OIKOS

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From antagonistic larvae to mutualistic adults: coevolution of diet niches within life cycles

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Oikos
128: 392–404, 2019
doi: 10.1111/oik.05128

Subject Editor: Carlos Melian
Editor-in-Chief: Dries Bonte
Accepted 5 September 2018

Population structures largely affect higher levels of organization (community structure, ecosystem functioning), especially when involving ontogenetic changes in habitat or diet. Along life cycles, partners and interaction type may change: for instance Lepidopterans are herbivores as larvae and pollinators as adults. To understand variations in diet niche from larvae to adults, we model a community of two plant species and one stage-structured insect species consuming plants as juvenile and pollinating them as adult. We model the coevolution of juvenile and adult diet specialization using adaptive dynamics to investigate when one should expect niche partitioning or niche overlap among life stages. We consider ecological and evolutionary implications for the coexistence of species. As predicted based on indirect effects among stages, we find that juvenile diet evolution increases niche overlap and favours the coexistence of plants, while the evolution of the adult diet decreases niche overlap and reduces plant coexistence, because of positive feedbacks emerging from the mutualistic interaction.

Keywords: ontogenetic diet shift, pollination, predation, coevolution, indirect density-dependent effects, tradeoff

Introduction

Ecological communities involve different interaction types, qualitatively classified depending on the effect of one species on another's growth rate. Mutualistic interactions benefit to both their partners, while antagonistic interactions have a negative effect on at least one of the two species (predation, competition). Most works in network ecology consider only one interaction type, such as food webs and mutualistic networks. The co-occurrence of different interactions types within networks has recently raised much interest, leading to theoretical and empirical integrative studies combining antagonistic and mutualistic interactions (Fontaine et al. 2011, Kéfi et al. 2012, Mougi and Kondoh 2012, Georgelin and Loeuille 2014, Ke and Nakazawa 2018).

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Such a coupling between interaction types does not have to rely on the addition of extra species within existing network studies. Indeed, the role of a single species may change due to ontogenetic shifts. Lepidoptera (butterflies and moths), for instance, are herbivores as larvae and pollinators as adults (Bronstein et al. 2009, Altermatt and Pearse 2011). In aquatic foodwebs, the size and stage of an individual often determine its trophic level: the species role varies along its life cycle (Werner and Gilliam 1984). Under such conditions, population structure largely impacts coexistence and stability properties of communities (Rudolf and Lafferty 2011, Miller and Rudolf 2011).

In this theoretical work, we study the evolution and coevolution of juvenile and adult diet specialization of a Lepidoptera species. Because of this ontogenetic change of role, Lepidoptera species can have impacts on natural communities and agricultural systems. Several cases where plants are consumed and pollinated by different stages of the same species have been described (Irwin 2010, Altermatt and Pearse 2011), among which some of agricultural importance, such as the tobacco plants *Nicotiana attenuata* and the hawkmoth *Manduca sexta* interaction (Kessler et al. 2010). Here, we consider a simple community of one insect and two plants. The insect predates plants as a juvenile and pollinates them as an adult, according to each stage specialization. Optimal foraging theory (Pyke et al. 1977) predicts that at equal profitability, the specialization on the most abundant resource should be selected. Thus, the two stages should specialize on the same plant and there should be a convergence between their optimal specialization strategies. Taking account of the indirect effects occurring in the system modifies this simple prediction. Changes in partner and interaction type along life cycles create qualitative changes in indirect effects within the network.

Indirect interactions are the effect of a species on another, transmitted through other species of the network (Strauss 1991, Wootton 1994). They have been well described for trophic interactions but emerge from all interaction types and can create positive or negative effects between species. Predictions on coexistence and diversity are derived by combining apparent competition (Holt 1977) – species sharing a common predator – and exploitative competition (Tilman 1980, Begon et al. 2006) – species sharing a common resource. Coexistence may then happen, based on a tradeoff between competitive ability and vulnerability to predation (Paine 1966, Holt et al. 1994). The analysis becomes more challenging when non-trophic interaction types are considered (Fontaine et al. 2011, Georgelin and Loeuille 2014). Consider a community of flower-producing plants interacting with pollinators and herbivores. Indirect effects resulting from these interactions are asymmetrical (Holland et al. 2013). Through plant density, pollinators have a positive effect on herbivores while herbivores have a negative effect on pollinators (Georgelin and Loeuille 2014). In our system, if the juvenile (herbivore) and adult (pollinator) are specialized on the same plant, the adult should have a positive indirect effect on the juvenile through pollination. The juvenile stage however competes with the adult as it consumes the plant.

