1   # Implications of (co)evolution of agriculture and resource foraging for the

2   # maintenance of species diversity and community structure

3   Aurore Picot[1,2], Thibaud Monnin[1] & Nicolas Loeuille[1]

4   [1] Sorbonne Université, Université de Paris, Université Paris-Est Créteil, CNRS, INRAE, IRD,

5   institute of Ecology and Environmental Science of Paris (iEES-Paris), Campus Pierre et Marie

6   Curie, 4 place Jussieu, 75005 Paris, France

7   [2] University of Lausanne, Département de Microbiologie Fondamentale, Groupe Mitri

8   **Corresponding author**: **picotaurore@gmail.com**

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11   **Abstract**: Agriculture is found in numerous taxa such as humans, ants, beetles, fishes and even

12   bacteria. This type of niche construction has evolved independently from hunting, though many

13   species remain primarily predators. When a consumer has a positive effect on its resource, we can

14   expect an allocative cost of agriculture, as the agricultural care diverts time and energy from other

15   activities. Defending the resource against predators may divert time from its consumption

16   (exploitation cost). The cost may also occur on the foraging of alternative resources, for instance if

17   the consumer spends more time nearby the farmed resource and underexploiting resources

18   elsewhere (opportunity cost). We here investigate transitions from predation to agriculture in a

19   simple three-species model of a farmer that consumes two resources and has a positive effect on

20   one. We study the conditions for the (co)evolution of the investment into agriculture and

21   specialization on the two resources, and its consequences on the ecological dynamics of the

22   community. Eco-evolutionary dynamics generate a feedback between the evolution of agriculture

23   and specialization on the helped resource, that can lead to varying selected intensity of agriculture,

24   from generalist strategies with no agriculture, to specialist farmers, with possible coexistence

25   between these two extreme strategies.

Introduction

Some of the species that display the greatest ecological success perform agriculture, that we here define as the cultivation of plants, algae, fungi and the herding of animal. Agriculture is a type of niche construction, an active modification of its environment by an organism, that potentially feed backs on the selective pressures acting upon it (Odling-Smee et al. 2013). A typical example is the impact of agriculture on the evolutionary history of humans and species affected by agriculture (Boivin et al. 2016). Humans have been causing both ecological and evolutionary change through their practice of agriculture, from direct effects such as artificial selection and domestication, to indirect effects such as climate change or introduction of invasive species, and causing the evolution of resistance to use of herbicides or pesticides (Thrall et al. 2011; Loeuille et al. 2013). The consequences of domestication, for instance, are important not only for the selected species (that can display drastic modifications of their phenotypic traits compared to the ancestral, undomesticated species (Thrall et al. 2011)) but also for other species within agricultural landscapes, as the domesticated species may become a dominant species exerting a strong selective force. Humans are not the only species to practice agriculture. Many ant species can use other insects, such as aphids, as cattle, or cultivate fungi (Mueller et al. 2005). Numerous taxa benefit from actively managing their resources: agriculture is also found in termites, beetles, fishes, nematodes and even microorganisms (Hata and Kato 2006; Boomsma 2011; Thutupalli et al. 2017; Brooker et al. 2020). The benefits associated with agriculture are easily understandable in changing, unpredictable and competitive environments: it potentially increases the resource availability, limits competition if the cattle or exploitation is privatized, and allows a greater predictability of resource abundance compared to foraging.

From a consumer-resource theory perspective, agriculture can be envisioned as a modification of a purely trophic interaction between a consumer and a resource. This interaction is then not only

50 consisting of consumption or predation, but contains an additional positive effect of the consumer

51 on the resource, which has been described in various contexts (Abrams 1992; Brown et al. 2004;

52 Terry et al. 2017). The ecological and evolutionary consequences of including positive effects into

53 trophic networks have recently received increasing attention (Fontaine et al. 2011; Kéfi et al. 2012;

54 Mougi and Kondoh 2012). Accounting for such non trophic interactions alters the stability of

55 networks and coexistence of species. Positive effects associated with agriculture can emerge from

56 different consumer behaviours (protection against predators, helped reproduction or dispersal, for

57 instance). It can impact the resource demography in various ways (increase of the carrying

58 capacity, increase of the growth rate) that are expected to increase the resource profitability for the

59 farmer species, compared to alternative foraged resources. The evolution of agriculture has been

60 envisioned in the niche construction perspective, particularly in the human context (Rowley-Conwy

61 and Layton 2011; Boivin et al. 2016; Zeder 2016) A classical example of the consequences of niche

62 construction through agriculture is the evolution of lactose tolerance in humans (Laland and

63 O'Brien 2011).

64 Jointly to the niche construction perspective, the ecological and evolutionary consequences of

65 agriculture can be conceived in the light of foraging theories (optimal foraging, (Charnov 1976;

66 Pyke et al. 1977), adaptive foraging, (Loeuille 2010)). This can help understand the question of the

67 potential transition between foraging strategies such as hunting, gathering, to agricultural strategies.

68 The evolution of agriculture can lead to full specialization and reciprocal dependency of the

69 agricultural partners, as in fungus-growing ants (Mueller et al. 2005). To understand those two

70 questions (transition to settled agriculture, extreme specialization), we can use the evolution of

71 specialization framework (Egas et al. 2004; Abrams 2006). Optimal foraging theory predicts that

72 the specialization of a consumer will evolve depending on the resources profitabilities. Agriculture

73 practice can then modify the resource profitability through the modification of its abundance.

74 Hence we expect that increasing agriculture selects for higher specialization on the cultivated

75 resource that becomes more profitable, in turn selecting for more agriculture, leading to a positive

76 feedback loop between agriculture and specialization on the cultivated resource. As a consequence,

77 we expect reciprocal evolutionary consequences (or coevolution) between the evolution of

78 specialization (*sensu* consumption, predation) on the resources, and the evolution of agriculture.

79 From this perspective, we can understand the evolution of agriculture as the addition of another

80 dimension to the classic evolution of specialization: an organism allocates energy or time between

81 the consumption of different resources, and the cultivation of one or several resources. Two types

82 of evolutionary outcomes are expected: either a high level of agriculture with a high specialization

83 on the managed resource, or no agriculture and generalism or a specialist on another resource

84 depending on the trade-off associated with the foraging activities.

85   This simple prediction can be modified by accounting for the cost of agriculture: the niche

86 constructing phenotype can first be threatened by cheaters, if niche construction benefits are shared

87 by all the population (potentially leading to a tragedy of commons, (Hardin 1968)). Farming can

88 then be considered a public good (Thutupalli et al. 2017). Although privatization might overcome

89 the threat of freerider invasion (through pleiotropy, (Chisholm et al. 2018), monopolization of the

90 niche (Krakauer et al. 2009) or benefits going to the closest relatives (Scheiner et al. 2021)), trade-

91 offs can still mitigate the evolution of agriculture by altering the profitabilities of the resources. If

92 the cultivated resource is initially much less profitable than an alternative resource, we predict that

93 agriculture may be counter-selected despite potential benefits. A cost to agricultural behaviour

94 could emerge because of a high presence of competitors, predators or pathogens of the resource

95 that needs to be actively protected (Hübner and Völkl 1996; Stadler and Dixon 2005; Adams et al.

96 2013; Fernández-Marín et al. 2013; Thutupalli et al. 2017). Here, we investigate the cost of

97 agriculture in the foraging theory perspective: increasing the niche construction activity occurs at a

98 cost on the consumption of resources, because of a limited energy or time budget available to the

99 farmer species. Agriculture can, as a type of resource exploitation, decrease the consumption of an

100   alternative resource ("opportunity cost", described in Picot et al. (2019)). It can as well decrease the

101   consumption of the managed resource, e.g. if defending it against predators or competitors implies

102   moving away from the resource site, or allocating more time to defense rather than consumption

103   ("exploitation cost" scenario, Picot et al. (2019)).

