Implications of the evolution of agriculture and resource foraging for the maintenance of species diversity and community structure

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Keywords: niche construction, evolution of specialization, indirect effects, agriculture, functional specialization

Abstract: Agriculture - cultivation of plants, algae, fungi and animal herding - is found in numerous taxa such as humans, but also ants, beetles, fishes and even bacteria. Such niche construction behaviours have evolved independently from hunter/predation behaviours, though many species remain primarily predators. We here investigate when such a transition from predation/hunter behaviour to agriculture is favoured. In these systems where a consumer has a positive effect on its resource, we can expect an allocative cost of agriculture for the farmer, hence modifying the selective pressures acting upon it. The management of the resource may have a negative effect on its consumption: for instance, when the consumer defends the resource against other predators (exploitation cost). In other situations, the cost may occur on the foraging of alternative resources, for instance if the consumer spends more time nearby the farmed resource (opportunity cost). Here, we develop a simple three-species model constituted by a farmer species that consumes two resource species, one of them receiving an additional positive effect from the consumer. We consider two trade-off scenarios based on how the cost of agriculture is implemented, either as an exploitation cost or as an opportunity cost. We use an adaptive dynamics approach to study the conditions for the evolution of the investment into agriculture and specialization on the two resources, and consequences on the ecological dynamics of the community. Eco-evolutionary dynamics generate a feedback between the evolution of agriculture and specialization on the helped resource, that can lead to varying selected intensity of agriculture, from generalist strategies with no agriculture, to farmer phenotypes that are entirely specialized on the farmed resource, with possible coexistence between those 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, that is the active modification of its environment by an organism, that potentially feedbacks on the selective pressures acting upon it (Odling-Smee, Laland, and Feldman 2003). We can obviously think of 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, Barot, and Georgelin 2013). The consequences of domestication, for instance, are important not only for the selected species (that can display drastic modification of their phenotypic traits contrary to the ancestral, undomesticated species, as in wheat (Thrall et al. 2011)) but also at the community level because biomass of the domesticated species will be largely higher than the wild ones. Humans are not the only species to practice agriculture. Some ant species can use other insects, such as aphids, as cattle, or cultivate fungi (Mueller et al. 2005). Numerous taxa in fact benefit from actively managing their resources: agriculture is also found in termites, beetles, fishes, nematodes and even microorganisms (Boomsma 2011; Hata and Kato 2006; Thutupalli et al. 2017). 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 the predictability of resource abundance can provide less risk than those associated to foraging.

In 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 not only consisting of consumption or predation, but contains an additional positive effect of the consumer on the

resource, which has been described in various contexts (Abrams 1992; Brown et al. 2004; Terry, Morris, and Bonsall 2017). The ecological and evolutionary consequences of including positive effects into trophic networks have received increasing attention (Kéfi et al. 2012; Fontaine et al. 2011; Mougi and Kondoh 2012). Accounting for such non trophic interaction alters for instance on stability of networks and coexistence of species. Positive effects associated with agriculture can emerge from different consumer behaviours (protection against predators, helped reproduction or dispersal, for instance) and impact for the resource demography in various ways (increase of the carrying capacity, increase of the growth rate) that are expected to increase the resource profitability for the farmer species, compared to alternative foraged resources. The evolution of agriculture has been envisioned in the niche construction perspective, particularly in the human context (Zeder 2016; Rowley-Conwy and Layton 2011; Boivin et al. 2016). A classical example of the consequences of niche construction through agriculture is the evolution of lactose tolerance in humans (Laland and O'Brien 2011). More generally, explicitly accounting for niche construction in models and theory leads to patterns that would not be predictable otherwise (Kylafis and Loreau 2011).

Jointly to the niche construction perspective, the ecological and evolutionary consequences of agriculture can naturally be conceived in the light of foraging theories (optimal foraging, (Charnov 1976; Pyke, Pulliam, and Charnov 1977), adaptive foraging, (Loeuille 2010)). This can help understand the question of the potential transition between foraging strategies such as hunting, gathering, to agricultural strategies. The evolution of agriculture can lead to full specialization and reciprocal dependency of the agricultural partners, as in fungus-growing ants (Mueller et al. 2005). To understand those two questions (transition to settled agriculture, extreme specialization), we can use the evolution of specialization framework (Egas, Dieckmann, and Sabelis 2004; Abrams 2006). Optimal foraging theory predicts that the specialization of a consumer will evolve depending on the resources profitabilities. Agriculture practice can then modify the resource profitability through the modification of its abundance. Hence we expect that increasing agriculture selects for higher

specialization on the cultivated resource that becomes more profitable, selecting for more agriculture, leading to a positive feedback between agriculture and specialization on the cultivated resource. As a consequence, we should expect reciprocal evolutionary consequences between the evolution of specialization (*sensu* consumption, predation) on the resources, and the evolution of agriculture. In this perspective, we can understand the evolution of agriculture as the addition of another dimension to the classic evolution of specialization: an organism allocates energy or time between the consumption of different resources, and the cultivation of one or several resources. We can then expect two types of evolutionary outcomes: either a high level of agriculture with a high specialization on the managed resource, or no agriculture and generalism or a specialist on another resource.

This simple prediction can be modified by taking account of the cost associated with agriculture: the niche constructing phenotype can first be threatened by cheaters, if niche construction benefits are shared by all the population (potentially leading to a tragedy of commons, (Hardin 1968)). Farming can then be considered a public good (Thutupalli et al. 2017). Even if the threat of freerider invasion is overcome for instance through privatization (pleiotropy, (Chisholm et al. 2018), monopolization of the niche (Krakauer, Page, and Erwin 2009)), trade-offs can still mitigate the evolution of agriculture by altering the profitabilities of the resources: if the cultivated resource is initially much less profitable than an alternative resource, we predict that agriculture may be counter-selected despite potential benefits. Behaviours associated with agriculture can be costly because of a high presence of competitors, predators or pathogens of the resource that needs to be actively protected (Stadler and Dixon 2005; Hübner and Völkl 1996; Adams et al. 2013; Fernández-Marín et al. 2013; Thutupalli et al. 2017). Here, we investigate the cost of agriculture in the foraging theory perspective: increasing the niche construction activity occurs at a cost on the consumption of resources, because of a limited energy or time budget available to the farmer species. Agriculture can, as a type of resource exploitation, decrease the consumption of an alternative resource (“opportunity cost”, described in Picot, Monnin, and Loeuille (2019)). It can as

well decrease the consumption of the managed resource, e.g. if defending it against predators or competitors implies moving away from the resource site, or allocating more time to defense rather than consumption (“exploitation cost” scenario, (Picot, Monnin, and Loeuille 2019)).

Because of the previously stated feedback loop, understanding the (co)evolution of agriculture and specialization requires to investigate its ecological consequences in terms of variations in resource abundances. In humans, agriculture is known to have drastic effects on the community and ecosystem level properties: for instance, by introducing invasive species that engage in apparent competition with native ones (Geslin et al. 2017; David et al. 2017). This question is more generally linked to those of maintaining biodiversity through agriculture (Emmerson et al. 2016). The study of indirect effects may give insights on the community consequences of evolution of agriculture, that we explore in a consumer-resource perspective. Indirect effects are effects of one species on another, transmitted by another species (Wootton 1994). Then, when a consumer consumes two resources, those resources engage in apparent competition (Holt 1977): an increase in density of one resource may decrease the other resource growth rate through their interaction with the consumer. In an ecological analysis of a consumer-resource model with niche construction, Picot, Monnin, and Loeuille (2019) show that cultivated and non-cultivated resources may then engage in apparent competition through the interaction with the consumer. Without considering any cost, increasing niche construction has a positive effect on the managed resource density, which translates in a bottom-up positive effect on the consumer density, and a negative effect on the alternative density, because of apparent competition. Considering costs of niche construction mitigates this result: in particular, if the cost of niche construction is high enough in terms of resource consumption, increasing it may lead to counter-intuitive increase in the alternative resource density: because of a decrease in its consumption rate (“opportunity cost” scenario) and/or a decrease of the consumer density (“exploitation cost” scenario and “opportunity cost”).