The diet overlap of adults and juveniles has implications for the coexistence of the plant communities. If the juvenile is not a full specialist, that is the two plant species share a predator (herbivore), then they are involved in apparent competition (Holt 1977). Similarly, even though pollen dilution may happen, observations suggest that pollinator sharing may create dominant facilitative effects among plant species (Tur et al. 2016). Therefore, apparent mutualism among plant species is possible, when the adult stage is not a full specialist. A meta-analysis of adult and juvenile diets from 995 species of European Lepidoptera showed a significant positive correlation between adult and juvenile diets (Altermatt and Pearse 2011). The authors suggest this is due to physiological and spatial constraints. In this study, we investigate the following alternative hypothesis: the indirect effect asymmetry resulting from coupling antagonism and mutualism may explain the positive correlation between adult and juvenile diets. We study the evolution and co-evolution of diet specialization of the two stages, using adaptive dynamics (Geritz et al. 1998). We allow juvenile and adult preferences for the two plants to evolve in response to community dynamics. We consider a tradeoff based on temporal and allocation constraints: an increased interaction (pollination or consumption) with one plant reduces the interaction with the other plant.

We address the following questions: 1) what are the conditions on diet overlap of the insect stages allowing the coexistence of the plant populations? We predict that coexistence requires a balance between pollination and herbivory between the two plants, therefore a strong diet overlap (Holt et al. 1994). 2) What are the evolutionary dynamics of each stage preference and how do these preferences coevolve? Based on the predicted indirect effects between the two stages, we expect that the evolution of the juvenile specialization at a fixed adult preference maximizes diet overlap while the evolution of adult specialization at a fixed juvenile preference minimizes diet overlap. The relative evolutionary constraints on the adult and juvenile traits should then determine the balance of the above-identified opposite selective pressures and thus the outcome of their coevolution. 3) What is the effect of evolutionary dynamics on the communities composition and ecological dynamics? Evolution should lead to coexistence of the two plants if it promotes a sufficient diet overlap, whether the two stages are generalist or specialized on the same plant. If evolution leads to specialization on different plants for the two stages we predict a decrease in coexistence following the decrease in density of one plant.

Methods

Ecological dynamics of the system

We formulate our model according to the following ordinary differential equations for the community:

$$
\begin{cases}
\dfrac{\mathrm{d}P_1}{\mathrm{d}t} = r_1 P_1 - s^g a_1 P_1 J + m^h w_1 b_1 P_1 A & \text{(a)} \\
\dfrac{\mathrm{d}P_2}{\mathrm{d}t} = r_2 P_2 - (1-s)^g a_2 P_2 J + (1-m)^h w_2 b_2 P_2 A & \text{(b)} \\
\dfrac{\mathrm{d}J}{\mathrm{d}t} = V_A(P_1,P_2) A - V_J(P_1,P_2) J - d_J J & \text{(c)} \\
\dfrac{\mathrm{d}A}{\mathrm{d}t} = V_J(P_1,P_2) J - d_A A & \text{(d)}
\end{cases}
\quad (1)
$$

$$
\begin{cases}
V_A(P_1,P_2) = m^h v_1 b_1 P_1 + (1-m)^h v_2 b_2 P_2 \\
V_J(P_1,P_2) = s^g k_1 a_1 P_1 + (1-s)^g k_2 a_2 P_2
\end{cases}
$$

