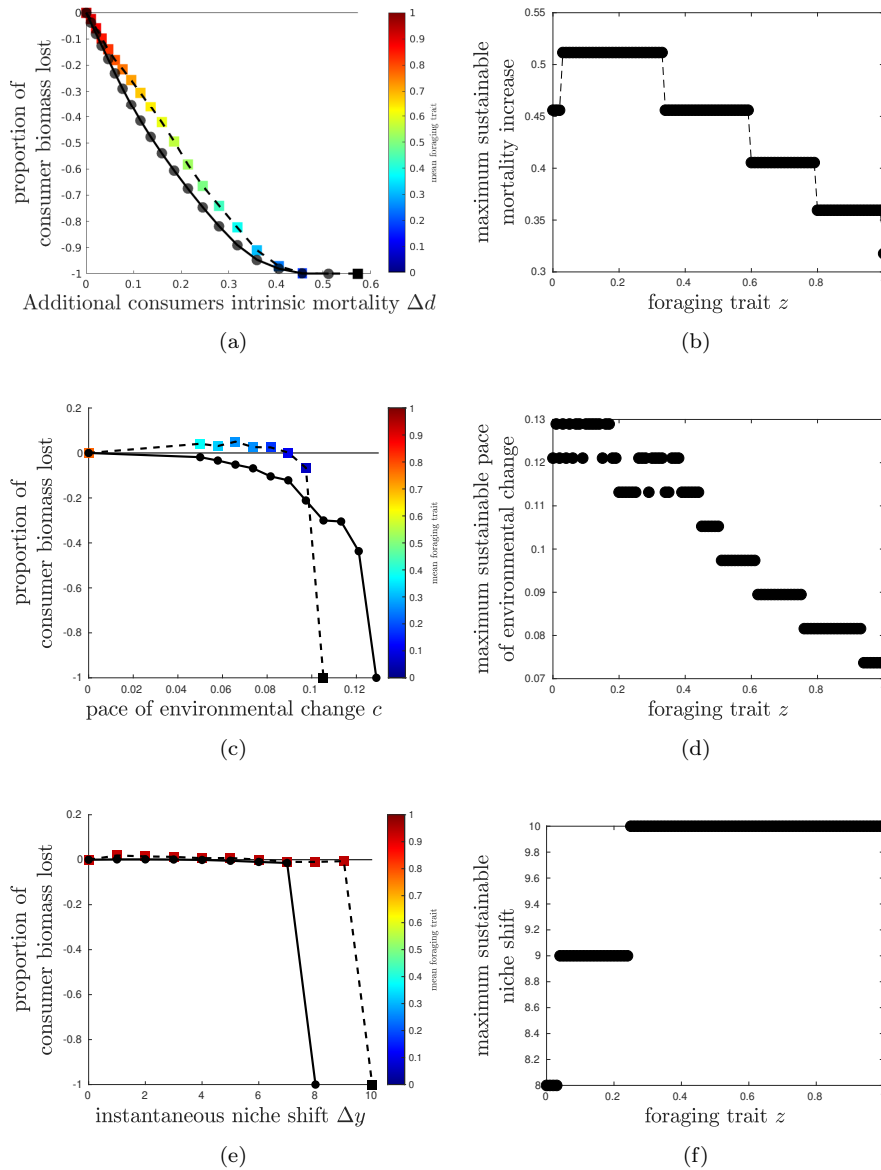


Figure 4: Effect of disturbances: (a, b) increased mortality Δd , (c, d) constant environment change c and (e, f) instantaneous niche shift Δy . Left column (a, c, e): variations of consumer biomass of systems with and without AF, in function of the intensity of the disturbance. A negative variation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

243 In reaction to increasing levels of consumer mortality, the system with AF evolution behaved as the system
 244 with fixed RF. Indeed, after each increment of mortality the new biomass of consumers was similar; and the
 245 consumers disappeared for the same mortality rate (Figure 4a). Moreover, at each mortality increase, consumers
 246 in the system with AF evolution gradually reduced their foraging trait, until AF ultimately disappeared (color
 247 scale in Figure 4a). Controlled monomorphic systems having low AF values better tolerated higher mortality rates
 248 (Figure 4b), which indicates that when AF was fixed it had a negative effect on the persistence of consumers
 249 facing increases in mortality.

250 Constant environmental change

251 The system with AF evolution tolerated the constant environmental change better than the system with fixed
252 RF, up to a certain point when it disappeared suddenly, earlier than its counterpart (Figure 4c). Moreover, as
253 in the case of ecosystem disturbance, the mean AF value decreased for faster environmental changes (color scale
254 in Figure 4c). Controlled monomorphic systems having low AF values tolerated faster environmental changes
255 (Figure 4d), which indicates that when AF was fixed it had a negative effect on the persistence of consumers
256 facing constant environmental change.

257 Sudden environmental change

258 After a sudden environmental change, either consumers disappeared or they persisted in a new state close to the
259 original one. In that case their niche traits shifted towards the new optimum and their foraging trait remained
260 unchanged, which is an indication of resilience. The variation of biomass before and after disturbance is therefore
261 uninformative; instead the maximal sudden environmental change that the consumer can tolerate was used to
262 quantify its stability (Figure 4e). The system with AF evolution resisted to a larger sudden change ($\delta_y = 10$)
263 compared with the system with fixed RF ($\delta_y = 8$). In order to disentangle the direct effect of AF on stability
264 from its indirect effect through diversity, the AF values of the consumers with AF were set to 0, while retaining
265 the original diversity of the niche traits x and y of both guilds. The resulting hybrid system tolerated a large
266 environmental change ($\delta_y = 10$), which indicates that the positive effect of AF on the persistence of consumers
267 was mainly due to its effects on diversity. In line with the above results, controlled monomorphic systems having
268 high AF values tolerated larger sudden environmental changes (Figure 4d).

269 4 Discussion

270 The evolutionary dynamics of adaptive foraging

271 Previous models exploring the effect of AF on community dynamics assumed that AF was a fixed trait of equal
272 intensity for all consumers (Kondoh, 2003; Uchida and Drossel, 2007; Beckerman et al., 2010; Heckmann et al.,
273 2012; Valdovinos et al., 2013). In these models, the foraging efforts of consumers changed in function of the
274 availability and suitability of their resources, but whether foraging efforts could change or not was itself not
275 subject to evolution. Egas et al. (2005) modelled the evolutionary dynamics of the consumers' niche width,
276 but not of their foraging selectivity. Therefore, the first motivation of this study was to explore under which
277 conditions the capacity to forage adaptatively can evolve by natural selection (Question 1 in the introduction).