104   Because of the previously stated feedback loop, understanding the (co)evolution of

105   agriculture and specialization requires to investigate its ecological consequences in terms of

106   variations in resource abundances. Explicitly accounting for niche construction in models and

107   theory leads to patterns that would not be predictable otherwise (Kylafis and Loreau 2011). In

108   humans, agriculture is known to have drastic effects on the community and ecosystem level

109   properties: for instance, by introducing invasive species that engage in apparent competition with

110   native ones (David et al. 2017; Geslin et al. 2017), so that agricultural has pervasive consequences

111   for the maintenance of species diversity and ecosystem functioning (Emmerson et al. 2016). The

112   study of indirect effects may give insights on the community consequences of the evolution of

113   agriculture. Indirect effects are effects of one species on another, transmitted by another species

114   (Wootton 1994), here the consumer species. When a consumer consumes two resources, those

115   resources engage in apparent competition (Holt 1977): an increase in density of one resource may

116   decrease the other resource growth rate through their interaction with the consumer. Agricultural

117   aspects modify this view. In an ecological analysis of a consumer-resource model with niche

118   construction, Picot et al. (2019) show that cultivated and non-cultivated resources may then engage

119   in various types of indirect interactions through the consumer. Without considering any cost,

120   increasing niche construction has a positive effect on the managed resource density, which

121   translates in a bottom-up positive effect on the consumer density, and a negative effect on the

122   alternative density, because of apparent competition. Considering costs of niche construction

123   mitigates this result. If the cost of niche construction is high enough in terms of resource

124   consumption, an increase in niche construction of the cultivated resource may lead to counter-

125 intuitive increase in the alternative resource density, because of a decrease in its consumption rate

126 ("opportunity cost" scenario) and/or a decrease of the consumer density ("exploitation cost"

127 scenario and "opportunity cost").

128 In this study, we use adaptive dynamics and numerical simulations to study the evolution

129 and coevolution of a consumer niche constructing trait and its specialization on two resources

130 (Geritz et al. 1998). We address the following questions: (1) How does a fixed foraging strategy

131 impact the selected investment into agriculture? We predict that a high specialization on the

132 managed resource favours the evolution of agriculture, while a high specialization on the

133 alternative resource prevents it. (2) How does the profitability of the different resources impact the

134 coevolution of the niche construction trait and the specialization on the resources? We predict a

135 positive correlation between the evolution of agriculture and specialization on the cultivated

136 resource. (3) How do the evolution of niche construction and its coevolution with specialization

137 impact the coexistence of the resources and the functioning of the system? We then predict that a

138 high selected level of agriculture leads to the exclusion of the alternative resource because of

139 increased apparent competition, while counter-selection of niche construction should lead to

140 coexistence of the resources.

Model presentation

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Ecological dynamics

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143 Our model is based on ordinary differential equations describing the ecological dynamics of the

144 consumer and two resource species. In this simple model (eq (1) and Fig 1 *A*), the consumer

145 species C interacts with the two resources R_1 and R_2. The resource R_1 is managed through

146 agriculture: we assume it receives a positive effect that increases its growth rate, but it is also

147 consumed. The alternative resource R_2 is only consumed:

$$\begin{cases} \dfrac{dC}{dt} = C\left(e_1(x)\,s_1(x)\,R_1 + e_2\,s_2(x)\,R_2 - m\right) & (a) \\[2mm] \dfrac{dR_1}{dt} = R_1\left(b_1 - g_1\,R_1 - s_1(x)\,C + w\,x\,C\right) & (b) \\[2mm] \dfrac{dR_2}{dt} = R_2\left(b_2 - g_2\,R_2 - s_2(x)\,C\right) & (c) \end{cases} \qquad (1)$$

148   The consumer *per capita* growth rate depends on its consumption of resources (modelled by

149   specialization on resource R_i, s_i, and consumption efficiency of resource R_i, e_i) and on its death rate

150   *m*. In the absence of the consumer, the two resources grow logistically (allowing for their

151   coexistence in such situations): b_i is the birth rate and g_i is the intraspecific competition rate for

152   resource R_i. Only apparent competition through the interactions with the consumer is considered

153   here: we do not consider any direct competition between resources, which allows us to single out

154   the impacts of the consumer. Finally, note that resource R_1 receives a positive effect from

155   agriculture, proportional to the investment into niche construction *x* and niche construction

156   efficiency *w*. We assume that all parameters e_i, s_i, b_i, g_i, x are positive. Niche construction is then

157   facultative for the maintenance of R_1, as both resources have positive intrinsic growth rates.

Trade-offs: costs and benefits of niche construction

159   As stated above, we assume that agriculture occurs at a cost for foraging on the resources. We

160   consider two trade-off scenarios that rely on a time or energy constraint: increasing the agricultural

161   intensity can decrease the consumption of the managed resource ("exploitation cost", $s_1'(x) < 0$) or

162   the consumption of the alternative resource ("opportunity cost", $s_2'(x) < 0$). We consider that the

163   three traits are linked through the following formula:

$$x^k + s_1^k + s_2^k = L \qquad (2)$$

164   *L* represents the total amount of time or energy that the consumer allocates between niche

165   construction and the consumption of the two resources. In the opportunity cost scenario, s_1 is fixed

166   while in the exploitation cost scenario, s_2 is fixed. In the coevolution scenario, the three traits may

167   evolve jointly along the trade-off surface (Fig 1 *B*). The exponent *k* shapes the trade-off

168   (accelerating for a convex trade-off, $k > 1$ or saturating for a concave trade-off, $k < 1$).

169   We also assume that niche construction provides a direct benefit for the organisms performing it:

170   for instance, agriculture can provide a more direct access to the managed resource and increase its

171   consumption efficiency, because of proximity, or through another adaptation. We positively link the

172   consumption efficiency to the agricultural trait through the following expression

$$e_1(x) = (1+x)^u \tag{3}$$

173   where *u<1* indicates saturating efficiency increase (diminishing returns, for instance if the

174   efficiency consumption is constrained by other factors, such as physiological ones) while *u>1*

175   indicates an accelerating response.

Ecological dynamics

177   The ecological dynamics of a similar system has been studied in Picot et al. (2019), assuming a

178   fixed level of niche construction, and differing only in the trade-off functions that are used. In this

179   previous work, niche construction intensity linearly decreased with specialization rates s_1 and s_2,

180   and no direct benefit of niche construction was assumed (this would mean *u=0* in our present

181   model). However, some general results of the ecological dynamics apply in the present model:

182   different types of ecological equilibria are obtained: either the coexistence of the two resources,

183   with or without the consumer, or the maintenance of one resource (still with or without the

184   consumer) or the extinction of all species. Note that this previous work only tackled ecological

185   dynamics, while we here focus on the evolution of the different traits.

Evolutionary dynamics

186

187   We first study the evolution of the phenotypic trait x using the adaptive dynamics framework

188   (Dieckmann and Law 1996; Geritz et al. 1998), assuming that the consumer diet (s_1, s_2) is fixed.

189   Adaptive dynamics allows to investigate evolutionary dynamics of phenotypic traits while defining

190   the fitness of a given phenotype based on its ecological dynamics. The analytical framework relies

191   on the separation of ecological and evolutionary timescales, while numerical simulations allows us

192   to more freely investigate the limits of this hypothesis. The evolution of a trait is studied through

193   several steps, assuming clonal reproduction, and small and rare mutations:

194   - the ecological equilibrium is determined, for a monomorphic population of resident trait x_{res}

195   (by nullifying equations 1(a) to 1(c))

196   - a rare mutant with trait x_{mut} is introduced and replaces the resident trait if its invasion fitness

197   (i.e., its *per capita* growth rate when rare, based on eq1(a)) is positive. Invasion fitness is given by:

$$W(x_{mut}, x_{res}) = e_1(x_{mut}) s_1(x_{mut}) R_1^*(x_{res}) + e_2 s_2(x_{mut}) R_2^*(x_{res}) - m \qquad (4)$$

198   The new ecological equilibrium is established and the process is iterated.

199   A deterministic approximation of the evolution of the trait is given by the canonical equation of

200   adaptive dynamics (Dieckmann and Law 1996) :

$$\frac{dx}{dt} = \frac{1}{2} \mu \sigma^2 N^0(x_{res}) \left. \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} \right|_{x_{mut} \to x_{res}} \qquad (5)$$

201    $\mu \sigma^2 N^0(x_{res})$ is the evolutionary potential, that is total phenotypic variability brought by

202   mutations with μ the *per capita* mutation rate, σ^2 the phenotypic variance associated to these

203   mutations and $N^0(x_{res})$ the resident population equilibrium density. The selection gradient

204    $\left.\dfrac{\partial W\left(x_{mut},x_{res}\right)}{\partial x_{mut}}\right|_{x_{mut}\to x_{res}}$ is derived from the invasion fitness (eq 4) and corresponds to the slope

205   of the fitness landscape around the resident population, therefore representing the selective

206   pressures acting on the phenotypic variability brought by mutations. The traits that nullify this

207   gradient are called singular strategies (Dieckmann and Law 1996). Dynamics around these singular

208   strategies are characterized by the second partial derivatives of fitness (Dieckmann and Law 1996;

209   Geritz et al. 1998). This allows to distinguish two stability-related properties: invasibility and

210   convergence. A singular strategy x^* is non-invasible (Maynard Smith 1982), or evolutionary stable

211   if:

$$\left.\frac{\partial^2 W\left(x_{mut},x_{res}\right)}{\partial x_{mut}^{\ 2}}\right|_{x_{mut}\to x_{res}\to x^*} < 0 \tag{6}$$

212   *i.e.* when the singular strategy is the resident population, no nearby mutant can invade.