Equations (a), (b), (c), (d) of system (1) represent the density variations of plant P_1, plant P_2, juvenile J and adult A insect stages. In the absence of the insect, plant populations exhibit exponential growth with r_i defined as the intrinsic growth rate of plant P_i. If $r_i < 0$, then P_i is an obligate mutualist while if $r_i > 0$, P_i is a facultative mutualist. The plants are consumed by the juvenile stage and pollinated by the adult stage of the insect. These interactions are modeled by a type I functional response (Holling 1959) where a_i is the predation rate and b_i is the pollination rate. k_i are energy conversion efficiencies associated with consumption rates. w_i corresponds to the conversion of pollination benefits by plant P_i while v_i scales the conversion of pollination benefits into growth for the adult stage (Fig. 1A). We define s^g and m^h the juvenile and adult preferences for P_1: the trait s quantifies how much the juvenile interacts with P_1 compared to P_2 while the trait m quantifies how much the adult interacts with P_1 compared to P_2 ($0 < s < 1$ and $0 < m < 1$). The tradeoff functions for each stage specialization are modeled by the exponents g for the juvenile preference and h for the adult preference. A concave tradeoff means specialization is costlier than generalism, while the costs associated to generalist strategies are higher under convex tradeoffs (Fig. 1B). The transition rates between stages are consumption-dependent (Schreiber and Rudolf 2008, Revilla and Encinas-Viso 2015, Ke and Nakazawa 2018) $V_A(P_1,P_2)$ is the reproduction rate, assumed to be proportional to adult energy intake. $V_J(P_1,P_2)$ is the maturation rate and is proportional to juvenile consumption resulting from predation on the plants. Parameters are further presented and discussed in Supplementary material Appendix 1.

Setting Eq. 1a–d to 0 gives the ecological equilibria. We investigate their feasibility by determining populations positivity conditions and their stability through the associated Jacobian matrix. We also analyzed the direct and indirect effects occurring in the system, using the negative inverse Jacobian matrix (Vázquez et al. 2015). The details of the analytical investigation of ecological dynamics is reported in Supplementary material Appendix 2, while we present the main results in the 'Ecological dynamics' section of the Results.

Evolutionary dynamics of the system

We study the evolution of the phenotypic traits s and m, that affect juvenile and adult specialization, using the adaptive dynamics framework (Dieckmann and Law 1996, Geritz et al. 1998). Adaptive dynamics allows to investigate evolutionary dynamics of phenotypic traits with explicit links to ecological dynamics. The analytical computations we present rely on the separation of ecological and evolutionary timescales. The evolution of a trait is studied through several steps, assuming clonal reproduction, and small and rare mutations:

1) the ecological equilibrium is determined, for a monomorphic population of resident trait x_{res} (by nulling Eq. 1a–d)

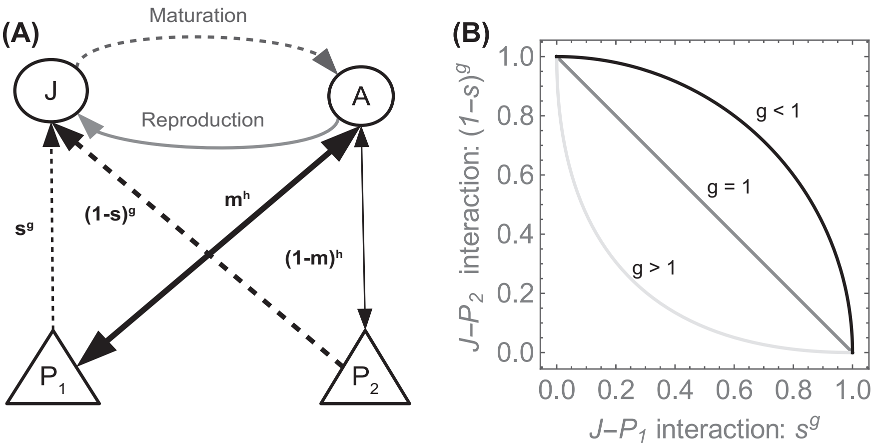

Figure 1. Community structure and tradeoff shapes. (A) Community structure. A and J are the adult and juvenile stages of the insect. P_1 and P_2 are the two plant species. Species interactions are represented in black lines (predation: dashed and single-arrowed lines, mutualism: solid and double-arrowed lines), while life history events are represented in gray lines: dashed for maturation, and solid for reproduction). (B) Tradeoff intensity for juvenile specialization on plants P_1 and P_2. The tradeoff is concave (being a specialist is costlier than generalism) for smaller values of the exponent ($g < 1$) and convex (being a generalist is costlier than specialism) for higher values of the exponent ($g > 1$). The tradeoff is linear when $g = 1$.