In this study, we theoretically investigate the evolution of agriculture in a two-resource, one consumer module. We assume two trade-offs scenario: either investing into agriculture decrease the consumption of the managed resource, or it decreases the consumption of the alternative resource. We use adaptive dynamics and numerical simulations to study the evolution of the niche constructing trait and the specialization on the two resources (Geritz et al. 1998). We address the following questions: (1) How does a fixed foraging strategy impact the selected investment into agriculture? We predict that a high specialization on the managed resource favours the evolution of agriculture, while a high specialization on the alternative resource prevents it. (2) How does the evolution of niche construction impact the coexistence of the resources and the functioning of the system? We then predict that a high selected level of agriculture leads to the exclusion of the alternative resource because of increased apparent competition, while counter-selection of niche construction should lead to coexistence of the resources.

Model presentation

Ecological dynamics

Our model is based on ordinary differential equations describing the ecological dynamics of the consumer and two resource species. In this simple model (eq (1)), the consumer species C interacts with the two resources R_1 and R_2. The resource R_1 is managed through agriculture: we assume it receives a positive effect that increases its growth rate, but it is also consumed. The alternative resource R_2 is only consumed:

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

The consumer *per capita* growth rate depends on its consumption of resources (modelled by specialization on resource R_i, s_i, and consumption efficiency of resource R_i, e_i) and on its death rate m. In the absence of the consumer, the two resources grow logistically (allowing for their coexistence in such situations): b_i is the birth rate and g_i is the intraspecific competition rate for resource R_i. Only apparent competition through the interactions with the consumer is considered here: we do not consider any direct competition between resources, which allows to clearly identify the impacts of the consumer. The resources variation also depends on their consumption by the consumer, modelled through consumption rate s_i (or specialization). Additionally, the resource R_1 receives a positive effect from agriculture, proportional to the investment into niche construction x and niche construction efficiency w. We assume that e_i, s_i, b_i, g_i, x are positive, so that the two resources have a positive intrinsic growth rate. Niche construction is then facultative for the maintenance of R_1.

Trade-offs: costs and benefits of niche construction

As stated above, we assume that agriculture occurs at a cost for foraging on the resources. We consider two trade-off scenarios that rely on a time or energy constraint: increasing the agriculture intensity can decrease the consumption of the managed resource ("exploitation cost", $s_1'(x) < 0$) or the consumption of the alternative resource ("opportunity cost", $s_2'(x) < 0$). We consider that the three traits are linked through the following formula:

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

L represents the total amount of time or energy that the consumer allocated between niche construction and the consumption of the two resources. In the opportunity cost scenario, s_1 is fixed while in the exploitation cost scenario, s_2 is fixed. The exponent k shapes the trade-off (accelerating for a concave trade-off or saturating for a convex trade-off).

We also assume that niche construction provides a direct benefit for the organisms performing it: for instance, agriculture can provide a more direct access to the managed resource and increase its

consumption efficiency, because of proximity, or another adaptation. This inclusion of a direct benefit (consumption efficiency is positively linked to the agricultural trait), has been shown to favor the evolution of niche construction (Chisholm et al. 2018). In our case, we consider the simple formula

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

where $u<1$ indicates saturating efficiency increase (diminishing returns, for instance if the efficiency consumption is constrained by other factors, such as physiological ones) while $u>1$ indicates an accelerating response.

Ecological dynamics

The ecological dynamics of a similar system has been studied in Picot, Monnin, and Loeuille (2019), assuming a fixed level of niche construction, and differing only in the trade-off function that are used: niche construction intensity decrease the specialization rates s_1 and s_2 linearly, by a factor β and no direct benefit of niche construction is assumed (this would mean $u=0$ in our present model). However, some general considerations apply in the present model: different types of ecological equilibria are obtained: either the coexistence of the two resources, with or without the consumer, or the maintaining of one resource (still with or without the consumer) or the extinction of all species.

Evolutionary dynamics

We study the evolution of the phenotypic trait x using the adaptive dynamics framework (Dieckmann and Law 1996; Geritz et al. 1998). Adaptive dynamics allows to investigate evolutionary dynamics of phenotypic traits while defining the fitness of a given phenotype based on its ecological dynamics. The analytical framework rely on the separation of ecological and evolutionary timescales, while numerical simulations may modulate the two timescales. The evolution of a trait is studied through several steps, assuming clonal reproduction, and small and rare mutations:

- the ecological equilibrium is determined, for a monomorphic population of resident trait x_{res} (by nulling equations 1(a) to 1(c))

- a rare mutant with trait x_{mut} is introduced and replaces the resident trait if its invasion fitness (ie, its *per capita* growth rate when rare, based on eq1(a)) is positive. The invasion fitness is given by:

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

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

A deterministic approximation of the evolution of the trait is given by the canonical equation of adaptive dynamics (Dieckmann et Law 1996) :

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{1}{2} \mu \sigma^2 N^0(x_{res}) \left. \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} \right|_{x_{mut} \to x_{res}} \tag{5}$$

$\mu \sigma^2 N^0(x_{res})$ is the evolutionary potential, that is total phenotypic variability brought by mutations with μ the *per capita* mutation rate, σ^2 the phenotypic variance associated to these mutations and $N^0(x_{res})$ the resident population equilibrium density. The selection gradient $\left. \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} \right|_{x_{mut} \to x_{res}}$ is derived from the invasion fitness (eq 4) and corresponds to the slope of the fitness landscape around the resident population, therefore representing the selective pressures acting on the phenotypic variability brought by mutations. The traits that nullify this gradient are called singular strategies (Dieckmann and Law 1996). Dynamics around these singular strategies are characterized by the second partial derivatives of fitness (Dieckmann and Law 1996; Geritz et al. 1998). This allows to distinguish two stability-related properties: invasibility and convergence. A singular strategy x^* is non-invasible (Maynard Smith 1982), or evolutionary stable if:

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

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

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

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

i.e., considering a resident population close to the singular strategy, mutants that are even closer to it are selected. The two trade-off scenarios lead to different fitness expression for each scenario, since in the "exploitation cost" scenario, s_2 is fixed and $s_1(x) = (L - s_2^k - x^k)^{\frac{1}{k}}$ while in the opportunity cost scenario s_1 is fixed leading to $s_2(x) = (L - s_1^k - x^k)^{\frac{1}{k}}$.

Using numerical simulations, we illustrate the evolution of x in the "exploitation cost" and "opportunity cost" scenarios given the constraint (equation (2)).

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 in function of 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 assume that s_1 decreases with x while e_1 increases with x.

Using the adaptive dynamics framework, we derive in eq (8) the fitness of a mutant of trait x_{mut} appearing in a resident population of consumer with trait x_{res}.

$$W(x_{mut}, x_{res}) = e_1(x_{mut}) s_1(x_{mut}) R_1^*(x_{res}) + e_2 s_2 R_2^*(x_{res}) - m \tag{8}$$

We then differentiate the fitness gradient to find singular strategies, that is potential endpoints of evolution (equation (9)): only the first part of the fitness depends on the mutant trait.

$$G(x_{mut}, x_{res}) = \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} = \left(e_1'(x_{mut}) s_1(x_{mut}) + e_1(x_{mut}) s_1'(x_{mut})\right) R_1^*(x_{res}) \tag{9}$$

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 non spatial model implicitly assumes that all consumers have access to the farmed resource. Let us consider from now that $e_1'(x_{mut})>0$. Assuming that the helped resource is not extinct, the position of singular strategies x^* can be obtained from eq (10) and does not depend on the resident trait x_{res}.

$$(e_1 s_1)'(x^*) = e_1'(x^*) s_1(x^*) + e_1(x^*) s_1'(x^*) = 0 \tag{10}$$

This mathematical condition means that the singular strategies correspond to an optimum of the realized consumption of the managed resource: if this strategy is an evolutionary endpoint, evolution optimize effective consumption of the managed resource, since the consumption efficiency and specialization rate vary oppositely with agriculture trait x. We then expect intermediate levels of agriculture to be selected for. In the scenario, we also note that the value of

the singular strategy only depends on this consumption-efficiency optimization: the densities of the resource do not matter.