213   A singular strategy is convergent or continuously stable (Eshel 1983) if:

$$\left.\frac{\partial^2 W\left(x_{mut},x_{res}\right)}{\partial x_{mut}^{\ 2}}\right|_{x_{mut}\to x_{res}\to x^*} + \left.\frac{\partial^2 W\left(x_{mut},x_{res}\right)}{\partial x_{mut}\partial x_{res}}\right|_{x_{mut}\to x_{res}\to x^*} < 0 \tag{7}$$

214   *i.e.*, considering a resident population close to the singular strategy, mutants that are even closer

215   to it are selected. The two trade-off scenarios lead to different fitness expressions for each scenario,

216   since in the "exploitation cost" scenario, s_2 is fixed and $s_1(x)=\left(L-s_2^k-x^k\right)^{\frac{1}{k}}$ while in the

217   opportunity cost scenario s_1 is fixed leading to $s_2(x)=\left(L-s_1^k-x^k\right)^{\frac{1}{k}}$.

218   We illustrate the evolution of x in the "exploitation cost" and "opportunity cost" scenarios using

219   numerical simulations. The simulation algorithm was built in C++.

220 Coevolutionary dynamics

221 In the coevolution scenario, we let the three traits s_1, s_2, and x vary while accounting for trade-

222 off constraints (equation (2)). This means we allow the two traits s_1 and x to evolve independently

223 and derive the trait s_2 from the trade-off. We approach this question both with semi-analytical

224 calculations, and using our evolutionary algorithm, by introducing mutations of the three traits.

225 When both x and s_1 jointly evolve, we derive two expressions of the fitness. The fitness $W_x(x_{mut},$

226 $x_{res},$ $s_{1res})$ of a mutant of trait x_{mut} and the fitness $W_{s1}(s_{1mut}, s_{1res}, x_{res})$ of a mutant of trait s_{1mut} appearing

227 in a resident population of traits x_{res} and s_{1res} are:

$$W_x(x_{mut}, x_{res}, s_{1res}) = e_1(x_{mut}) s_{1res} R_1 *(x_{res}, s_{1res}) + e_2 s_2(x_{mut}, s_{1res}) R_2 *(x_{res}, s_{1res}) - m$$
$$W_{s_1}(s_{1mut}, s_{1res}, x_{res}) = e_1(x_{res}) s_{1mut} R_1 *(x_{res}, s_{1res}) + e_2 s_2(x_{res}, s_{1mut}) R_2 *(x_{res}, s_{1res}) - m \qquad (8)$$

228 We can then compute the two coupled fitness gradients:

$$\left. \frac{\partial W_x(x_{mut}, x_{res}, s_{1res})}{\partial x_{mut}} \right|_{x_{mut} \to x_{res}} = e_1'(x_{mut}) s_{1res} R_1 *(x_{res}, s_{1res}) + e_2 \frac{\partial s_2(x_{mut}, s_{1res})}{\partial x_{mut}} R_2 *(x_{res}, s_{1res}) = 0$$

$$\left. \frac{\partial W_{s_1}(s_{1mut}, s_{1res}, x_{res})}{\partial s_{1mut}} \right|_{s_{1mut} \to s_{1res}} = e_1(x_{res}) R_1 *(x_{res}, s_{1res}) + e_2 \frac{\partial s_2(x_{res}, s_{1mut})}{\partial s_{1mut}} R_2 *(x_{res}, s_{1res}) = 0 \qquad (9)$$

229 The coevolutionary dynamics of the traits are then described by a system of coupled canonical

230 equations (Dieckmann and Law 1996):

$$\frac{dx}{dt} = \frac{1}{2} \mu_x \sigma_x^2 N^0(x_{res}, s_{1res}) \left. \frac{\partial W_x(x_{mut}, x_{res}, s_{1res})}{\partial x_{mut}} \right|_{x_{mut} \to x_{res}}$$

$$\frac{ds_1}{dt} = \frac{1}{2} \mu_{s_1} \sigma_{s_1}^2 N^0(x_{res}, s_{1res}) \left. \frac{\partial W_{s_1}(s_{1mut}, x_{res}, s_{1res})}{\partial s_{1mut}} \right|_{s_{1mut} \to s_{1res}} \qquad (10)$$

231   The singularities are obtained by solving the system (10), which means finding x and s_1 values

232   that simultaneously nullify the two fitness gradients, (x^*, s_1^*). This is done by numerically solving

233   the equations in Mathematica with fixed parameter values. From the equations of the

234   coevolutionary dynamics, we can derive the Jacobian matrix and evaluate the conditions to obtain a

235   stable coalition (evolutionary attractor) for the singularity (x^*, s_1^*) (Marrow et al. 1996).

236   The Jacobian matrix J of the system (10) at the equilibrium (x^*, s_1^*) is:

$$J = \frac{1}{2} N^0 \begin{bmatrix} \mu_x \sigma_x^2 \left(\frac{\partial^2 W_x}{\partial^2 x_{mut}} + \frac{\partial^2 W_x}{\partial x_{mut} \partial x_{res}} \right) & \mu_x \sigma_x^2 \frac{\partial^2 W_x}{\partial x_{mut} \partial s_{1res}} \\ \mu_{s_1} \sigma_{s_1}^2 \frac{\partial^2 W_{s_1}}{\partial s_{1mut} \partial x_{res}} & \mu_{s_1} \sigma_{s_1}^2 \left(\frac{\partial^2 W_{s_1}}{\partial^2 s_{1mut}} + \frac{\partial^2 W_{s_1}}{\partial s_{1mut} \partial s_{1res}} \right) \end{bmatrix}_{\substack{x_{mut} \to x_{res} \to x^* \\ s_{1mut} \to s_{1res} \to s_1^*}} \tag{11}$$

237   The condition to have a stable equilibrium (x^*, s_1^*) is that $Tr(J) < 0$ and $Det(J) > 0$. We note that the

238   diagonal terms correspond to the criteria of convergence in the monomorphic evolution, so if these

239   terms are negative, then $Tr(J) < 0$. The second condition is that $Det(J) > 0$ (which is the condition for

240   absolute convergence in Kisdi (2006). This condition can be expressed as:

$$\left[\left(\frac{\partial^2 W_x}{\partial^2 x_{mut}} + \frac{\partial^2 W_x}{\partial x_{mut} \partial x_{res}} \right) \left(\frac{\partial^2 W_{s_1}}{\partial^2 s_{1mut}} + \frac{\partial^2 W_{s_1}}{\partial s_{1mut} \partial s_{1res}} \right) > \frac{\partial^2 W_x}{\partial x_{mut} \partial s_{1res}} \frac{\partial^2 W_{s_1}}{\partial s_{1mut} \partial x_{res}} \right]_{\substack{x_{mut} \to x_{res} \to x^* \\ s_{1mut} \to s_{1res} \to s_1^*}} \tag{12}$$

241   We then numerically check that the two conditions are met at the singularities. We also adapt our

242   evolutionary algorithm in C++ to take account for the coevolution of the three traits and check that

243   the algorithm converges to the analytically obtained singularity values.

Results

1) Evolutionary dynamics of agriculture in the two trade-off scenarios

"Exploitation cost" scenario: managing the resource or consuming it.