278 As expected, elevated costs of AF (S_{max} , Table 1) disfavored its evolution, which is in accordance with the
279 existence of a trade-off between AF and other life-history traits like predation (Pangle et al., 2012; Wang et al.,
280 2013; McArthur et al., 2014; Costa et al., 2019), thermoregulation (du Plessis et al., 2012; Van de Ven et al.,
281 2019) and time budget (Randolph and Cameron, 2001; Fortin et al., 2004). In the present model the trade-off was
282 only incorporated into the handling time of the type II functional response, where high handling times reduced
283 resource absorption rates. We are nevertheless confident that similar results would have been obtained if the
284 trade-off had concerned mortality.

285 The evolution of AF was instead favored by the niche width of consumers (parameter σ). In nature, a positive
286 correlation between total niche width and inter-individual niche variation was found for herbivores (Bison et al.,
287 2015) and predators (Bolnick et al., 2007). Inter-individual niche variation reflects the existence of contrasting
288 foraging strategies, which may be the result of adaptive foraging. Baboons also combine niche breadth with
289 selectivity in resource use (Whiten et al., 1991). Since the evolution of consumer niche width may itself depend
290 on environmental heterogeneity (Kassen, 2002) (i.e. on resource diversity in the model), the coevolution of AF,
291 niche width and niche position is a possible avenue for future research. Niche width fostered AF because consumers
292 depleted the whole range of resources when their niche width was large, therefore competition between consumers
293 was more intense, which led to the evolution of AF. Empirical studies have indeed found that generalist consumers
294 competing for resources forage adaptatively. For instance generalist bumblebee species visited the larkspur
295 *Delphinium barbeyi* when the most abundant bumblebee species was experimentally removed, but preferred other
296 plant species otherwise, likely to avoid competition for nectar (Brosi and Briggs, 2013). A similar behavior has
297 been reported for syrphid flies, which preferentially foraged on open rather than tubular flowers when competing
298 with bumblebees (Fontaine et al., 2006). In the case of predators, intraspecific competition between sticklebacks
299 (*Gasterosteus aculeatus*) enhanced the diversity of foraging behaviors and increased the correlation between diet
300 and morphology (Svanbäck and Bolnick, 2007), as found here (Figure A4).

301 The present model further predicted that AF evolution is favoured by direct competition between consumers
302 I (other than for resources) as well as by increased consumer mortality δ . This is in line with the above results,
303 in the sense that constrained environmental condition for consumers strengthen the need for AF. On the other
304 hand AF becomes useful when resources are diversified enough, hence the positive effect of the resources niche
305 width σ_K .

306 The results discussed above are based on the mean foraging trait \bar{z} , but consumers positioned at the niche
307 edge foraged adaptatively much more often than those at the niche center (Figure 2b). Indeed, scarce resources
308 located at the niche edge were consumed significantly by adaptive foragers only, whereas abundant resources
309 located at the niche center could be consumed in large amounts by random foragers. This model prediction calls
310 for empirical testing, as we are not aware of any existing work reporting this pattern.

311 The effects of AF on functional diversity

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

319 As expected, the evolution of AF decreased niche overlap between consumers (Figure 3d). AF also decreased
320 niche overlap between pollinators in the model of Valdovinos et al. (2013) and in the experiments discussed
321 above (Fontaine et al., 2006; Brosi and Briggs, 2013). At the intraspecific level, niche overlap between individuals
322 of the same species decreases in function of their abundance (Svanbäck and Bolnick, 2007; Tur et al., 2014),
323 suggesting the existence of a plastic behavior. Since abundance favors intraspecific competition, this is consistent
324 with our findings that competition between consumers promotes the evolution of AF. The decrease of niche
325 overlap between consumers corresponds to niche partitioning, which may favor their coexistence (Behmer and
326 Joern, 2008; Turcotte and Levine, 2016). Indeed, in the model the evolution of AF enhanced the functional
327 diversity of both consumers and resources (Figure 3b), due to an eco-evolutionary loop between resources and
328 consumers situated at the niche edge. Following the evolution of AF some consumers foraged at the niche edge,

329 thereby reducing the density of the corresponding resources. This decreased competition among these resources
330 and promoted the emergence of new resource phenotypes at the niche edge. The diversification of resources
331 triggered the apparition of consumers standing even further away from the niche centre, and so on until the
332 resources reached the limits of the exploitable niche. This emphasizes that adaptive phenotypic plasticity like
333 AF can subsequently fuel evolutionary change (Baldwin, 1896; Crispo, 2007; Laland et al., 2014). Instead, when
334 no AF evolution was introduced, the few resources standing far away from the niche centre were barely used by
335 consumers, which could not forage preferentially on them. This prevented the emergence of new resources further
336 away from the niche centre, due to competition between resources. Since the evolution of AF occurred when the
337 diversity of resources was initially large enough (large σ_K), causation was reciprocal: AF both promoted and was
338 promoted by resource diversity.

339 Following the evolution of AF, the functional complementarity and diversity of consumers increased their
340 biomass at the expense of resources (Figure 3a). This fits with empirical studies showing a relationship between
341 resource consumption and consumer diversity (Deraison et al., 2015; Lefcheck et al., 2019; Milotić et al., 2019).
342 The effects of AF on productivity, defined as the net production of biomass by consumers following resource ab-
343 sorption (Table A1) were instead contrasted (Figure 3c). Moderate values of AF ($\bar{z} < 0.5$) increased productivity
344 thanks to functional complementarity between consumers (Poisot et al., 2013), but higher AF values decreased
345 productivity because consumers impacted resources too heavily.

346 The effects of AF on consumer persistence

347 After a sudden environmental change corresponding to an instantaneous shift of the niche center, consumers with
348 AF evolution withstood larger disturbances (Figure 4e). Previous theoretical studies have shown that AF can
349 stabilize foodwebs by favoring more robust topologies able to buffer environmental disturbances (Kondoh, 2003;
350 Heckmann et al., 2012). In the present model, the mechanisms responsible for this observation also rely on the
351 dynamical nature of the interaction webs produced by AF, but not on the emergence of robust topologies. One
352 of these mechanisms is caused by a direct effect of AF (Question 3a), and the other by an indirect effect through
353 diversity (Question 3b), as detailed in the results. The direct effect of AF on consumer persistence relies on
354 the mitigation of the lag load faced by consumers. Indeed, resources became adapted to the new niche center
355 more quickly than consumers, which suffered from a trait mismatch (e.g. Post and Forchhammer, 2008; Miller-
356 Struttmann et al., 2015; Damien and Tougeron, 2019). This indicates that phenotypic plasticity acted as a rapid
357 response mechanism to environmental change (Fox et al., 2019), in that case. Since random foragers consumed
358 the most abundant resources (but not the most suitable), after a sudden niche shift they fed on sub-optimal
359 resources, which hampered their resilience to environmental change. In contrast adaptive foragers selected less
360 abundant but more suitable resources, which favored their survival. In the meantime their traits evolved towards
361 the new niche optimum and ultimately caught up the resources, which illustrates that adaptive plasticity can
362 promote persistence in new environmental conditions (Ghalambor et al., 2007).