Replacing the fitness gradient with the chosen functions of equations 2 and 3 (in equation (10)) leads to:

$$\left(L-s_2^k-x^{*k}\right)^{\frac{1-k}{k}}\left(x^{*k}-\left(L-s_2^k\right)u\,x^{*u}+\left(1+u\right)x^{*k+u}\right)=0 \qquad (11)$$

And the condition for non-invasibility and convergence (that are equivalent here, see Supplementary Information for details) is:

$$\left(u-1\right)u\,x^{*u} - \frac{2u\,x^{*k+u}}{L-s_2^k-x^{*k}} - \frac{\left(k-1\right)\left(L-s_2^k\right)x^{*k}\left(1+x^{*u}\right)}{\left(L-s_2^k-x^{*k}\right)^2}<0 \qquad (12)$$

In the linear case ($u=k=1$), the equation (11) becomes $\left(x^*-\left(L-s_2\right)x^*+2x^{*2}\right)=0$. We obtain two possible singularities: $x^* = 0$ (which is a neutral case in the sense that the second derivative is null) or $x^*=\frac{\left(L-s_2-1\right)}{2}$ which is always convergent and non-invasible (CSS) (the second derivative expressed in (12) is $\frac{-2x^{*2}}{L-s_2-x^*}$ and is negative): it is an evolutionary endpoint.

While a completely general study using non-linear trade-offs is not possible, note that a sufficient condition to obtain a CSS is that $u < 1$ and $k > 1$ (see equation (12)), in other terms having diminishing returns of niche construction on resource consumption efficiency and a concave trade-off between specialization and niche construction. If $u>1$ and $k<1$ (accelerating efficiency and convex trade-off) the strategy may be characterized as a repellor (an unstable evolutionary point) depending of the sign of our expression. In this case, directional selection brings the trait to either

zero niche construction (and total consumption), or total niche construction (and zero consumption), the latter case being less likely biologically. We show the possible evolutionary dynamics for different trade-off shapes in Supplementary Figure S1.

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

When increasing agriculture occurs at a cost of the consumption of the alternative resource, the invasion fitness of a mutant of trait x_{mut} appearing in a resident population of consumer with trait x_{res} is derived:

$$W(x_{mut}, x_{res}) = e_1(x_{mut}) s_1 R_1^*(x_{res}) + e_2 s_2(x_{mut}) R_2^*(x_{res}) - m \tag{13}$$

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

$$G(x_{mut}, x_{res}) = \frac{\partial W(x_{mut}, x_{res})}{\partial x_{mut}} = e_1'(x_{mut}) s_1 R_1^*(x_{res}) + e_2 s_2'(x_{mut}) R_2^*(x_{res}) \tag{14}$$

Singularities x^* are obtained through nulling $G(x^*,x^*)$. The position of the singularity depends on optimizing both the consumption efficiency and the cost on the alternative resource consumption. Contrary to the previous scenario, the resident agricultural trait x_{res} matters for the position of the singularity. The non-invasibility condition is given for a general trade-off and for our chosen trade-off functions in equation (14):

$$\begin{gathered} e_1''(x^*) s_1 R_1^*(x^*) + e_2 s_2''(x^*) R_2^*(x^*) < 0 \\ e_1(u-1) u x^{u-2} s_1 R_1^*(x^*) + e_2(1-k)(L - s_1^k) x^{k-2} (L - x^{*k} - s_1^k)^{\frac{1}{k}-2} R_2^*(x^*) < 0 \end{gathered} \tag{15}$$

In the linear case (u=k=1), the invasibility criteria is null, but not necessarily the convergence criteria. This can lead us to identify parameters set for which the strategy is convergent, and invasible.

As in the previous scenario, we can get partial information in the non-linear cases. We obtain a sufficient condition for non-invasibility of the singular strategy (equation (15)) (i.e. if this level of agriculture is reached, it is an ESS): $u < 1$ and $k > 1$. A sufficient condition for the invasibility of the point is that if $u > 1$ and $k < 1$. Those conditions are the same as for the "exploitation cost" scenario invasibility condition, but are not conditions for the evolutionary convergence that we only study numerically (see Supplementary Information for the convergence condition).

2) Effect of specialization patterns on the evolutionary dynamics of agriculture and feedbacks on the ecological dynamics

In the "exploitation cost" scenario, when we consider linear functions, we obtain a continuously stable strategy (CSS) that is both convergent and non-invasible. Moreover we obtain the value of this selected level of agriculture expressed in eq 16:

$$x^* = \frac{(L - s_2 - 1)}{2} \tag{16}$$

This singular strategy is positive if $s_2 < L - 1$. If $s_2 > L - 1$, the value of the singularity becomes negative and the niche constructing trait evolves to 0. From the expression of the singularity (eq 16) we show that the selected level of niche construction is is negatively correlated to specialization on resource R_2. This is an intuitive result that we predicted in the introduction. The consumption of the managed resource at the evolutionary equilibrium ($s_1(x^*)$) is

$s_1(x^*) = L - s_2 - \frac{(L - s_2 - 1)}{2} = \frac{(L - s_2 + 1)}{2}$. We plot the value of the selected agriculture level and consequent consumption of the managed resource, as a function of specialization on resource 2 in Figure 2 a. We also plot the evolutionary equilibrium densities in Figure 2 b. We represent the area of stable coexistence of the species when resource 2 specialization s_2 and x vary (ecologically). We show that the selected value of agriculture, x^* (represented as a black line) falls in the coexistence area (the black arrows indicated the direction of evolution, meaning that starting from a high value of agriculture, evolution brings the trait back into a coexistence area.

We show that the slope of the selected x^* and ($s_1(x^*)$) levels is the same (the lines are parallel), meaning that the cost of increasing consumption of resource 2 is equally shared between niche constructing activities and exploitation of the managed resource. This comes directly from our trade-off expression: mathematically, we assume that the total amount of energy or time L is a linear combination of all the traits and here they all have the same coefficient (ie, 1). If we consider different coefficients, that is that the variation of each trait does not have the same impact on the energy allocation, then at the evolutionary equilibrium, modifying the specialization on resource 2 would lead to weighted cost on agriculture investment and the resource 1 consumption (see Supplementary Figure S2). In the non-linear CSS cases, we also obtain a negative correlation between the intensity of alternative resource consumption and the evolved level of agriculture (figure not shown). When the strategy is a repellor, the singular strategy value is now positively related to the specialization on R_2. That means that the higher s_2, the larger the range of initial traits that lead to zero niche construction (see Supplementary Figure S3).