In this scenario, increasing the intensity of niche construction negatively impacts the consumption of the helped resource. We first study the general possible evolutionary dynamics depending on the trade-off shape, then focus on the linear trade-off scenario to get a more thorough mathematical investigation. As a first step, we do not specify the various functions implied in the biological trade-off, in order to have a general analysis of possible evolutionary dynamics: we ignore equations 2 and 3 and simply assume that s_1 decreases with x while e_1 increases with x.

Considering these assumptions in the fitness function definition (eq (4)) allows us to compute the fitness gradient (eq (13)):

$$G(x_{mut}, x_{res}) = \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} = \left(e_1{}'(x_{mut}) s_1(x_{mut}) + e_1(x_{mut}) s_1{}'(x_{mut})\right) R_1{}^*(x_{res}) \qquad (13)$$

From this equation, we immediately note that if we do not consider a direct benefit to niche construction ($e_1{}'(x_{mut})=0$), the fitness gradient becomes negative (as $s_1{}'(x_{mut})<0$). This leads to gradual decrease of the trait and counter-selection of niche construction. This is consistent with the result of Chisholm et al. (2018): considering a direct benefit (from pleiotropy or pseudo-spatialization) is necessary to avoid a tragedy of the commons. That is inevitable given that our completely mixed model implicitly assumes that all consumers have access to the farmed resource (i.e., interaction is modeled by a mass action function). Variation in spatial access is a well-known way to avoid this situation (Lion et al. 2011). To keep the model simple and tractable, we thus consider an easier access to the constructed ressource, i.e.that $e_1{}'(x_{mut})>0$.

264   Assuming that the helped resource is not extinct ($R_1{}^*(x^*) > 0$), the position of singular strategies

265   x^* can be obtained from eq (14).

$$(e_1 s_1)'(x^*) = e_1'(x^*) s_1(x^*) + e_1(x^*) s_1'(x^*) = 0 \tag{14}$$

266   This mathematical condition means that the singular strategies correspond to an optimum of the

267   realized consumption of the managed resource: if this strategy is an evolutionary endpoint,

268   evolution optimize total effective consumption of the managed resource, since the consumption

269   efficiency and specialization rate vary oppositely with agriculture trait x. We then expect

270   intermediate levels of agriculture to be selected for. In the scenario, we also note that the value of

271   the singular strategy only depends on this consumption-efficiency optimization: the densities of the

272   resources do not matter.

273   Replacing the fitness gradient with the chosen functions of equations 2 and 3 (in equation (14))

274   leads to:

$$\left(L - s_2^k - x^{*k}\right)^{\frac{1-k}{k}}\left(x^{*k} - \left(L - s_2^k\right) u\, x^{*u} + (1+u)\, x^{*k+u}\right) = 0 \tag{15}$$

275   The condition for non-invasibility and convergence (that are equivalent here, see Supplementary

276   Information for details) is:

$$(u-1) u\, x^{*u} \ - \ \frac{2u\, x^{*k+u}}{L - s_2^k - x^{*k}} \ - \ \frac{(k-1)\left(L - s_2^k\right) x^{*k}\left(1 + x^{*u}\right)}{\left(L - s_2^k - x^{*k}\right)^2} < 0 \tag{16}$$

277   In the linear case ($u=k=1$), the equation (15) becomes $\left(x^* - \left(L - s_2\right) x^* + 2 x^{*2}\right) = 0$. We obtain

278   two possible singularities: $x^* = 0$ (which is a neutral case in the sense that the second derivative is

279   null) or $x* = \dfrac{(L - s_2 - 1)}{2}$ which is always convergent and non-invasible (CSS) (the second

280   derivative expressed in (16) is $\dfrac{-2 x*^2}{L - s_2 - x*}$ and is negative), it is an evolutionary endpoint.

281   While a completely general study using non-linear trade-offs is not possible, note that a

282   sufficient condition to obtain a CSS is that $u < 1$ and $k > 1$ (see equation (16)), in other terms

283   having diminishing returns of niche construction on resource consumption efficiency and a concave

284   trade-off between specialization and niche construction. If $u > 1$ and $k < 1$ (accelerating efficiency

285   and convex trade-off) the strategy may be characterized as a repellor (an unstable evolutionary

286   point) depending of the sign of our expression. In this case, directional selection brings the trait to

287   either zero niche construction (and total consumption), or total niche construction (and zero

288   consumption), the latter case being less likely biologically. We show the possible evolutionary

289   dynamics for different trade-off shapes in Supplementary Figure S1.

290   *"Opportunity cost" scenario: managing one resource or foraging on another resource*

291   When increasing agriculture occurs at a cost of the consumption of the alternative resource, the

292   invasion fitness of a mutant of trait x_{mut} appearing in a resident population of consumer with trait

293   x_{res} is derived:

$$W(x_{mut}, x_{res}) = e_1(x_{mut}) s_1 R_1{}^*(x_{res}) + e_2 s_2(x_{mut}) R_2{}^*(x_{res}) - m \tag{17}$$

294   To obtain the fitness gradient $G(x_{mut},x_{res})$ we consider the derivation of the fitness with respect to the

295   mutant trait x_{mut}:

$$G(x_{mut}, x_{res}) = \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} = e_1{}'(x_{mut}) s_1 R_1{}^*(x_{res}) + e_2 s_2{}'(x_{mut}) R_2{}^*(x_{res}) \tag{18}$$

296   Singularities $x*$ are obtained through nulling $G(x*,x*)$. The position of the singularity depends on

297   optimizing both the consumption efficiency and the cost on the alternative resource consumption.

298   Contrary to the previous scenario, the resident agricultural trait x_{res} matters for the position of the

299   singularity. The non-invasibility condition is given for a general trade-off and for our chosen trade-

300   off functions in equation (18):

$$e_1''(x*)s_1 R_1*(x*) + e_2 s_2''(x*)R_2*(x*) < 0$$
$$e_1(u-1)u\,x^{u-2}s_1 R_1*(x*) + e_2(1-k)(L-s_1^k)x^{k-2}(L-x*^k-s_1^k)^{\frac{1}{k}-2}R_2*(x*) < 0 \tag{19}$$

301   In the linear case ($u = k = 1$), the invasibility criteria is null, but not necessarily the convergence

302   criteria. This can lead us to identify parameters set for which the strategy is convergent, and

303   invasible.

304   As in the previous scenario, we can get partial information in the non-linear cases. We obtain a

305   sufficient condition for non-invasibility of the singular strategy (equation (19)) (i.e. if this level of

306   agriculture is reached, it is an ESS): $u < 1$ and $k > 1$. A sufficient condition for the invasibility of

307   the point is that if $u > 1$ and $k < 1$. Those invasibility conditions are the same as for the

308   "exploitation cost" scenario invasibility condition. Conditions for evolutionary convergence are

309   however not tractable in the general case, and we only study numerically (see Supplementary

310   Information for the convergence condition).

311   2) Effect of specialization patterns on the evolutionary dynamics of

312   agriculture and feedbacks on the ecological dynamics

313   In the "exploitation cost" scenario, when we consider linear functions, we obtain a continuously

314   stable strategy (CSS) that is both convergent and non-invasible. The value of this selected level of

315   agriculture is expressed in eq 20:

$$x* = \frac{(L - s_2 - 1)}{2} \tag{20}$$

316 This singular strategy is positive if $s_2 < L-1$. If $s_2 > L-1$, the value of the singularity becomes

317 negative and the niche constructing trait evolves to 0. From the expression of the singularity (eq

318 20) we show that the selected level of niche construction is is negatively correlated to

319 specialization on resource R_2, consistent with our predictions.

320 The consumption of the managed resource at the evolutionary equilibrium ($s_1(x*)$) is

$$s_1(x*) = L - s_2 - \frac{(L - s_2 - 1)}{2} = \frac{(L - s_2 + 1)}{2} \tag{21}$$

321 We plot the value of the selected agriculture level and consequent consumption of the managed

322 resource, as a function of specialization on resource 2 in Figure 2 *A*. We represent the area of stable

323 coexistence of the species when resource 2 specialization s_2 and x vary (ecologically). We show

324 that the selected value of agriculture, $x*$ (represented as a black line) falls in the resource

325 coexistence area (the black arrows indicated the direction of evolution, meaning that starting from a

326 high value of agriculture, evolution brings the trait back into a coexistence area. The corresponding

327 equilibrium densities are shown on Figure 2 *B*. Increasing the consumption of the alternative

328 resource leads to a decrease in its evolutionary equilibrium density. The highest consumer

329 equilibrium density is obtained when the specialization on the alternative resource is intermediate

330 (and when the cultivated resource density is the lowest).