363 Turning to the indirect effect of AF on consumer persistence (Question 3b), when AF increased the diversity
364 of both resources and consumers this favored the emergence of extreme phenotypes far away from the niche center.
365 The extreme phenotypes were pre-adapted to the niche shift and therefore persisted, unlike the central species.
366 The positive effect of biodiversity on ecosystem functioning can be caused by complementarity and selection effects
367 (e.g. Loreau and Hector, 2001). In the present case, a few well-adapted phenotypes determined the resilience
368 to the niche shift : this corresponds to a selection effect. Although AF also increased complementarity between
369 species as discussed earlier, this did not created any synergy between phenotypes, at least with respect to the
370 resilience to the niche shift.

371 In the cases of ecosystem disturbance and constant environmental change, AF had this time a negative
372 effect on consumer persistence, as indicated by simulations with fixed AF values (Figures 4 b and d). For
373 both disturbances the cost of AF became larger than the benefits, and choosy consumers went extinct earlier
374 than random consumers. In particular, constant environmental changes weathered resource diversity to such a
375 point that RF and AF consumers had a similar diet, which annihilated the benefits of AF. It has been stressed
376 that phenotypic plasticity can retard adaptation to environmental change, shielding suboptimal phenotypes from
377 natural selection (Fox et al., 2019), but in the present model phenotypic plasticity was limited to the foraging
378 strategy of consumers. Instead, niche traits were not plastic and were therefore entirely sensitive to selection; the
379 negative effect of AF on consumer persistence was therefore only due to its cost. In nature however, niche trait
380 can also be plastic (e.g. Rossiter, 1987), but this was ignored by the model.

381 In figures 4 b and d AF was fixed but when AF could evolve, it gradually decreased in function of the intensity
382 of the disturbances (see color scales in Figures 4 a and c). In the case of a particularly fast environmental change,
383 consumers did not have enough time to reduce their AF searching behaviour and became extinct slightly earlier
384 (Figure 4c). The constant environmental change created a lag load to consumers, whose niche traits ran after those
385 of resources; in addition AF imposed a second lag load, corresponding to the time needed for the evolutionary
386 regression of AF. In the case of ecosystem disturbance, however, since optimal foragers quickly turned into random
387 foragers, both types of foraging strategies responded in a similar way (Figure 4a). A purely ecological model
388 ignoring the evolutionary dynamics of AF would have missed the possibility of its evolutionary regression, and
389 would have therefore overestimated the negative effect of AF on consumer persistence. In the simulations, the

390 various disturbance types have been applied independently, but in nature they can be combined. In such cases,
391 ecosystem disturbance and/or constant environmental change might first lead to the evolutionary regression of
392 the AF behaviour, and a sudden shift might then facilitate the extinction of consumers, since they would not be
393 protected by AF any more.

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

399 Assumption and limitations of the model

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

403 First, in previous works the absence of AF corresponded to a constant interaction matrix between resources
404 and consumers (e.g. Kondoh, 2003; Valdovinos et al., 2013). Instead, in the present model the alternative to
405 adaptive foraging consists in random foraging, where resources are consumed according to their density. The
406 interaction matrix is therefore highly dynamic for both foraging strategies, although for different reasons. In the
407 case of RF the resources exploited by a given consumer change according to their abundance only, whereas in
408 the case of AF they also change according to their traits, the consumer’s trait, and their degree of exploitation
409 by other consumers. In previous models allowing the evolutionary diversification of niche traits, the interaction
410 matrices were dynamic but consumers did not forage adaptatively (Loeuille and Loreau, 2005; Allhoff et al.,
411 2015). In those cases as well as here, new phenotypes constantly appear and need to be incorporated into the
412 food web, which is therefore inherently dynamic (Appendix A.2). In comparison to RF, a consumer having fixed
413 interaction coefficients would ignore these new phenotypes even if its favorite resources had gone extinct, which
414 would make little sense. Besides, AF alone can produce non-equilibrium dynamics even with a fixed community
415 composition, by triggering consumer-resource cycles (Abrams, 1992; Abrams and Matsuda, 2004).

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

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

428 Conclusion

429 The present model illustrates how phenotypic plasticity can be simultaneously a result and a factor of evolution.
430 On the one hand, adaptive foraging (AF) evolved by natural selection acting on consumers. On the other hand,
431 it stimulated the diversification of ecological characters not only of consumers but also of resources, stressing that
432 phenotypic plasticity can have far-reaching evolutionary consequences at the community-level (Fordyce, 2006).
433 Moreover, functional diversity itself promoted the evolution of AF, creating an eco-evolutionary feedback loop
434 between phenotypic plasticity, natural selection and community composition. This had intricate consequences on
435 the response of the resource-consumer community to disturbances. In the case of sudden environmental change,
436 the evolution of AF had a positive effect on community stability, partly via its effects on functional diversity.
437 However for other disturbance types like constant change and increases in mortality, the AF behavior was less
438 fit than random foraging and therefore declined. In contrast to previous studies, these results stress that the
439 relationship between AF and community stability depends on the type of the disturbance as well as on the
440 evolutionary dynamics of AF itself.