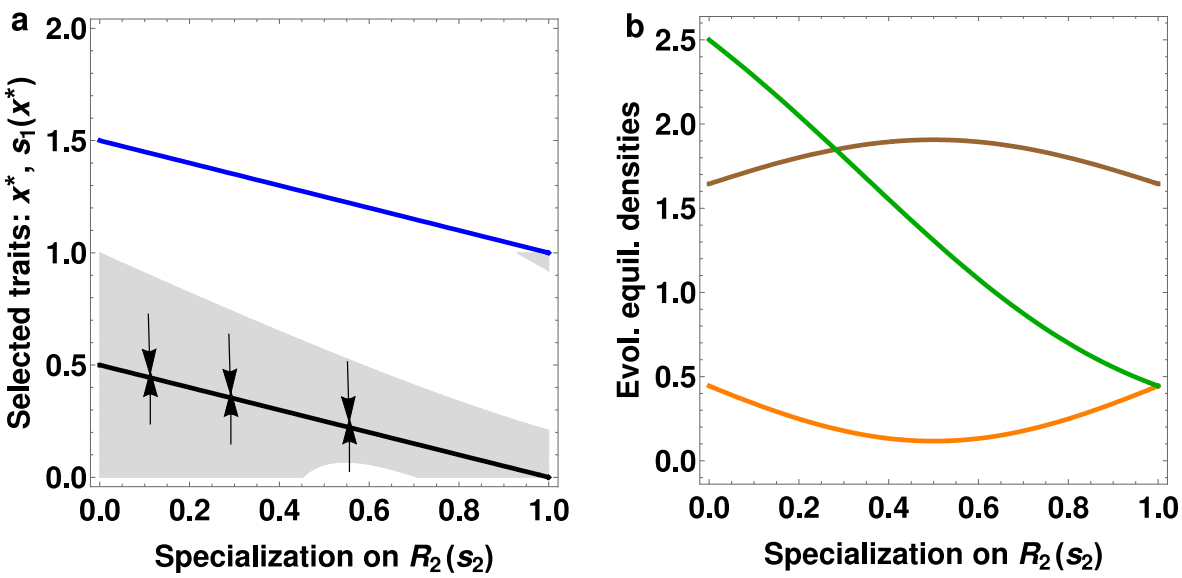

Figure 2: Effect of specialization on resource 2 on the evolutionary and ecological dynamics in the "exploitation cost" scenario. a) effect on the selected level of niche construction x (in black) and subsequent consumption of resource 1, $s_1(x^*)$ (in blue). The area of stable ecological coexistence of the three species when varying agriculture and the specialization on R_2 (ie, 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. $b_1 = b_2 = 2$, $g_1 = g_2 = 0.8$, $e_1 = e_2 = 1$, $L = 2$, $w = 1$, $m = 0.8$, $k=1$, $u=1$

In the "opportunity cost" scenario, we do not obtain an analytical value of the expected evolved level of agriculture: it is obtained by numerically nulling the fitness gradient (equ. (14)), and then computing the dynamics (convergence and invasibility criteria). We do this for a range of s_1 traits in order to investigate our prediction stating that the more the consumer is specialized on the managed resource, the more it should allocate to agriculture. On figure 3 we present the selected investment into agriculture in CSS cases (evolutionary endpoint), as well as the resulting specialization on the alternative resource, and the densities of the species at the evolutionary equilibrium.

When specialization on the managed resource is relatively low (left part of figure 3 a), consistently with our prediction, increasing the level of specialization leads to an increase in the selected agriculture intensity. Meanwhile, the level of foraging on resource 2 decreases. However, when specialization is higher (right part of figure 3a), this pattern is reversed: now, increasing specialization leads to a lower selected level of agriculture. We can explain this by considering the evolutionary equilibrium densities (figure 3 b): because an increase in specialization decreases the foraging on resource 2 (blue line, fig 3 a), the alternative resource suffers less from the indirect effects: in the second part of the graph, it increases in density (green line). This increases its profitability and then selects for less niche construction.

As in the "exploitation cost" scenario, the selected agriculture level (x^*, black line) falls in the coexistence area represented in gray for all specialization values. However, this is not always the case and in particular seems to depend on the trade-off shapes, and effect of niche construction on the helped resource, that mediates apparent competition and hence coexistence. We can obtain insight from how evolution could reduce coexistence from figure 3 b: at low s_1, increasing specialization on the helped resource decreases the alternative resource density at the evolutionary equilibrium, because it selects for more niche construction. Then we can imagine that if this pattern is even stronger, it could lead to the extinction of the alternative resource. This is indeed what is

observed when the helped resource obtains even higher benefits from niche construction (high conversion efficiency w): this makes apparent competition stronger and for intermediate R_1 specializations, R_2 may become extinct (see Supplementary Figure S4). In this case, evolution kills the alternative resource but also destabilizes the community: it increases the agriculture trait to levels where the consumer and helped resource display exponential growth.

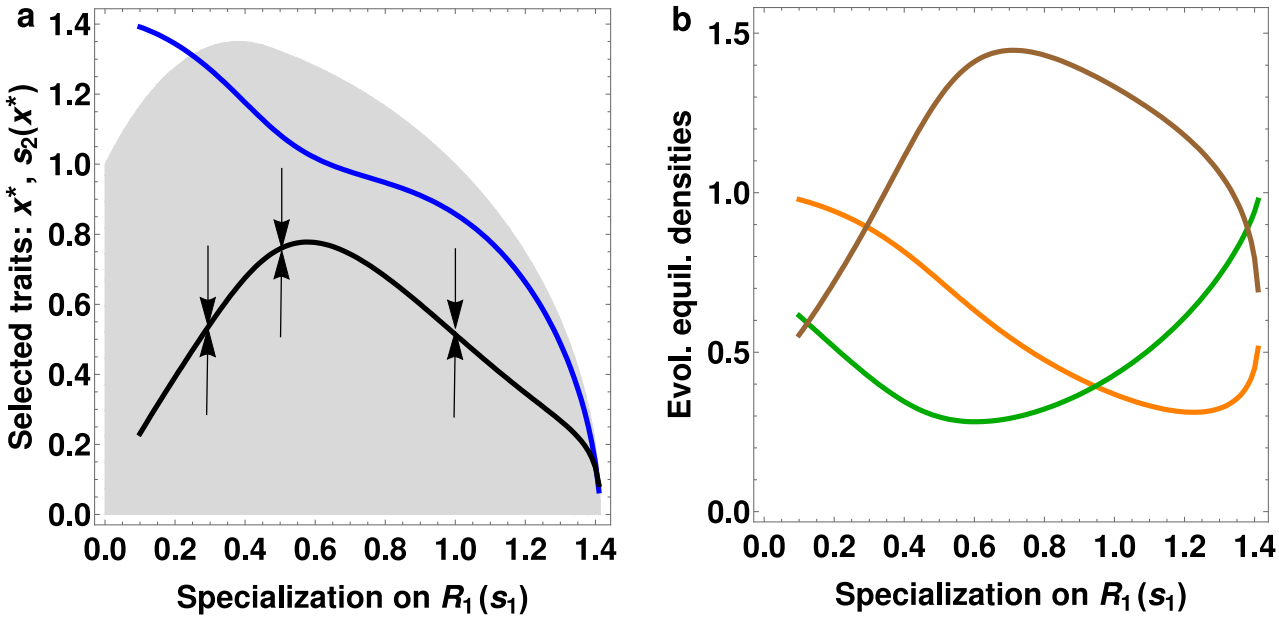

Figure 3: Effect of specialization on resource 1 on the evolutionary and ecological dynamics in the "opportunity cost" scenario. a) effect on the selected level of niche construction x (in black) and subsequent consumption of resource 2, $s_2(x^*)$ (in blue). The area of stable ecological coexistence of the three species when varying agriculture and the specialization on R_1 (ie, in a (s_1,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. $b_1 = b_2 = 2$, $g_1 = g_2 = 2$, $e_1 = e_2 = 2$,, $L = 2$, $w = 0.1$, $m=2$, $k=2$, $u=0.5$*

Can evolution increase the diversity of the system?

In the "exploitation cost" scenario, because the non-invasibility and convergence criteria are equivalent, the two only types of evolutionary dynamics are evolutionary endpoints (CSS) that select for intermediate agriculture levels, or repellors leading to runaway evolution towards no

niche construction, full niche construction (potentially destabilizing for the community) or to intermediate levels of niche construction (see supplementary figure S1).