331 The slopes of the selected $x*$ and $s_1(x*)$ are the same (the lines are parallel), meaning that a higher

332 specialization on resource 2 equally impact niche constructing activities and exploitation of the

333 managed resource. This comes directly from our trade-off expression: mathematically, we assume

334 that the total amount of energy or time L is a linear combination of all the traits and here they all

335 have the same coefficient (i.e., 1). Were we to weight the different traits through different

336 coefficients, so that the variation of each trait does not have the same impact on the energy

337 allocation, then at the evolutionary equilibrium, modifying the specialization on resource 2 would

338   lead to weighted cost on agriculture investment and the resource 1 consumption (see

339   Supplementary Figure S2). In the non-linear CSS cases as well, the intensity of alternative resource

340   consumption is negatively correlated with the evolved level of agriculture (figure not shown). This

341   result is qualitatively the same when the strategy is a repellor. The singular strategy value is

342   positively related to the specialization on R_2, so that a higher specialization s_2 on the alternative

343   resource creates a larger basin of attraction for the zero niche construction state, i.e., niche

344   construction is more often counter-selected.(see Supplementary Figure S3).

345   In the "opportunity cost" scenario, we do not obtain an analytical value of the expected selected

346   level of agriculture: it is obtained by numerically nullifying the fitness gradient (equ. (18)), and

347   then computing convergence and invasibility criteria. We do this for a range of s_1 values in order to

348   investigate our prediction that higher specialization on the managed resource should select for

349   higher investment in agriculture. On Figure 3, we show the selected investment into agriculture in

350   CSS cases (evolutionary endpoint), as well as the resulting specialization on the alternative

351   resource, and the densities of the species at the evolutionary equilibrium.

352   When specialization on the managed resource s_1 is relatively low (left part of Fig 3 A), as predicted,

353   increasing s_1 leads to an increase in the selected agriculture intensity x^*. The level of foraging on

354   resource 2, $s_2(x^*)$ consequently decreases due to trade-off constraints. However, when s_1 is higher

355   (right part of Fig 3 A), the pattern is reversed: increasing s_1 selects for less agriculture. We can

356   explain this by considering the evolutionary equilibrium densities (Fig 3 B): because an increase in

357   s_1 decreases the foraging on resource 2 (blue line, Fig 3 A), the alternative resource suffers less

358   from the indirect effects. In the second part of the graph, it increases in density (green line). This

359   increases its profitability which selects for less niche construction.

360   As in the "exploitation cost" scenario, the selected agriculture level (x^*, purple line) falls in the

361   coexistence area represented in gray for all specialization values. Evolution of agriculture therefore

362   again favors the persistence of the system. This however depends on the trade-off shapes, and on

363   the effect of niche construction on the helped resource, that mediates apparent competition and

364   hence coexistence. We can obtain insight from how evolution could reduce coexistence from Fig 3

365   *B*: at low s_1, increasing specialization on the helped resource decreases the alternative resource

366   density at the evolutionary equilibrium. The evolution selects for more niche construction

367   (advantaging its competitor) and higher consumer densities at the equilibrium, then the alternative

368   resource suffers from a higher apparent competition. A even stronger pattern can lead to the

369   extinction the alternative resource. When the helped resource obtains even higher benefits from

370   niche construction (high conversion efficiency *w*), apparent competition is strong enough that for

371   intermediate R_1 specializations, R_2 may become extinct (see Supplementary Figure S4). In this case,

372   evolution kills the alternative resource but also destabilizes the community since it increases the

373   agricultural trait to levels where the consumer and the helped resource are involved in a very strong

374   positive feedback that produce an ever increasing dynamics.

375   *Can evolution increase the diversity of the system?*

376   We have seen that even though evolution mostly maintains the diversity in CSS scenarios (since

377   the selected trait *x** falls in the coexistence area) it can also disrupt it if apparent competition is too

378   strong. We now investigate whether the diversity in the system can be increased, in particular

379   through dimorphism in the consumer population.

380   In the "exploitation cost" scenario, because the non-invasibility and convergence criteria are

381   equivalent, the two only types of evolutionary dynamics are evolutionary endpoints (CSS) that

382   select for intermediate agriculture levels, or repellors leading to runaway evolution towards either

383   no niche construction or full niche construction (potentially destabilizing for the community) or to

384   intermediate levels of niche construction (see supplementary figure S1).

385   In the "opportunity cost", all types of singular strategies can be potentially obtained, combining

386   convergence and non-convergence, invasibility and non-invasibility. In particular, it is possible to

387 obtain convergent points that are invasible: evolutionary branching points. In such conditions, the

388 traits evolve towards the singularity value where disruptive selection is experienced. Dimorphism

389 can then be maintained in the consumer population. We illustrate these dynamics in Figure 4. If the

390 initial level of niche construction is high enough (that is, higher than the repellor value of the

391 singularity, around 0.4 in the example), it evolves towards the singularity (around 1.2) where it

392 experiences disruptive selection. We then observe the coexistence of two consumers in the

393 population, a "farmer" strategy with a high value of niche construction investment and a "predator"

394 strategy, not investing at all into niche construction. If initial niche construction investment is too

395 low, it is then counter-selected and evolves towards zero (which is consistent with the positive

396 nature of the feedbacks, we can expect threshold-dependent dynamics). This evolution leads to the

397 coexistence of the two resources. The farmer strategy is a full specialist on the helped resource. The

398 predator strategy consumes both preys, and is a relative generalist (here we have a higher

399 specialization on the alternative resource, which is a property of our parameters: we fixed s_1 to 0.5,

400 so evolution towards zero niche construction automatically brings s_2 to 1.5). The evolutionary

401 branching point that we obtain here is not linked to the trade-off between specialization and niche

402 construction shape ($k=1$) but to the niche "privatization" effect, that is the accelerating positive

403 effect of agriculture intensity on the consumption efficiency on the resource ($u=2$). This is intuitive:

404 providing diminishing returns to the farmer should favor generalism, while providing increasing

405 returns favors specialization and more niche construction.

406 3) Coevolution of the specialization and the agriculture investment

407 traits.

408 Until now we have fixed one trait and considered two trade-off scenarios, namely the

409 opportunity cost and exploitation cost scenarios. We now assume that the three traits evolve

410 simultaneously while still respecting the trade-off constraint, which means that we are looking at

411   the coevolution of two traits, for instance x and s_1, and with s_2 being deduced from the two first and

412   trade-off (eq (2)).

413   We investigate whether our prediction of a correlation between the profitability of the cultivated

414   resource and the coevolution of specialization and agriculture on this resource. To do this, we vary

415   the intrinsic growth rates of the two resources (b_1 and b_2) which can represent a proxy for their

416   profitabilities, and explore how the values of the three traits at the coevolutionary equilibrium are

417   impacted. We present these results in Figure 5. In Fig 5 A, b_1 is varied and the values of the traits is

418   plotted. We show that as the profitability of R_1 increases, both x^* and s_1^* increase, which means an

419   increase in the consumer specialization on R_1 and the investment in its cultivation. Inversely, when

420   b_2 is increased (Fig 5 B), the profitability of resource R_2 increases, thus decreasing the evolution

421   towards specialization and agriculture on R_1. We then explore how the joint variation of the two

422   profitabilities determine the ecological state at the coevolutionary equilibrium. We show how the

423   selected agriculture investment (Fig 5 C) and relative preference on R_1 (Fig 5 D) increase with

424   increased relative profitability of R_1 compared to R_2. In Fig 5 E, we summarize the different

425   possible states of the system with three areas. When b_2 is high and b_1 is low (area 1), the consumer

426   is mostly specialized on the non cultivating resource at the equilibrium and investing less in

427   constructing R_1. When b_1 is intermediate and b_2 is high (area 2), the consumer is a generalist that

428   cultivates R_1 and consumes R_1 and R_2. When b_1 is high, the consumer evolves to predominantly

429   agricultural strategies with high investment into the cultivation and consumption of R_1.