441 **A Appendix**

442 **A.1 Model details**

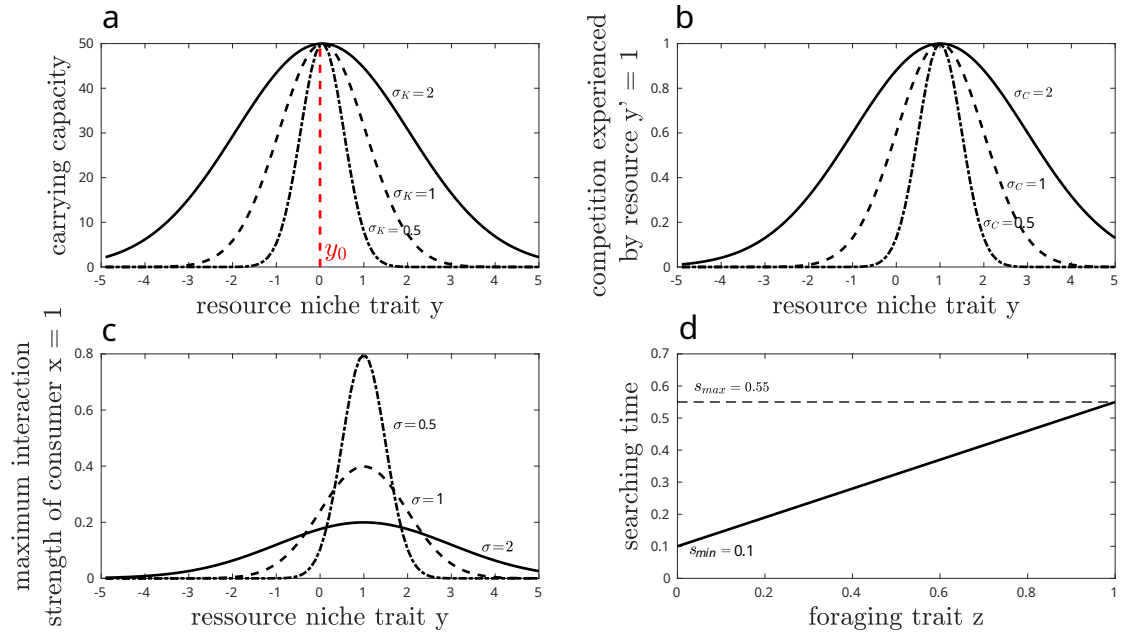


Figure A1: a) Carrying capacity $K(y)$ of resources for various niche width values $\sigma_K = \{0.5, 1, 2\}$. The niche centre fixed at $y_0 = 0$ corresponds to the maximal carrying capacity. b) Competition kernel K_{eff} for various neighbourhood size $\sigma_C = \{0.5, 1, 2\}$ between a focal resource $y' = 1$ and all resources in function of their niche trait y . c) Interactions kernel Δ for various generalization levels ($\sigma = \{0.5, 1, 2\}$) between a focal consumer ($x = 1$) and all the resources in function of their niche trait y . d) Searching time s in function of the foraging trait z . Parameter values as in Table 1.

| Quantitative traits | | Ranges |
|-----------------------------|--|---|
| x | Consumers niche trait | $[-5; 5]$ |
| y | Resources niche trait | $[-5; 5]$ |
| z | Consumers foraging trait | $[0; 1]$ |
| State variables | | Shapes |
| $r(t, y)$ | Resource density | see Eq. (1) |
| $R(t)$ | Total resource biomass | $R(t) = \int r(t, y) dy$ |
| $\bar{y}(t)$ | Mean resource trait | $\bar{y}(t) = \int y \frac{r(t, y)}{R(t)} dy$ |
| $c(t, x, z)$ | Consumer density with foraging trait z | see Eq. (2) |
| $\bar{c}(t, x)$ | Consumer biomass with trait x | $\bar{c}(t) = \int c(t, x, z) dz$ |
| $C(t)$ | Total consumer biomass | $C(t) = \iint c(t, x, z) dx dz$ |
| $\bar{x}(t)$ | Mean consumer niche trait | $\bar{x}(t) = \int x \frac{\bar{c}(t, x)}{C(t)} dx$ |
| $\bar{z}(t)$ | Mean foraging trait | $\bar{z}(t) = \iint z \frac{c(t, x, z)}{C(t)} dx dz$ |
| $\phi_{RF}(t, y)$ | Random Foraging efforts | $\phi_{RF}(t, y) = \frac{r(t, y)}{R(t)}$ |
| $\phi_{AF}(t, x, y, z)$ | Relative Foraging efforts | see Eq. (7) |
| $\phi(t, x, y, z)$ | Effective Foraging efforts | $\phi = z\phi_{AF} + (1 - z)\phi_{RF}$ |
| Functional responses | | Shapes |
| $F_r[r, c, \phi](t, y)$ | Resource consumption | see Eq. (4) |
| $F_c[r, \phi](t, x, z)$ | Resource absorption | see Eq. (5) |
| $K(y)$ | Carrying capacity | $K(y) = \frac{e^{-\frac{y^2}{2\sigma_K^2}}}{\sqrt{2\pi\sigma_K^2}}$ |
| $K_{eff}(y)$ | 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. (3) |
| $\Delta(x, y)$ | 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 gain of a consumer | see Eq. (8) |
| $s(z)$ | Searching time | $s(z) = s_{min} + z(s_{max} - s_{min})$ |
| $\mathcal{M}_y(r)(t, y)$ | Resource niche trait mutations | see Eq. (10) |
| $\mathcal{M}_x(c)(t, x, z)$ | Consumer niche trait mutations | see Eq. (10) |
| $\mathcal{M}_z(c)(t, x, z)$ | Foraging trait mutations | see Eq. (10) |
| 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 | $FDis_c(t) = \int \frac{ x - \bar{x}(t) (t, x)}{\int (t, x) dx} dx$ |
| $Prod$ | Productivity | $Prod = \iint c(T, x, z) F_c[r, \phi](T, x, z) dx dz$ |
| ρ_{ij} | Niche overlap between foraging traits | see Eq. (14) |
| $FM(t)$ | Functional match | see Eq. (15) |

Table A1: List of the quantitative traits subject to evolutionary change, the state variables, the functions and the aggregate system-level properties involved the model.

443 A.2 Stationary regime

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

452 A.3 Effect of a fixed AF trait

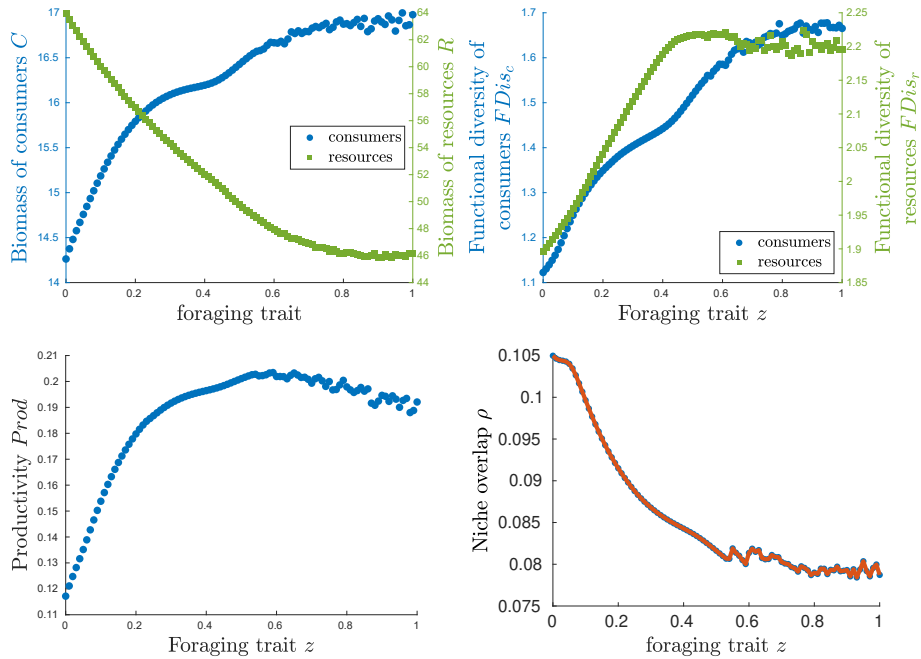


Figure A3: Effect of a fixed foraging trait value z on systems where only the niche traits x and y of resources and consumers can evolve. The measured characteristics are biomass, functional diversity, productivity, and niche overlap.