In the “opportunity cost”, all types of singular strategies can be potentially obtained, combining convergence and non-convergence, invasibility and non-invasibility. In particular, it is possible to obtain convergent points that are invasible: evolutionary branching points. In such dynamics, the traits evolves towards the singularity value where disruptive selection is experienced: then dimorphism can appear in the consumer population. We illustrate these dynamics in figure 4: if the initial level of niche construction is high enough (that is, higher than the repellor value of the singularity, around 0.4 in the example), it evolves towards the singularity (around 1.2) where it experiences disruptive selection: we then observe the coexistence of two consumers in the population, one with a high value of niche construction investment, one not investing at all into niche construction. If initial niche construction investment is too low, it is then counter-selected and evolves towards zero (which is consistent with the positive nature of the feedbacks: we can expect threshold-dependent dynamics). This evolution leads to the coexistence of the two plants, one of the consumer phenotypes is a full specialist on the helped resource, and has a high investment into agriculture. The other consumer phenotype is a forager-only, it consumes both preys, and is a relative generalist (here we have a higher specialization on the alternative resource, which is a property of our parameters: we fixed s_1 to 0.5, so evolution towards zero niche construction automatically brings s_2 to 1.5). The evolutionary branching point that we obtain here is not linked to the trade-off between specialization and niche construction shape (k=1) but to the niche “privatization” effect, that is the accelerating positive effect of agriculture intensity on the consumption efficiency on the resource (u=2). This is intuitive: providing diminishing returns to the farmer should favor generalism, while providing increasing returns favors specialization and more niche construction.

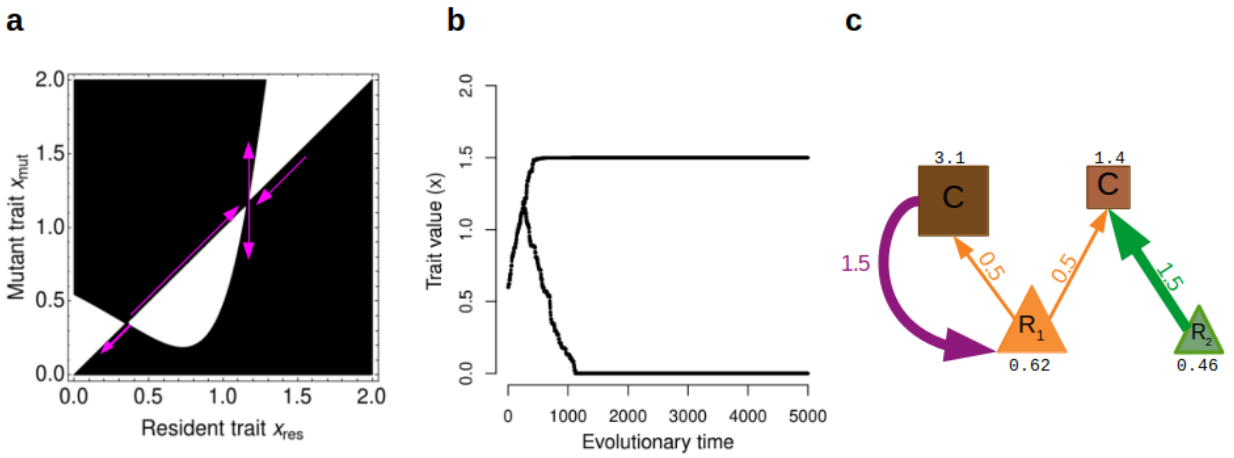

Figure 4: Evolutionary branching leading to dimorphism in agriculture investment, in the "opportunity cost" scenario. a: Pairwise Invasibility Plot, the sign of the fitness of a mutant of trait x_{mut} appearing in a population of trait x_{res} is shown (white for negative, black for positive). The pink 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.

Discussion

Evolution of agriculture in our model assumed two main hypotheses: first, that agriculture occurs at a cost, that is there is a trade-off between agriculture and the foraging of resources (either the cultivated one or the alternative one), second that agriculture provides a direct benefit to the organism that performs it. This direct benefit can also be interpreted as a trade-off between the consumption efficiency of resource 1 and its non-cultivation, and allow for the evolution of agriculture because it limits the invasion of cheaters that would not pay the cost of agriculture investment. This scenario has been recently described in a model of niche construction in which pleiotropy allow for the maintenance of niche construction (Chisholm et al. 2018): if there is a positive correlation between the investment and the returns (which is exactly what we have in our model), costly niche construction may evolve. These considerations have also be applied to a more specific biological setting. Thutupalli et al have investigated farming as a public good in nematodes that disperse ("seed") bacteria which they use as food resource (Thutupalli et al. 2017). Experimentally the authors could not find any trade-off or cost to this "agricultural" behaviour: there was no fitness difference between the nematodes that disperse bacteria and others, suggesting that this behaviour might be a by-product. They discuss scenarios in which this behaviour could be costly and include this assumption in their theoretically study.

In our model, considering a direct benefit is a necessary condition to observe the evolution of agriculture, but it is not sufficient. The evolution of the trait, if the invasion by cheaters is avoided, is still determined by the associated fitness costs and benefits, and depends on the trade-off shape and specialization patterns. Especially, our initial prediction is that intuitively, cultivating a resource that the consumer is not consuming (ie a resource that is not profitable) is not adaptive and is counter-selected. This general prediction translates in two predictions when considering our scenarios: first, that the increasing the (fixed) specialization on the alternative resource should decrease the investment into agriculture in the "exploitation cost" scenario, second that increasing

the (fixed) specialization on the cultivated resource should increase the investment into agriculture (in the “opportunity cost” scenario). These predictions are partly consistent with our results: indeed, increasing the profitability of (specialization on) the alternative resource decreases the investment for agriculture in the “exploitation cost” scenario. Conversely, increasing the profitability of (specialization on) the cultivated resource increases the selected level of agriculture, at least when this specialization level is not too high. An aspect that is missing from our current model is that of the joint evolution of the three traits, in order to obtain a complete picture of the coevolution of agriculture and specialization and potentially get insights on evolutionary transitions from foraging-only to settled agriculture behaviours. In such coevolution scenario, the three traits would evolve jointly along the trade-off surface. Then, the profitability of the resources itself should evolve in such coevolution scenario, since the three-components trade-off allow to vary investment into agriculture and the level of specialization.

The analysis of the evolution of niche construction in different specialization regimes show an eco-evolutionary feedback between the specialization or preference of the plant and level of agriculture. In particular, this gives insights on the transitions from foraging-only to agriculture-only strategies, that may be observed in the model, as well as transitions from foraging-only to facultative farmers (or facultative foragers). This general model that we envision in a niche construction/agriculture perspective is very well suited to understand the evolution of mutualism or symbiosis: for instance, some ants perform facultative agriculture (on aphids or fungi) while other taxa are obligate farmers of fungi (Chapela et al. 1994) or aphids (Ivens et al. 2016). This full specialization may be explained by physiological constraints and here we show that such dynamics may arise from foraging theory constraints (that may be linked to physiology, but also to resource densities, dynamics). In our model, we do not investigate whether the net interaction is mutualistic for the helped resource, because this has been proven difficult to measure experimentally (context-dependency of interactions (Chamberlain, Bronstein, and Rudgers 2014), multiple components of fitness) but we rather decide to implement both a positive and a negative aspect of the interaction.

For instance, in the ant-aphid interaction, it is unclear whether this can be qualified as mutualism or exploitation (Offenberg 2001; Billick et al. 2007; Stadler and Dixon 2005).