Discussion

431   In this work, we have studied the evolution of niche constructing agriculture in a consumer-

432   resource perspective. Our initial prediction is that intuitively, cultivating a resource that the

433   consumer is not consuming (so, a resource that is not profitable) is not adaptive and is counter-

434   selected. We show a positive correlation between the evolution of agriculture and specialization on

435   the cultivated resource, both in the two trade-off scenarios (although the cost of agriculture

436   mitigates this result) and in the coevolution study.

437   In the "exploitation cost" scenario, we predicted that increasing the (fixed) specialization on the

438   alternative resource should decrease the investment into agriculture. In the "opportunity cost"

439   scenario, increasing the (fixed) specialization on the cultivated resource should increase the

440   investment into agriculture. These predictions are partly confirmed by our results. Indeed,

441   increasing the profitability of the alternative resource (via increased specialization) decreases the

442   investment for agriculture in the "exploitation cost" scenario. Conversely, increasing the

443   specialization on the cultivated resource increases the selected level of agriculture in the

444   "opportunity cost" scenario, although a further increase mitigate the profitability of the cultivated

445   resource through indirect effects, leading to a decrease in the selected level of agriculture.

446   The joint evolution of specialization and agriculture is analyzed in the coevolution scenarios,

447   where an increase in the profitability of the cultivated resource leads to an increase in the level of

448   investment into both specialization of this resource and cultivation of the resource, via the

449   emergence of an eco-evolutionary feedback between these two traits. This gives important insights

450   on the transitions from foraging-only to agriculture-only strategies, that may be observed in the

451   model, as well as on transitions from foraging-only to facultative farmers (or facultative foragers).

452   This question that we here investigated here from a niche construction/agriculture perspective is

453   well suited to understand the evolution of mutualism or symbiosis. For instance, some ants perform

454   facultative agriculture (on aphids or fungi) and usually remain generalist, while other taxa are

455   obligate farmers of fungi (Chapela et al. 1994; Stadler and Dixon 2005) or aphids (Ivens et al.

456   2016) in which cases many specialized traits are observed. We here show that such dynamics may

457   emerge from foraging theory constraints (that may be linked to physiology, but also to resource

458   densities, dynamics). In our model, we do not investigate whether the net interaction is mutualistic

459   for the helped resource, because this has been proven difficult to measure experimentally (context-

460   dependency of interactions (Chamberlain et al. 2014), multiple components of fitness) but we

461   implement both a positive and a negative aspect of the interaction. For instance, in the ant-aphid

462   interaction, it is unclear whether this can be qualified as mutualism or exploitation (Offenberg

463   2001; Stadler and Dixon 2005; Billick et al. 2007).

464   One of the two questions that stimulated our study was to improve our understanding of the

465   conditions under which agriculture may evolve. The other one, is the effect of this evolution on the

466   ecological dynamics and in particular the coexistence of cultivated and non-cultivated resources.

467   This aspect is here mediated by the indirect interactions occurring in the system, particularly

468   apparent competition. Apparent competition has been experimentally described in agricultural

469   systems where a predator has a positive effect of one of its preys, notably in aphid-tending ant

470   increasing the predation on other arthropods (Warrington and Whittaker 1985; Wimp and Whitham

471   2001). In our model, we note that evolution does not optimize densities: this result that could seem

472   counter-intuitive is rather well known when considering adaptive dynamics studies (Metz et al.

473   2008; Boudsocq et al. 2011). Second, we show that evolution of agriculture may favor coexistence

474   in the system. In the "exploitation cost" scenario, without evolution, we expect that increasing

475   specialization on the alternative resource should reduce coexistence, as it increases predation

476   pressure on the resource which does not benefit from niche construction. When we consider

477   evolution though, the decreased selected level of niche construction compensates for this effect and

478   rescues the alternative resource, thus favoring coexistence. We can observe similar patterns in the

479   "opportunity cost" scenario. Adaptive foraging is also known to improve coexistence of resources

480   by mitigating apparent competition in purely trophic systems (Abrams 2010). We note however

481   that this evolutionary facilitation of coexistence is dependent on costs and benefits. Especially, in

482   cases where the efficiency of niche construction is very high, even if the evolution mitigates the

483   stronger apparent competition that the alternative resource suffers from, it might not be enough to

484   rescue it. Such effects may be linked to natural observations. In devil's gardens, ants kill

485   competitors of their host plant species thereby actively limiting coexistence at a local scale

486   (Frederickson et al. 2005). In our model, runaway evolution toward high niche construction may

487   yield large positive feedbacks, potentially destabilizing the system and leading to the exponential

488   growth of the consumer and helped resource. Such infinite increases could be avoided if we

489   considered diminishing returns of niche construction, for instance, if niche construction is limited

490   by other parameters. This addition to the model has been shown to stabilize the ecological

491   dynamics within this module (Picot et al. 2019).

492   Evolution of agriculture in our model assumed two main hypotheses. First, that agriculture

493   occurs at a cost, here constraining the foraging of resources (either the cultivated one or the

494   alternative one) ; second, that agriculture provides a direct benefit to the organism that performs it.

495   This direct benefit can also be interpreted as a trade-off between the consumption efficiency of

496   resource 1 and its non-cultivation, and allows the evolution of agriculture because it limits the

497   invasion of cheaters that would not pay the cost of agriculture investment. Such a scenario has been

498   described in a model of niche construction in which pleiotropy allows the maintenance of niche

499   construction (Chisholm et al. 2018). If there is a positive correlation between the investment and

500   the returns, costly niche construction may evolve. If the direct benefits of niche construction are

501   accelerating with increasing niche construction intensity, evolution can lead to dimorphism in the

502   consumer population. We then observe the coalition of a highly specialized farmer, that invests a lot

503   in niche construction and only preys on the helped resource, and of a generalist predator strategy

504   that performs no or very low agriculture. This latter could be considered a cheater in the evolution

505   of cooperation terminology: it consumes the resource that is maintained by niche construction,

506   without paying the cost of agriculture (but see Ghoul et al. (2013). Because of the direct benefit

507   that the farmer obtains from the exploitation of the helped resource ("privatization" or "monopoly"

508   (Krakauer et al. 2009; Chisholm et al. 2018; Scheiner et al. 2021), the invasion of the cheater is

509   avoided and the two phenotypes coexist.

510   Increasing the number of consumers also stabilizes the system: similar to exploitative

511   competition where two consumers may coexist when consuming two shared resources (according

512   to the R^* rule, (Tilman 1980)), in apparent competition, resources are more likely to coexist if they

513   are consumed by n consumers because it balances apparent competition (similarly to the P^* rule,

514   (Holt et al. 1994)). If the consumer population is considered as a whole comprised of two

515   subpopulations, we can then interpret this coalition as division of labor, or functional

516   specialization, between farmers and foragers. This type of division of labour has been investigated

517   in theoretical works which stress the importance of considering high benefits to specialization or

518   accelerating returns (Rueffler et al. 2012; Cooper and West 2018). This is consistent with our

519   model, and recalls the importance of trade-off geometries in evolutionary dynamics of

520   specialization (de Mazancourt and Dieckmann 2004; Egas et al. 2004; Ravigné et al. 2009; Kisdi

521   2014). From an evolution of specialization perspective, the coalition between niche-constructors

522   and non-constructors is also a coalition between a specialist and a generalist. The question of the

523   coexistence of specialists and generalists have often been frequently investigated from a purely

524   trophic context (Egas et al. 2004; Abrams 2006; Rueffler et al. 2006). Our model provides various

525   dynamics that emerge from simple assumptions, and these results can be understood both in the

526   evolution of cooperation and evolution of specialization framework. The coevolution analysis

527   allows to describe situations where if a potentially cultivable resource is profitable enough, it might

528   be advantageous to switch from a generalist forager to a specialized farmer, which can explain

529   evolutionary transitions from foraging-only to settled agriculture behaviours.