453 A.4 Functional match between resources and consumers

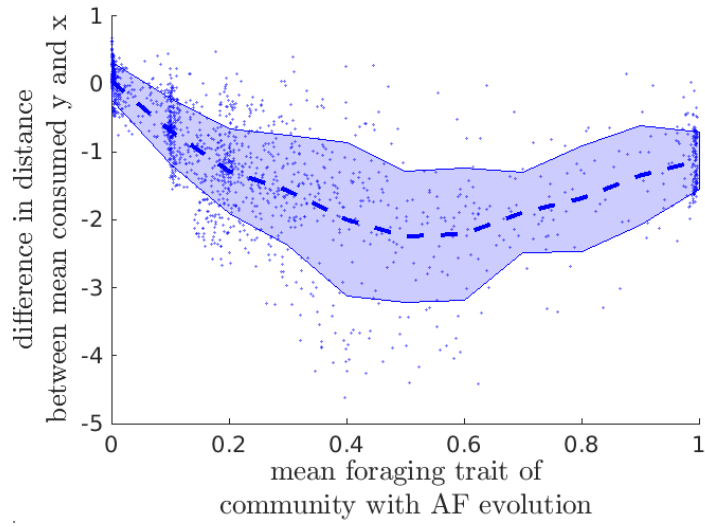


Figure A4: Difference in functional matching between systems with AF evolution and systems with fixed RF. 500 pairs of systems were compared, each pair having the same parameter set randomly sampled in the ranges specified in Table 1. Dashed lines: median; areas: 75% confidence intervals.

454 References

- 455 P.A. Abrams. Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology*, 6(1):
456 56–72, 1992. doi: 10.1007/BF02285334.
- 457 P.A. Abrams. Can adaptive evolution or behaviour lead to diversification of traits determining a trade-off between
458 foraging gain and predation risk? *Evolutionary Ecology Research*, 5(5):653–670, 2003.
- 459 P.A. Abrams. Implications of flexible foraging for interspecific interactions: Lessons from simple models. *Func-*
460 *tional Ecology*, 24(1):7–17, 2010. doi: 10.1111/j.1365-2435.2009.01621.x.
- 461 P.A. Abrams and H. Matsuda. Consequences of behavioral dynamics for the population dynamics of predator-prey
462 systems with switching. *Population Ecology*, 46(1):13–25, 2004. doi: 10.1007/s10144-003-0168-2.
- 463 K.T. Allhoff, D. Ritterskamp, B.C. Rall, B. Drossel, and C. Guill. Evolutionary food web model based on body
464 masses gives realistic networks with permanent species turnover. *Scientific Reports*, 5(1):10955, 2015. doi:
465 10.1038/srep10955.
- 466 F. Altermatt. Tell me what you eat and I’ll tell you when you fly: Diet can predict phenological changes in
467 response to climate change: Phenological change and diet breadth. *Ecology Letters*, 13(12):1475–1484, 2010.
468 doi: 10.1111/j.1461-0248.2010.01534.x.
- 469 J.M. Baldwin. A new factor in evolution. *The american naturalist*, 30(354):441–451, 1896.
- 470 J.S. Bale, G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse,
471 J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press,
472 I. Symrnioudis, A.D. Watt, and J.B. Whittaker. Herbivory in global climate change research: Direct effects
473 of rising temperature on insect herbivores. *Global Change Biology*, 8(1):1–16, 2002. doi: 10.1046/j.1365-2486.
474 2002.00451.x.
- 475 A. Beckerman, O.L. Petchey, and P.J. Morin. Adaptive foragers and community ecology: Linking individuals to
476 communities and ecosystems. *Functional Ecology*, 24(1):1–6, 2010. doi: 10.1111/j.1365-2435.2009.01673.x.
- 477 A.P. Beckerman, O.L. Petchey, and P.H. Warren. Foraging biology predicts food web complexity. *Proceedings of*
478 *the National Academy of Sciences*, 103(37):13745–13749, 2006. doi: 10.1073/pnas.0603039103.
- 479 S.T. Behmer and A. Joern. Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings*
480 *of the National Academy of Sciences*, 105(6):1977–1982, 2008. doi: 10.1073/pnas.0711870105.
- 481 L. Berec, J. Eisner, and V. Křivan. Adaptive foraging does not always lead to more complex food webs. *Journal*
482 *of Theoretical Biology*, 266(2):211–218, 2010. doi: 10.1016/j.jtbi.2010.06.034.
- 483 C.M. Bergman, J.M. Fryxell, C.C. Gates, and D. Fortin. Ungulate foraging strategies: Energy maximizing or
484 time minimizing? *Journal of Animal Ecology*, 70(2):289–300, 2001. doi: 10.1111/j.1365-2656.2001.00496.x.
- 485 M.G. Bidart-Bouzat and A. Imeh-Nathaniel. Global change effects on plant chemical defenses against insect
486 herbivores. *Journal of Integrative Plant Biology*, 50(11):1339–1354, 2008. doi: 10.1111/j.1744-7909.2008.
487 00751.x.
- 488 M. Bison, S. Ibanez, C. Redjadj, F. Boyer, E. Coissac, C. Miquel, D. Rioux, S. Said, D. Maillard, P. Taberlet,
489 N.G. Yoccoz, and A. Loison. Upscaling the niche variation hypothesis from the intra- to the inter-specific level.
490 *Oecologia*, 179(3):835–842, 2015. doi: 10.1007/s00442-015-3390-7.
- 491 M. Boersma, K.A. Mathew, B. Niehoff, K.L. Schoo, R.M. Franco-Santos, and C.L. Meunier. Temperature driven
492 changes in the diet preference of omnivorous copepods: No more meat when it’s hot? *Ecology Letters*, 19(1):
493 45–53, 2016. doi: 10.1111/ele.12541.
- 494 D.I. Bolnick, R. Svanbäck, M.S. Araújo, and L. Persson. Comparative support for the niche variation hypothesis
495 that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of*
496 *Sciences*, 104(24):10075–10079, 2007. doi: 10.1073/pnas.0703743104.
- 497 B.J. Brosi and H.M. Briggs. Single pollinator species losses reduce floral fidelity and plant reproductive function.
498 *Proceedings of the National Academy of Sciences*, 110(32):13044–13048, 2013. doi: 10.1073/pnas.1307438110.
- 499 L. Buisson, G. Grenouillet, S. Villéger, J. Canal, and P. Laffaille. Toward a loss of functional diversity in stream
500 fish assemblages under climate change. *Global change biology*, 19(2):387–400, 2013. doi: 10.1111/gcb.12056.
- 501 A. Charmantier, R.H. McCleery, L.R. Cole, C. Perrins, L.E.B. Kruuk, and Ben C. Sheldon. Adaptive phenotypic
502 plasticity in response to climate change in a wild bird population. *science*, 320(5877):800–803, 2008. doi:
503 10.1126/science.1157174.
- 504 P. Chesson and J.J. Kuang. The interaction between predation and competition. 2008.
- 505 L.-M. Chevin, S. Collins, and F. Lefèvre. Phenotypic plasticity and evolutionary demographic responses to climate
506 change: Taking theory out to the field. *Functional Ecology*, 27(4):967–979, 2013. doi: 10.1111/j.1365-2435.
507 2012.02043.x.
- 508 F.J. Clissold, G.D. Sanson, J. Read, and S.J. Simpson. Gross vs. net income: How plant toughness affects
509 performance of an insect herbivore. *Ecology*, 90(12):3393–3405, 2009. doi: 10.1890/09-0130.1.