One of the two questions that stimulated our study was the conditions for evolution of agriculture. The other one, is the effect of this evolution on the ecological dynamics and in particular the coexistence of cultivated and non-cultivated resources, which is mediated by the indirect interactions occurring in the system, particularly apparent competition. Apparent competition has been experimentally described in systems where a predator has a positive effect of one of its preys, notably in aphid-tending ant increasing the predation on other arthropods (Warrington and Whittaker 1985; Wimp and Whitham 2001). In our model, we note that evolution does not optimize densities: this result that could seem counter-intuitive is rather well known when considering adaptive dynamics studies (Metz, Mylius, and Diekmann 2008; Boudsocq, Barot, and Loeuille 2011). Second, we show that evolutionary rescue may happen (Ferriere and Legendre 2012). In the “exploitation cost” scenario, for instance, we expect that increasing specialization on the alternative resource should reduce coexistence (because of increased predation pressure on the resource which does not benefit from niche construction). However when we consider evolution, since increasing this level of specialization leads to a decrease in the evolved niche constructing trait, this mitigates the negative effect of increased predation pressure by reducing apparent competition: evolution then helps coexistence by rescuing the alternative resource, even if the initial agriculture intensity did not allow its maintain. We can observe the same patterns in the “opportunity cost” scenario. In a community perspective, this can have consequences for the coexistence of cultivated and non-cultivated resources: because of the trade-off and evolutionary dynamics, the evolution of agriculture may allow for the coexistence of the two resources. Adaptive foraging has been shown to improve coexistence of resources by mitigating apparent competition (Abrams 2010). However, this pattern is not a general one and can be mitigated by the costs and benefits. Especially, if niche construction has a very strong positive impact on the helped resource, the decreased evolutionary agriculture levels may not be sufficient to rescue the alternative

resource that suffers from important apparent competition, and lead to the murder of the alternative resource. In devil's gardens, ants kill competitors of their host plant species: this limits coexistence at a local scale (Frederickson, Greene, and Gordon 2005). In our model, runaway evolution of the positive feedback may destabilize the system and lead to exponential growth of the consumer and helped resource. We think this pattern could be avoided if we considered diminishing returns in terms of the effect of niche construction on the helped resource, for instance, if its growth is constrained by other parameters. This addition to the model has been shown to stabilize the dynamics in the ecological analysis of this module (Picot, Monnin, and Loeuille (2019)).

If the direct benefits of niche construction are accelerating when increasing niche construction intensity, the evolution of the agricultural trait can lead to dimorphism in the consumer population. We then observe the coalition of a highly specialize farmer, that invests a lot in niche construction and only preys on the helped resource, and a forager phenotype that performs no or very low agriculture and consumer both resources. This latter could be considered a cheater in the evolution of cooperation terminology: it consumes the resource that is maintained by niche construction, without paying the cost of agriculture. Because of the direct benefit that the farmer obtains from the exploitation of the helped resource (“privatization” or “monopoly” (Krakauer, Page, and Erwin 2009; Chisholm et al. 2018)), the invasion of the cheater is avoided and the two phenotypes coexist. The coexistence of cheaters and cooperators is a question that has been studied elsewhere in the context of social evolution. A variety of mechanisms can explain this coexistence. We consider in this model a preferential access of the benefits of cooperation by cooperators through higher consumption efficiency. This preferential access can emerge from spatial structure or specificity of the resource use (Kümmerli et al. 2009; Niehus et al. 2017). Such coexistence can also emerge from cyclic dynamics such as rock-paper-scissors (or green beard) dynamics (Biernaskie, Gardner, and West 2013; Lee, van Baalen, and Jansen 2012) and snowdrift dynamics (Gore, Youk, and van Oudenaarden 2009). Here, because the cooperators retain a higher benefit from niche construction that the cheaters, it might be inadequate to qualify the latter as “true

cheaters" (Ghoul, Griffin, and West 2013). However, the decrease of niche construction in the generalist "cheater" phenotype could be interpreted as an evolutionary loss of function (since this decrease of niche construction level occurs at a branching point where the trait is at an intermediate value), that depends on the presence of the other phenotype that maintains a necessary resource. Such an evolutionary loss of trait driven by indirect positive of facilitation effects has been described in the "Black Queen Hypothesis" literature (Morris and Zinser 2012; Morris, Papoulis, and Lenski 2014).

This coexistence between niche constructors and non-constructors also allows the coexistence of the two resources: we then have an increase of the diversity in the module. Increasing the number of consumers should then stabilize the system: similar to exploitative competition where two consumers may coexist when consuming two shared resources (according to the R^* rule, (Tilman 1980)), in apparent competition, resources are more likely to coexist if they are consumed by n consumers because it balances apparent competition (similarly to the P^* rule, Holt, Grover, and Tilman (1994)). If the consumer population is considered as a whole comprised of two subpopulations, we can then interpret this coalition as division of labor, or functional specialization, between farmers and foragers. This type of division of labour linked to the evolution of specialization has recently been investigated in several theoretical works (Rueffler, Hermisson, and Wagner 2012; Cooper and West 2018): both underline the importance of considering high benefits to specialization or accelerating returns to favour division of labour, which is also something observed in our model and recalls the importance of trade-off geometries in evolutionary dynamics of specialization (Egas, Dieckmann, and Sabelis 2004; de Mazancourt and Dieckmann 2004; Kisdi 2006; Ravigné, Dieckmann, and Olivieri 2009). We have discussed our results in terms of evolution of cooperation, but our study of the evolution of niche construction is also rooted in the evolution of specialization framework. The coalition between niche-constructor and non-constructor is also a coalition between a specialist and a generalist. The question of the coexistence of specialists and generalists have been frequently investigated in the evolution of

specialization (Egas, Dieckmann, and Sabelis 2004; Abrams 2006; Rueffler, Egas, and Metz 2006). The model studied in this work provides various dynamics that emerge from simple assumptions, and these results can be understood both in the evolution of cooperation and evolution of specialization framework.

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Supplementary Information

1) Mathematical analysis: details

“Exploitation cost” scenario: convergence and invasibility

The convergence and invasibility properties are expressed as functions of second derivatives of fitness. The singularity is non-invasible (evolutionary stable) if:

$$\left.\frac{\partial^2 W(x_{mut},x_{res})}{\partial x_{mut}^{\ 2}}\right|_{x_{mut}\to x_{res}\to x^*} < 0 \Leftrightarrow \qquad (17)$$
$$e_1''(x^*)s_1(x^*)+2e_1'(x^*)s_1'(x^*)+e_1(x^*)s_1''(x^*)<0$$

The term $2e_1'(x^*)s_1'(x^*)$ is negative. Hence, the non-invasibility condition is dependent on trade-off concavity between x et s_1 ($s_1''(x^*_t)$), as well as on the benefit from niche construction ($e_1''(x^*)$). The singularity is convergent if:

$$\left.\frac{\partial^2 W(x_{mut},x_{res})}{\partial x_{mut}^{\ 2}}\right|_{x_{mut}\to x_{res}\to x^*} + \left.\frac{\partial^2 W(x_{mut},x_{res})}{\partial x_{mut}\partial x_{res}}\right|_{x_{mut}\to x_{res}\to x^*} < 0 \qquad (18)$$

Given that $\frac{\partial^2 W(x_{mut},x_{res})}{\partial x_{mut}\partial x_{res}}=\left(e_1'(x_{mut})s_1(x_{mut})+e_1(x_{mut})s_1'(x_{mut})\right)\frac{\partial R_1^*(x_{res})}{\partial x_{res}}$, we have

$$\left.\frac{\partial^2 W(x_{mut},x_{res})}{\partial x_{mut}\partial x_{res}}\right|_{x_{mut}\to x_{res}\to x^*}=\left(e_1'(x^*)s_1(x^*)+e_1(x^*)s_1'(x^*)\right)\frac{\partial R_1^*(x_{res})}{\partial x_{res}}_{x_{mut}\to x_{res}\to x^*}=0 \qquad (19)$$

Hence we conclude that the singularity is convergent if and only if it is non-invasible.