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678 # **Figures**

convex trade-off   concave trade-off
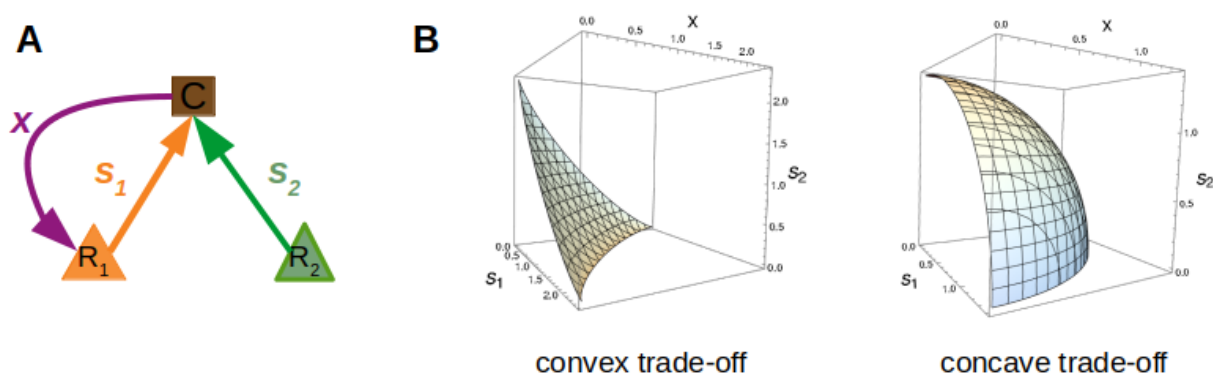
679   Figure 1: A) The module: the consumer C (in brown) consumes resources R_1 (in orange) and R_2 (in

680   green) according to respective specialization rates s_1 and s_2. The resource R_1 receives an additional

681   positive effect through niche construction (agriculture) performed by the consumer. B) Different

682   trade-off shapes determine the dependency between the three traits. Typically, concave trade-offs

683   (here $k=2$) and convex trade-offs are considered ($k=0.8$).
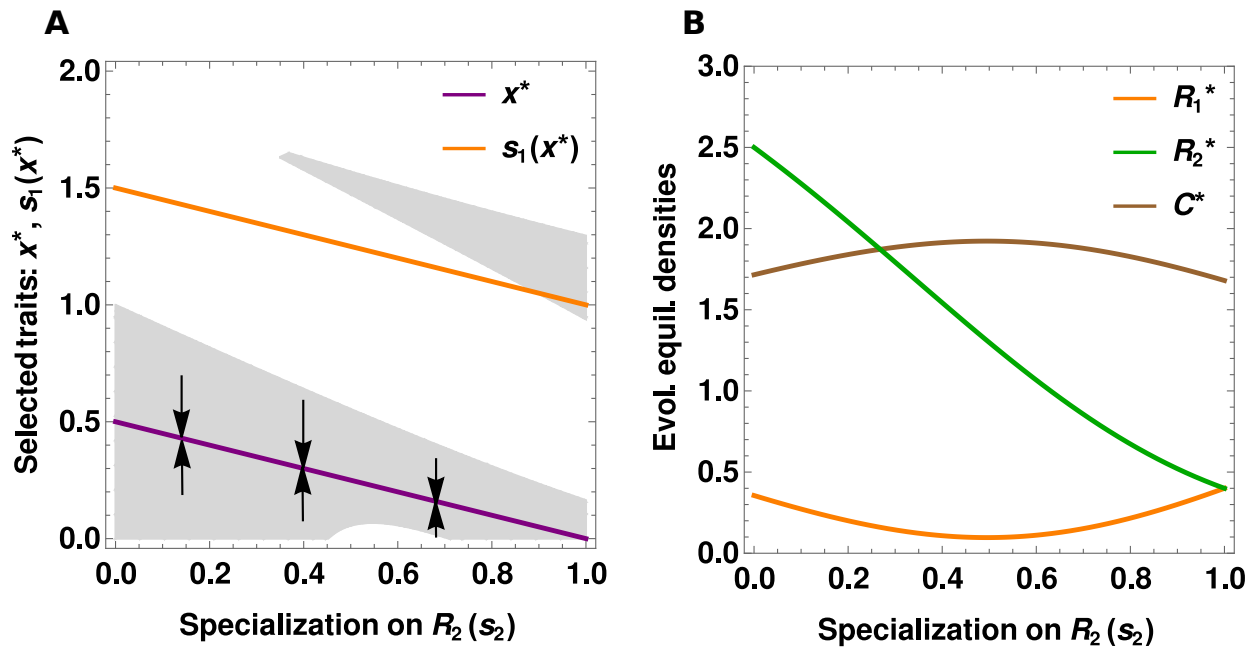
Figure 2: Effect of specialization on resource 2 on the evolutionary and ecological dynamics in the "exploitation cost" scenario. A) effect on the selected level of niche construction x^* (in purple, the arrows indicate the direction of evolution) and subsequent consumption of resource 1, $s_1(x^*)$ (in orange). The area of stable ecological coexistence of the three species when varying agriculture and the specialization on R_2 (i.e., in a (s_2,x) plane) is represented in grey. B) effect on the species densities at the ecological evolutionary equilibrium (that is at the selected niche construction): the consumer is in brown, R_1 is in orange, R_2 is in green. $b_1 = b_2 = 2$, $g_1 = g_2 = 0.8$, $e_1 = e_2 = 1$, $L = 2$, $w = 1$, $m = 0.8$, $k=1$, $u=1$
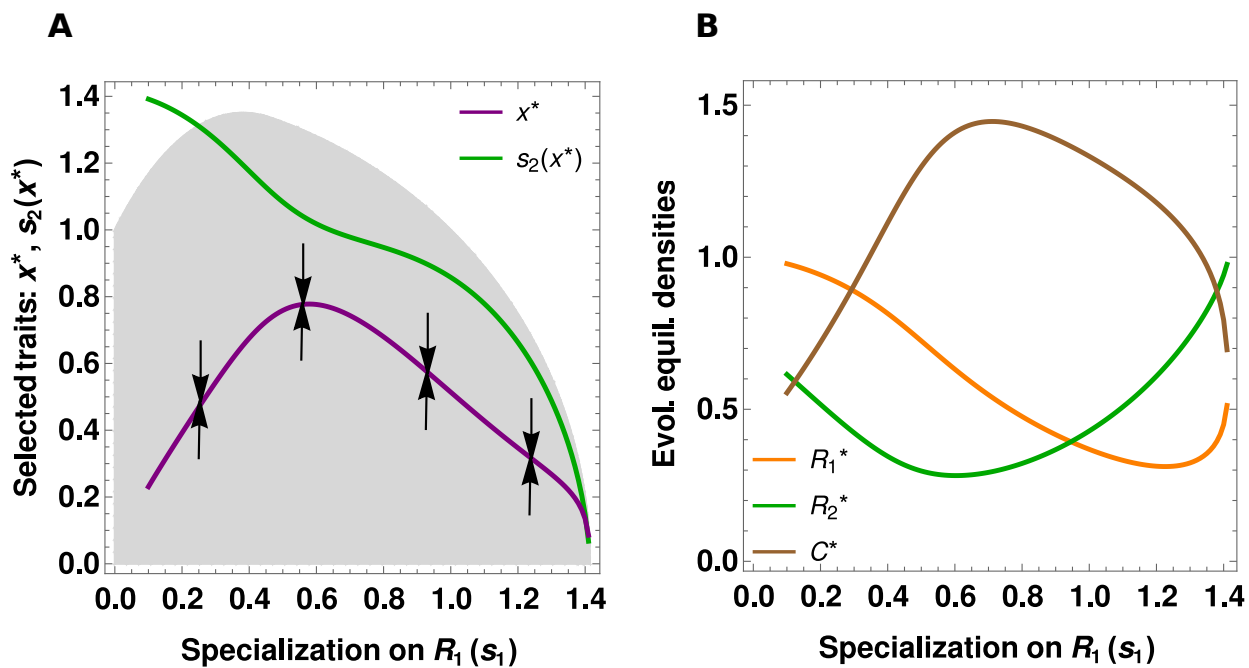
692   Figure 3: Effect of specialization on resource 1 on the evolutionary and ecological dynamics in the

693   "opportunity cost" scenario. A) effect on the selected level of niche construction x^* (in purple, the

694   arrows indicate the direction of evolution) and subsequent consumption of resource 2, $s_2(x^*)$ (in

695   green). The area of stable ecological coexistence of the three species when varying agriculture and