- 510 A.N. Costa, H.L. Vasconcelos, E.H.M. Vieira-Neto, and E.M. Bruna. Adaptive foraging of leaf-cutter ants to
511 spatiotemporal changes in resource availability in Neotropical savannas. *Ecological Entomology*, 44(2):227–238,
512 2019. doi: 10.1111/een.12697.
- 513 E. Crispo. The Baldwin effect and genetic assimilation: Revisiting two mechanisms of evolutionary change
514 mediated by phenotypic plasticity. *Evolution: International Journal of Organic Evolution*, 61(11):2469–2479,
515 2007. doi: 10.1111/j.1558-5646.2007.00203.x.
- 516 M. Damien and K. Tougeron. Prey–predator phenological mismatch under climate change. *Current opinion in
517 insect science*, 35:60–68, 2019. doi: 10.1016/j.cois.2019.07.002.
- 518 H. Deraison, I. Badenhauer, N. Loeuille, C. Scherber, and N. Gross. Functional trait diversity across trophic
519 levels determines herbivore impact on plant community biomass. *Ecology letters*, 18(12):1346–1355, 2015. doi:
520 10.1111/ele.12529.
- 521 U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400(6742):354, 1999.
522 doi: 10.1038/22521.
- 523 L.M. Dill. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic
524 Sciences*, 40(4):398–408, 1983. doi: 10.1139/f83-058.
- 525 V. Domínguez-García, V. Dakos, and S. Kéfi. Unveiling dimensions of stability in complex ecological networks.
526 *Proceedings of the National Academy of Sciences*, page 201904470, 2019. doi: 10.1073/pnas.1904470116.
- 527 K.L. du Plessis, R.O. Martin, P.A.R. Hockey, S.J. Cunningham, and A.R. Ridley. The costs of keeping cool in
528 a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an
529 arid-zone bird. *Global Change Biology*, 18(10):3063–3070, 2012. doi: 10.1111/j.1365-2486.2012.02778.x.
- 530 M. Egas, M.W. Sabelis, and U. Dieckmann. Evolution of specialization and ecological character displacement of
531 herbivores along a gradient of plant quality. *Evolution*, 59(3):507–520, 2005. doi: 10.1111/j.0014-3820.2005.
532 tb01011.x.
- 533 C. Fontaine, I. Dajoz, J. Meriguet, and M. Loreau. Functional Diversity of Plant–Pollinator Interaction Webs
534 Enhances the Persistence of Plant Communities. *PLoS Biol*, 4(1):e1, 2006. doi: 10.1371/journal.pbio.0040001.
- 535 J.A. Fordyce. The evolutionary consequences of ecological interactions mediated through phenotypic plasticity.
536 *Journal of Experimental Biology*, 209(12):2377–2383, 2006. doi: 10.1242/jeb.02271.
- 537 D. Fortin, M.S. Boyce, E.H. Merrill, and J.M. Fryxell. Foraging costs of vigilance in large mammalian herbivores.
538 *Oikos*, 107(1):172–180, 2004. doi: 10.1111/j.0030-1299.2004.12976.x.
- 539 R.J. Fox, J.M. Donelson, C. Schunter, T. Ravasi, and J.D. Gaitán-Espitia. Beyond buying time: The role of
540 plasticity in phenotypic adaptation to rapid environmental change. *Philosophical Transactions of the Royal
541 Society B: Biological Sciences*, 374(1768):20180174, 2019. doi: 10.1098/rstb.2018.0174.
- 542 S.A.H. Geritz, E. Kisdi, G. Meszéna, and J.A.J. Metz. Evolutionarily singular strategies and the adaptive growth
543 and branching of the evolutionary tree. *Evolutionary ecology*, 12(1):35–57, 1998. doi: 10.1023/A:1006554906681.
- 544 C.K. Ghalambor, J.K. McKay, S.P. Carroll, and D.N. Reznick. Adaptive versus non-adaptive phenotypic plasticity
545 and the potential for contemporary adaptation in new environments. *Functional ecology*, 21(3):394–407, 2007.
546 doi: 10.1111/j.1365-2435.2007.01283.x.
- 547 A. Gonzalez, O. Ronce, R. Ferriere, and M.E. Hochberg. Evolutionary rescue: An emerging focus at the inter-
548 section between ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
549 368(1610):20120404, 2013. doi: 10.1098/rstb.2012.0404.
- 550 M.P. Hassell and T.R.E. Southwood. Foraging strategies of insects. *Annual review of ecology and systematics*, 9
551 (1):75–98, 1978. doi: 10.1146/annurev.es.09.110178.000451.
- 552 L. Heckmann, B. Drossel, U. Brose, and C. Guill. Interactive effects of body-size structure and adaptive foraging
553 on food-web stability. *Ecology letters*, 15(3):243–250, 2012. doi: 10.1111/j.1461-0248.2011.01733.x.
- 554 S. Ibanez, C. Gallet, and L. Després. Plant insecticidal toxins in ecological networks. *Toxins*, 4(4):228–243, 2012.
555 doi: 10.3390/toxins4040228.
- 556 K. Jensen, D. Mayntz, S. Toft, F.J. Clissold, J. Hunt, D. Raubenheimer, and S.J. Simpson. Optimal foraging for
557 specific nutrients in predatory beetles. *Proceedings of the Royal Society of London B: Biological Sciences*, 279
558 (1736):2212–2218, 2012. doi: 10.1098/rspb.2011.2410.
- 559 R. Kassen. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of
560 evolutionary biology*, 15(2):173–190, 2002. doi: 10.1046/j.1420-9101.2002.00377.x.
- 561 J.T. Kerby, C.C. Wilmers, and E. Post. Climate change, phenology, and the nature of consumer–resource
562 interactions: Advancing the match/mismatch hypothesis. In *Trait-Mediated Indirect Interactions: Ecological
563 and Evolutionary Perspectives*, pages 508–25. 2012.
- 564 M. Kondoh. Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. *Science*,
565 299(5611):1388–1391, 2003. doi: 10.1126/science.1079154.
- 566 M. Kopp and S. Matuszewski. Rapid evolution of quantitative traits: Theoretical perspectives. *Evolutionary*