“Opportunity cost” scenario: convergence and invasibility

The strategy is non-invasible if:

$$e_1''(x^*)s_1R_1^*(x^*)+e_2s_2''(x^*)R_2^*(x^*)<0 \tag{20}$$

And it is convergent if:

$$\begin{aligned} &e_1''(x^*)s_1R_1^*(x^*)+e_2s_2''(x^*)R_2^*(x^*) \\ &+e_1'(x^*)s_1\frac{dR_1^*(x_{res})}{dx_{res}}_{x_{res}\to x^*}+e_2s_2'(x^*)\frac{dR_2^*(x_{res})}{dx_{res}}_{x_{res}\to x^*}<0 \end{aligned} \tag{21}$$

With the trade-off functions that we considered, the fitness gradient at the singularity becomes:

$$G(x^*,x^*)=\frac{\partial W(x_{mut},x_{res})}{\partial x_{mut}}_{x_{mut}\to x_{res}\to x^*}=e_1ux^{*u-1}s_1R_1^*(x^*)-e_2x^{*\frac{1}{k}-1}(L-x^{*k}-s_1^k)^{\frac{1}{k}-1}R_2^*(x^*)$$

We note that in this scenario, the resource densities at the ecological equilibrium can have an effect on the dynamics. In the linear case, the singular strategy cannot be studied (degenerate case with the nulling of the invasibility and convergence properties).

The non-invasibility condition becomes:

$$e_1(u-1)ux^{u-2}s_1R_1^*(x^*)+e_2(1-k)(L-s_1^k)x^{k-2}(L-x^{*k}-s_1^k)^{\frac{1}{k}-2}R_2^*(x^*)<0$$

We get a sufficient condition for non-invasibility: $u < 1$ and $k > 1$. A sufficient condition for the invasibility is that if $u>1$ and $k<1$.

2) Supplementary Figures

"Exploitation cost" scenario

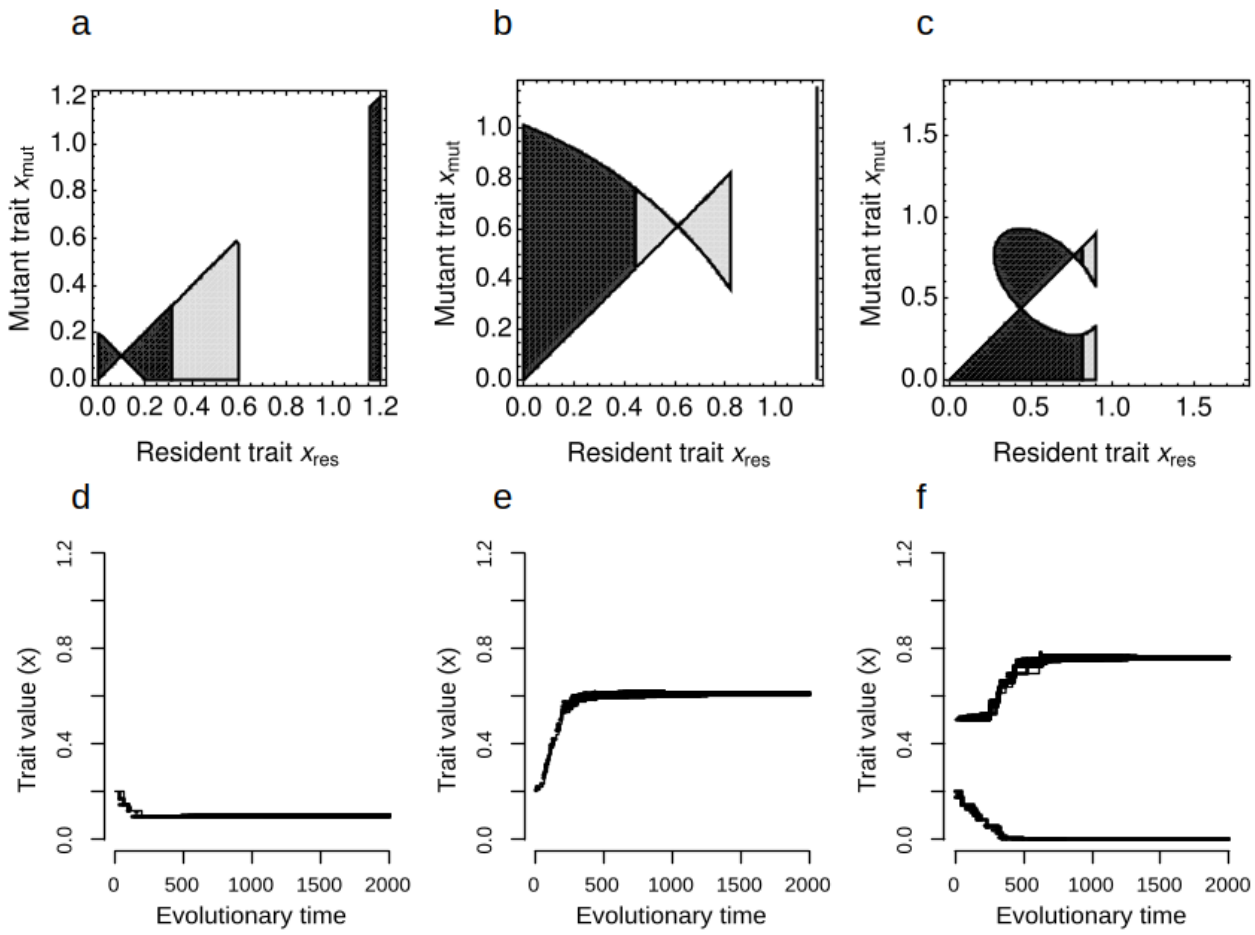

Figure S1: Pairwise Invasibility Plot and corresponding evolutionary trajectories in the "exploitation cost" scenario. For panels a,b,c: the sign of the fitness of a mutant of trait x_{mut} appearing in a population of trait x_{res} is shown (white for negative, black and grey for positive). In the black area, the three species coexist stably, while in the gray area only the constructor and R_1 coexist. a: k=2, u=1, s_2=0.8 (CSS, evolutionary attractor) illustrated in d. b: k=1, u=1, s_2=0.8 (CSS), illustrated in e. c: k=1, u=2, s_2=0.2 (repellor and CSS, evolutionary bistability, illustrated in f). Other parameter values are $b_1 = b_2 = 2$, $g_1 = g_2 = 0.8$, $e_1 = e_2 = 1$, L =2, w = 1, m = 0.8.

On panel 3a,b we obtain a CSS: the evolution leads the trait to an intermediate level of niche construction. On panel 3c, there is a repellor and a CSS: that is starting from less than 0.5 (the position of the repellor), evolution leads to zero niche construction, while starting from above 0.5,

the evolution leads to the CSS that is an intermediate value of niche construction (0.8). The evolution brings the trait to a coexistent zone on panel 3b,c while it reduces diversity by killing resource 2 on panel a.

We present the effect of specialization on the selected level of agriculture when varying the weight of each trait in the trade-off function:

$$\gamma x^k + \beta s_1^k + \alpha s_2^k = L \tag{22}$$

This leads to altered distribution of the cost of increased specialization on R_2 between the selected agriculture level and specialization on R_1 (figure S2).