696   the specialization on R_1 (i.e., in a (s_1,x) plane) is represented in grey. B) effect on the species

697   densities at the ecological evolutionary equilibrium (that is at the selected niche construction): the

698   consumer is in brown, R_1 is in orange, R_2 is in green. $b_1 = b_2 = 2$, $g_1 = g_2 = 2$, $e_1 = e_2 = 2$, $L = 2$, w
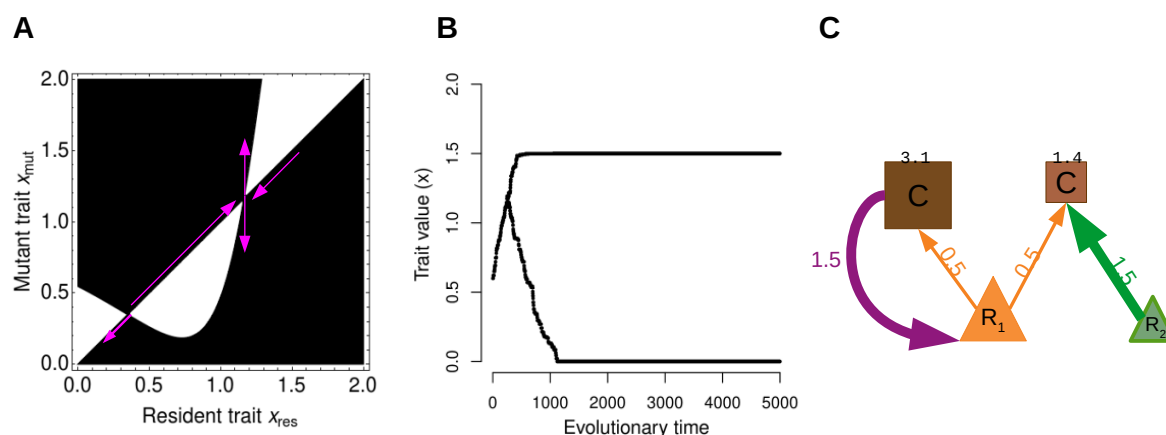
699     $= 0.1$, $m=2$, $k=2$, $u=0.5$

Figure 4: Evolutionary branching leading to dimorphism in agriculture investment, in the "opportunity cost" scenario. A: Pairwise Invasibility Plot, the sign of the fitness of a mutant of trait x_{mut} appearing in a population of trait x_{res} is shown (white for negative, black for positive). The pink arrows indicated the direction of evolution. B: Evolution trajectory of the investment into agriculture: the trait experiences disruptive selection at the convergent singularity leading to two coexisting phenotypes. C: final module with traits values (in color) and population densities (in black): the width of the arrows represents the trait value, not the net interaction (eg, the net per capita effect of C on R_1 is $s_1 - w\,x = 0.35$). Values are: $s_1=0.5$, $k=1$, $u=2$, $w=0.1$, $b_1=b_2=3$, $g_1=g_2=2$, $e_1=e_2=2$, $m=2$.
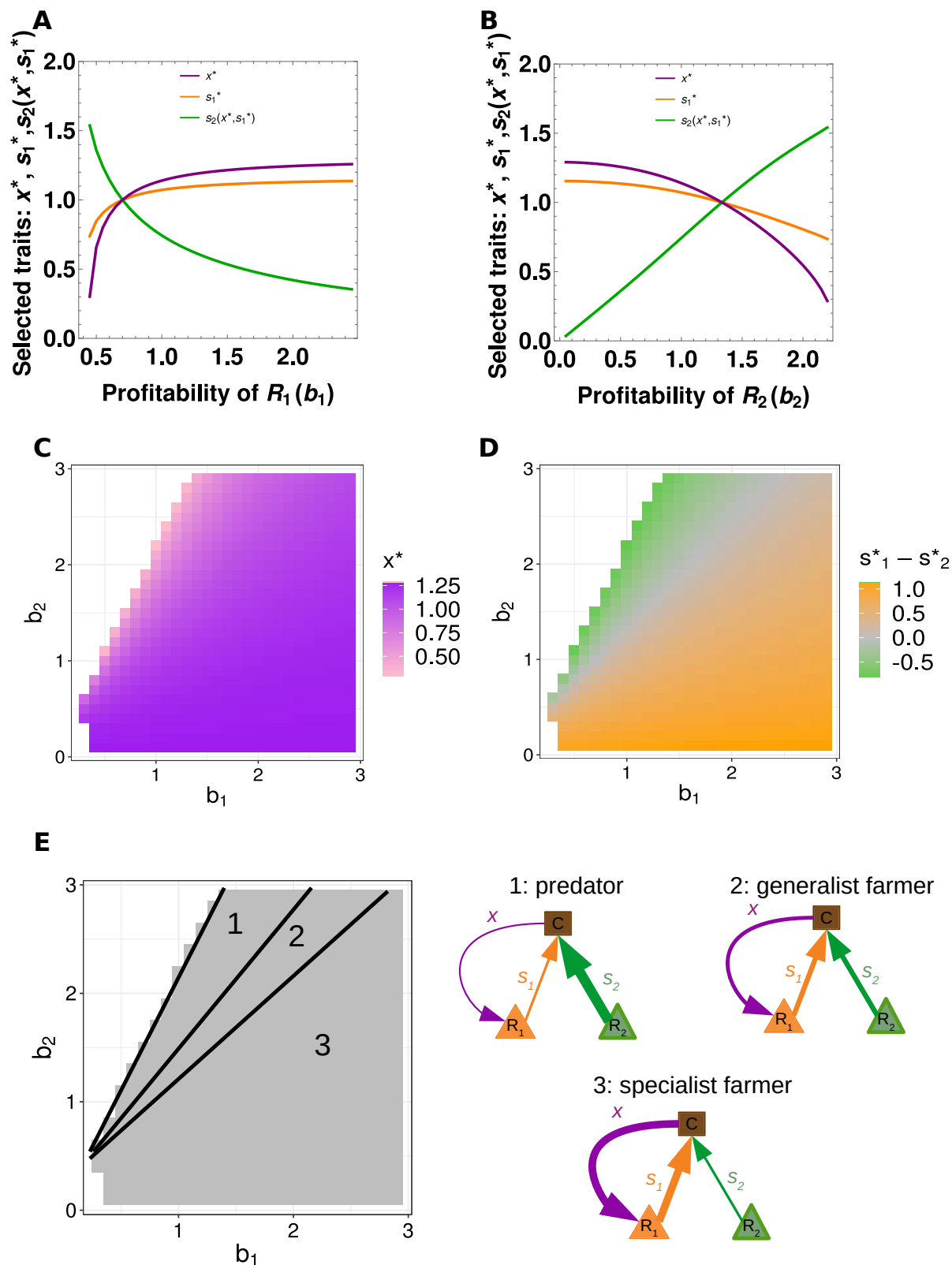
709   Figure 5: Coevolutionary dynamics. A) Correlation between the profitability of R_1 and the

710   values of the traits at the coevolutionary equilibrium (attractor, CSS): x^* is shown in purple, s_1^* in

711   orange, and s_2^* in green. B) Correlation between the profitability of R_2 and the values of the traits

712   at the coevolutionary equilibrium (attractor, CSS): x^* is shown in purple, s_1^* in orange, and s_2^* in

713   green. C) Values of the niche construction trait at the coevolutionary equilibrium in the two

714   resources profitabilities plane. D) Relative resource preference at the coevolutionary equilibrium:

715   the consumer is more specialized on R_1 in the orange area and more specialized on R_2 in the green

716   area. E) Module state in the different areas defined by the profitabilities of the resources. When b_2

717   is high and b_1 is low (area 1), the consumer is mostly specialized on the non cultivating resource at

718   the equilibrium and investing less in constructing R_1. When b_1 is intermediate and b_2 is high (area

719   2), the consumer is a generalist that cultivates R_1 and consumes R_1 and R_2. When b_1 is high, the

720   consumer evolves to predominantly agricultural strategies with high investment into the cultivation

721   and consumption of R_1.

722   Values are: $g_1=g_2=2$, $e_1=e_2=2$, $L=3$, $w=0.1$, $k=2$, $u=2$, $m=1$. In panel A, $b_2=1$. In panel B, $b_1 = 1$.