- 567 *Applications*, 7(1):169–191, 2014. doi: 10.1111/eva.12127.
- 568 C. Kovach-Orr and G.F. Fussmann. Evolutionary and plastic rescue in multitrophic model communities.
569 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1610):20120084, 2013. doi:
570 10.1098/rstb.2012.0084.
- 571 R. Kowalczyk, J.M. Wójcik, P. Taberlet, T. Kamiński, C. Miquel, A. Valentini, J.M. Craine, and E. Coissac.
572 Foraging plasticity allows a large herbivore to persist in a sheltering forest habitat: DNA metabarcoding diet
573 analysis of the European bison. *Forest Ecology and Management*, 449:117474, October 2019. doi: 10.1016/j.
574 foreco.2019.117474.
- 575 V. Křivan and O.J. Schmitz. Adaptive foraging and flexible food web topology. *Evolutionary Ecology Research*,
576 5(5):623–652, 2003.
- 577 K. Laland, T. Uller, M. Feldman, K. Sterelny, G.B. Müller, A. Moczek, E. Jablonka, J. Odling-Smee, G.A.
578 Wray, H.E. Hoekstra, D.J. Futuyma, R.E. Lenski, T.F.C. Mackay, D. Schluter, and J.E. Strassmann. Does
579 evolutionary theory need a rethink? *Nature News*, 514(7521):161, 2014. doi: 10.1038/514161a.
- 580 E. Laliberté and P. Legendre. A distance-based framework for measuring functional diversity from multiple traits.
581 *Ecology*, 91(1):299–305, 2010. doi: 10.1890/08-2244.1.
- 582 J.S. Lefcheck, A.A. Innes-Gold, S.J. Brandl, R.S. Steneck, R.E. Torres, and D.B. Rasher. Tropical fish diversity
583 enhances coral reef functioning across multiple scales. *Science Advances*, 5(3):eaav6420, March 2019. doi:
584 10.1126/sciadv.aav6420.
- 585 W.C. Lemon. Heritability of selectively advantageous foraging behaviour in a small passerine. *Evolutionary
586 Ecology*, 7(4):421–428, July 1993. doi: 10.1007/BF01237873.
- 587 N. Loeuille. Consequences of adaptive foraging in diverse communities. *Functional Ecology*, 24(1):18–27, February
588 2010. doi: 10.1111/j.1365-2435.2009.01617.x.
- 589 N. Loeuille and M. Loreau. Evolutionary emergence of size-structured food webs. *Proceedings of the National
590 Academy of Sciences*, 102(16):5761–5766, 2005. doi: 10.1073/pnas.0408424102.
- 591 M. Loreau and A. Hector. Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412
592 (6842):72–76, July 2001. doi: 10.1038/35083573.
- 593 R.H. MacArthur and E.R. Pianka. On optimal use of a patchy environment. *The American Naturalist*, 100(916):
594 603–609, 1966.
- 595 C. McArthur, P.B. Banks, R. Boonstra, and J.S. Forbey. The dilemma of foraging herbivores: Dealing with food
596 and fear. *Oecologia*, 176(3):677–689, 2014. doi: 10.1007/s00442-014-3076-6.
- 597 J. Merilä and A.P. Hendry. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence.
598 *Evolutionary applications*, 7(1):1–14, 2014. doi: 10.1111/eva.12137.
- 599 N.E. Miller-Struttman, J.C. Geib, J.D. Franklin, P.G. Kevan, R.M. Holdo, D. Ebert-May, A.M. Lynn, J.A.
600 Kettenbach, E. Hedrick, and C. Galen. Functional mismatch in a bumble bee pollination mutualism under
601 climate change. *Science*, 349(6255):1541–1544, 2015. doi: 10.1126/science.aab0868.
- 602 T. Milotić, C. Baltzinger, C. Eichberg, A.E. Eycott, M. Heurich, J. Müller, J.A. Noriega, R. Menendez, J. Stadler,
603 and R. Ádám. Functionally richer communities improve ecosystem functioning: Dung removal and secondary
604 seed dispersal by dung beetles in the Western Palearctic. *Journal of Biogeography*, 46(1):70–82, 2019. doi:
605 10.1111/jbi.13452.
- 606 B.G. Miner, S.E. Sultan, S.G. Morgan, D.K. Padilla, and R.A. Relyea. Ecological consequences of phenotypic
607 plasticity. *Trends in ecology & evolution*, 20(12):685–692, 2005. doi: 10.1016/j.tree.2005.08.002.
- 608 D.H. Nussey, E. Postma, P. Gienapp, and M.E. Visser. Selection on heritable phenotypic plasticity in a wild bird
609 population. *Science*, 310(5746):304–306, 2005. doi: 10.1126/science.1117004.
- 610 K.L. Pangle, T.D. Malinich, D.B. Bunnell, D.R. DeVries, and S.A. Ludsins. Context-dependent planktivory:
611 Interacting effects of turbidity and predation risk on adaptive foraging. *Ecosphere*, 3(12):1–18, 2012. doi:
612 10.1890/ES12-00224.1.
- 613 S.I. Peluc, T.S. Sillett, J.T. Rotenberry, and C.K. Ghalambor. Adaptive phenotypic plasticity in an island songbird
614 exposed to a novel predation risk. *Behavioral Ecology*, 19(4):830–835, 2008. doi: 10.1093/beheco/arn033.
- 615 D.W. Pfennig. *Phenotypic Plasticity & Evolution: Causes, Consequences, Controversies*. Taylor & Francis, 2021.
- 616 T. Poisot, N. Mouquet, and D. Gravel. Trophic complementarity drives the biodiversity–ecosystem functioning
617 relationship in food webs. *Ecology Letters*, 16(7):853–861, 2013. doi: 10.1111/ele.12118.
- 618 S.M.J. Portalier, J. Candau, and F. Lutscher. A temperature-driven model of phenological mismatch provides
619 insights into the potential impacts of climate change on consumer–resource interactions. *Ecography*, n/a(n/a):
620 e06259. doi: 10.1111/ecog.06259.
- 621 E. Post and M.C. Forchhammer. Climate change reduces reproductive success of an Arctic herbivore through
622 trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1501):2367–2373,
623 2008. doi: 10.1098/rstb.2007.2207.