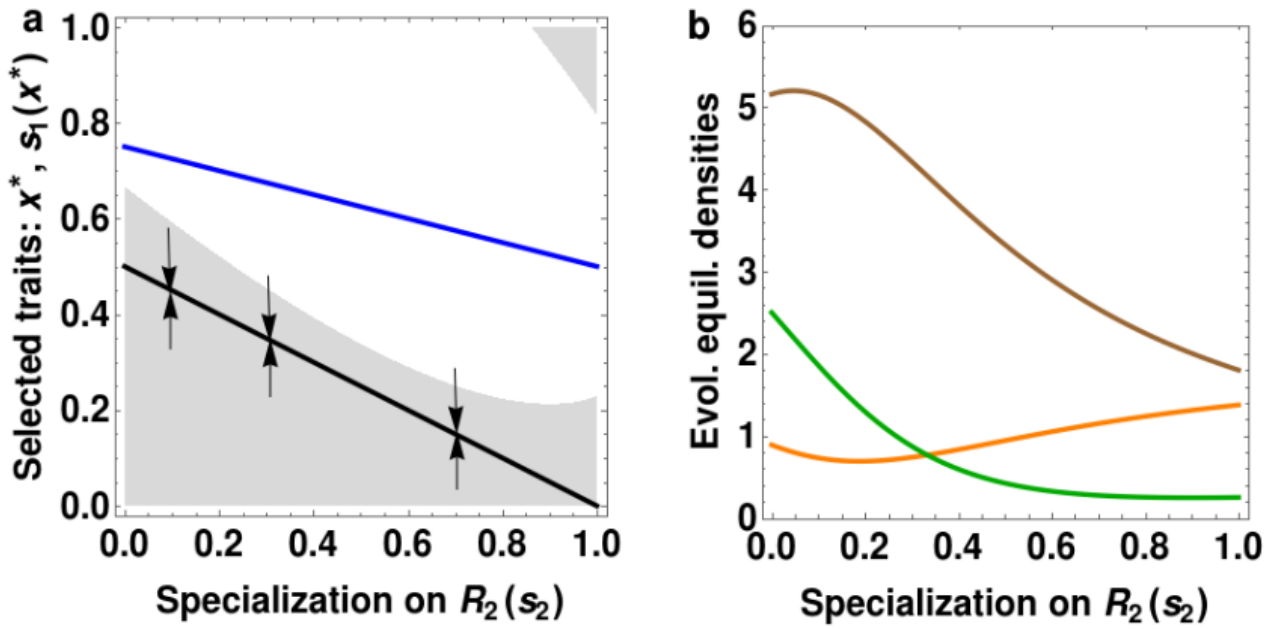

Figure S2: Effect of specialization on resource 2 on the evolutionary and ecological dynamics in the "exploitation cost" scenario. a) effect on the selected level of niche construction x (in black) and subsequent consumption of resource 2, $s_1(x^*)$ (in blue). The area of stable ecological coexistence of the three species when varying agriculture and the specialization on R_2 (ie, 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. $b_1 = b_2 = 2$, $g_1 = g_2 = 0.8$, $e_1 = e_2 = 1$, $L = 2$, $w = 1$, $m = 0.8$, $k = 1$, $u = 1$, $\alpha = 1$, $\gamma = 1$, $\beta = 2$

When the strategy is a repellor, we obtain a positive correlation between its value and the specialization on R_2 (figure S3): this leads to a negative correlation in terms of outcome of evolution, because the higher the specialization on R_2, the higher the repellor singular strategy, and the lower the range of initial values that lead to a high niche construction.

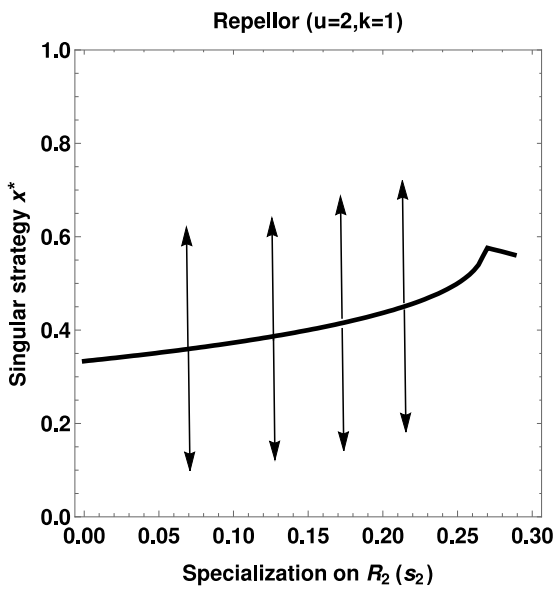

Figure S3: The effect of specialization on resource 2 on the evolutionary dynamics. We plot the value of the repellor singular strategy (unstable evolutionary equilibrium) against the value of s_2. $b_1 = b_2 = 2$, $g_1 = g_2 = 0.8$, $e_1 = e_2 = = 1$, $L = 2$, $w = 1$, $m = 0.8$, $k = 1$, $u = 2$

“Opportunity cost” scenario

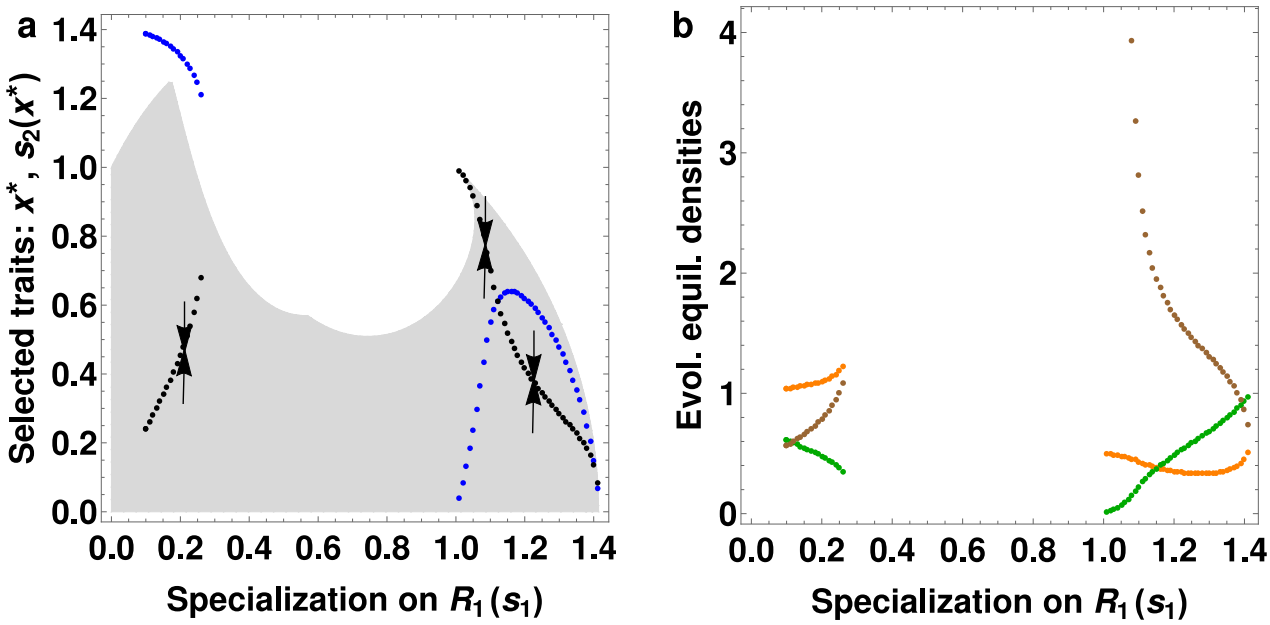

Figure S4: Effect of specialization on resource 1 on the evolutionary and ecological dynamics in the “opportunity cost” scenario. a) effect on the selected level of niche construction x (in black) and subsequent consumption of resource 2, $s_2(x^*)$ (in blue). The area of stable ecological coexistence of the three species when varying agriculture and the specialization on R_1 (ie, in a (s_1,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. $b_1 = b_2 = 2$, $g_1 = g_2 = 2$, $e_1 = e_2 = 2$,, $L = 2$, $w = 1$, $m=2$, $k=2$, $u=0.5$*