- 624 J.C. Randolph and G.N. Cameron. Consequences of diet choice by a small generalist herbivore. *Ecological*
625 *Monographs*, 71(1):117–136, 2001. doi: 10.1890/0012-9615(2001)071[0117:CODCBA]2.0.CO;2.
- 626 S. Rasmann and L. Pellissier. Adaptive responses of plants to insect herbivores under climate change. In *Climate*
627 *Change and Insect Pests*, pages 38–53. 2015.
- 628 S. Rasmann, L. Pellissier, E. Defosse, H. Jactel, and G. Kunstler. Climate-driven change in plant–insect inter-
629 actions along elevation gradients. *Functional Ecology*, 28(1):46–54, 2014. doi: 10.1111/1365-2435.12135.
- 630 A.E. Rosenblatt and O.J. Schmitz. Climate Change, Nutrition, and Bottom-Up and Top-Down Food Web
631 Processes. *Trends in Ecology & Evolution*, 31(12):965–975, 2016. doi: 10.1016/j.tree.2016.09.009.
- 632 M.C. Rossiter. Genetic and phenotypic variation in diet breadth in a generalist herbivore. *Evolutionary Ecology*,
633 1(3):272–282, 1987. doi: 10.1007/BF02067557.
- 634 A. Saltelli, S. Tarantola, F. Campolongo, and M. Ratto. *Sensitivity Analysis in Practice: A Guide to Assessing*
635 *Scientific Models*. Chichester, England, 2004. doi: 10.1111/j.1467-985X.2005.358_13.x.
- 636 C. Scherber, D.J. Gladbach, K. Stevnbak, R.J. Karsten, I.K. Schmidt, A. Michelsen, K.R. Albert, K.S. Larsen,
637 T.N. Mikkelsen, and C. Beier. Multi-factor climate change effects on insect herbivore performance. *Ecology*
638 *and evolution*, 3(6):1449–1460, 2013. doi: 10.1002/ece3.564.
- 639 G.G. Simpson. The baldwin effect. *Evolution*, 7(2):110–117, 1953. doi: 10.2307/2405746.
- 640 M.S. Singer, E.A. Bernays, and Y. Carriere. The interplay between nutrient balancing and toxin dilution in
641 foraging by a generalist insect herbivore. *Animal Behaviour*, 64(4):629–643, 2002. doi: 10.1006/anbe.2002.3082.
- 642 J.T. Staley and S.N. Johnson. Climate change impacts on root herbivores. In *Root Feeders: An Ecosystem*
643 *Perspective*, pages 192–215. 2008. doi: 10.1079/9781845934613.019.
- 644 J. Sundell, J.A. Eccard, R. Tiilikainen, and H. Ylönen. Predation rate, prey preference and predator switching:
645 Experiments on voles and weasels. *Oikos*, 101(3):615–623, 2003. doi: 10.1034/j.1600-0706.2003.12264.x.
- 646 R. Svanbäck and D.I. Bolnick. Intraspecific competition drives increased resource use diversity within a natural
647 population. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611):839–844, 2007. doi: 10.1098/
648 rspb.2006.0198.
- 649 W. Thuiller, S. Lavorel, M.T. Sykes, and M.B. Araújo. Using niche-based modelling to assess the impact of
650 climate change on tree functional diversity in Europe. *Diversity and Distributions*, 12(1):49–60, 2006. doi:
651 10.1111/j.1366-9516.2006.00216.x.
- 652 C; Tur, J.M. Olesen, and A. Traveset. Increasing modularity when downscaling networks from species to indi-
653 viduals. *Oikos*, 2014. doi: 10.5061/dryad.63fp5.
- 654 M.M. Turcotte and J.M. Levine. Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*,
655 31(10):803–813, 2016. doi: 10.1016/j.tree.2016.07.013.
- 656 S. Uchida and B. Drossel. Relation between complexity and stability in food webs with adaptive behavior. *Journal*
657 *of theoretical biology*, 247(4):713–722, 2007. doi: 10.1016/j.jtbi.2007.04.019.
- 658 S.B. Unsicker, A. Oswald, G. Köhler, and W.W. Weisser. Complementarity effects through dietary mixing
659 enhance the performance of a generalist insect herbivore. *Oecologia*, 156(2):313–324, 2008. doi: 10.1007/
660 s00442-008-0973-6.
- 661 F.S. Valdovinos, P. Moisset de Espanés, J.D. Flores, and R. Ramos-Jiliberto. Adaptive foraging allows the
662 maintenance of biodiversity of pollination networks. *Oikos*, 122(6):907–917, 2013. doi: 10.1111/j.1600-0706.
663 2012.20830.x.
- 664 T.M. Van de Ven, A.E. McKechnie, and S. Cunningham. The costs of keeping cool: Behavioural trade-offs between
665 foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, 191
666 (1):205–215, 2019. doi: 10.1007/s00442-019-04486-x.
- 667 M. Van Kleunen and M. Fischer. Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology*, 82
668 (12):3309–3319, 2001. doi: 10.1890/0012-9658(2001)082[3309:AEOFR]2.0.CO;2.
- 669 J. Varner and M.D. Dearing. Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal*
670 *of Mammalogy*, 95(1):72–81, 2014. doi: 10.1644/13-MAMM-A-099.1.
- 671 O. Vedder, S. Bouwhuis, and B.C. Sheldon. Quantitative Assessment of the Importance of Phenotypic Plasticity
672 in Adaptation to Climate Change in Wild Bird Populations. *PLOS Biology*, 11(7):e1001605, 2013. doi:
673 10.1371/journal.pbio.1001605.
- 674 A. Wallin. The genetics of foraging behaviour: Artificial selection for food choice in larvae of the fruitfly,
675 *Drosophila melanogaster*. *Animal Behaviour*, 36(1):106–114, 1988. doi: 10.1016/S0003-3472(88)80253-7.
- 676 M.F. WallisDeVries. Effects of resource distribution patterns on ungulate foraging behaviour: A modelling
677 approach. *Forest Ecology and Management*, 88(1):167–177, 1996. doi: 10.1016/S0378-1127(96)03822-4.
- 678 L. Wang, D. Wang, Y. Bai, G. Jiang, J. Liu, Y. Huang, and Y. Li. Spatial distributions of multiple plant species
679 affect herbivore foraging selectivity. *Oikos*, 119(2):401–408, 2010. doi: 10.1111/j.1600-0706.2009.17774.x.

- 680 M-Y. Wang, T.C. Ings, M.J. Proulx, and L. Chittka. Can bees simultaneously engage in adaptive foraging
681 behaviour and attend to cryptic predators? *Animal Behaviour*, 86(4):859–866, 2013. doi: 10.1016/j.anbehav.
682 2013.07.029.
- 683 M.J. West-Eberhard. *Developmental Plasticity and Evolution*. Oxford University Press, 2003.
- 684 A. Whiten, R.W. Byrne, R.A. Barton, P.G. Waterman, and S.P. Henzi. Dietary and foraging strategies of
685 baboons. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 334(1270):
686 187–197, 1991. doi: 10.1098/rstb.1991.0108.