2) a rare mutant with trait x_{mut} is introduced and replaces the resident trait if its invasion fitness is positive. The new ecological equilibrium is established and the process is iterated.

Dieckmann and Law (1996) derived a deterministic approximation of this process, the canonical equation of adaptive dynamics (Eq. 2):

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

$\mu\sigma^2 N^0\left(x_{res}\right)$ represents the total phenotypic variability resulting from mutations; μ and σ^2 are the mutation rate per individual and associated phenotypic variance and $N^0(x_{res})$ is the density of the population (or reproductive class for a structured population) at the equilibrium determined by the resident.

The selection gradient $\left.\frac{\partial W\left(x_{mut}, x_{res}\right)}{\partial x_{mut}}\right|_{x_{mut} \to x_{res}}$ represents the selective pressures acting on the phenotypic variability brought by mutations. By nulling it, one obtain the fixed points of the canonical equation, called singular strategies. Dynamics around these singular strategies are characterized by the second partial derivatives of fitness. 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:

$$\left.\frac{\partial^2 W\left(x_{mut}, x_{res}\right)}{\partial {x_{mut}}^2}\right|_{x_{mut} \to x_{res} \to x^*} < 0 \tag{3}$$

i.e. if no nearby mutant can invade the singularity.

A singular strategy is convergent (Eshel 1983) if:

$$\left.\frac{\partial^2 W\left(x_{mut}, x_{res}\right)}{\partial {x_{mut}}^2}\right|_{x_{mut} \to x_{res} \to x^*} + \left.\frac{\partial^2 W\left(x_{mut}, x_{res}\right)}{\partial x_{mut}\partial x_{res}}\right|_{x_{mut} \to x_{res} \to x^*} < 0 \tag{4}$$

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

Invasion fitness in a structured population: a matrix-based approach

In unstructured population models, the relative fitness of the mutant is determined by its per capita population growth rate when rare in the resident population. Based on a similar idea, in a structured model, the mutant may invade when rare, provided its population is repelled from the extinction equilibrium. This approach is analogous to fitness criterion for meta-populations (Metz and Gyllenberg 2001, Massol et al. 2009). Based on this idea, we define the fitness function in Supplementary material Appendix 3.

We illustrate evolutionary dynamics using pairwise invasibility plots (PIP) that represent areas of positive and negative fitness of a mutant of trait s_{mut} (or m_{mut}) in the equilibrium set by the resident s_{res} (or m_{res}).

Simulations of trait evolution and trait co-evolution

We simulated trait evolutionary trajectories to illustrate analytical results and study the coevolution of the two preferences (see the algorithm structure in Supplementary material Appendix 5), presented on Fig. 5. Because the 'single trait' evolution anaylsis above suggests that tradeoff structures matter much for juvenile evolution and not much for adult evolution, we run simulations following two tradeoff scenarios (concave and convex) for the juvenile preference, and with a convex tradeoff for the adult preference. Because we expect conflicting selective pressures on the adult and juvenile traits, the outcome of coevolution should depend on the relative evolution speed allowed for each trait. We therefore manipulate the standing phenotypic variability by changing adult and juvenile mutation rates on a logarithmic grid (10^{-14} to 10^{-11}). Each set is replicated 50 times starting from the same initial conditions (high diet overlap, generalist stages, coexisting plants) and run for 10 000 time steps (i.e. random mutational events on the adult and/or juvenile traits). We define diet overlap D_f as the similarity between the two plant-stages interaction frequencies (Eq. 5): F_A is the adult mean frequency of interaction with P_1, and F_J is the juvenile mean frequency of interaction with P_1. $D_f = 1$ corresponds to a maximal diet overlap, while $D_f = 0$ is the minimal diet overlap.

$$\begin{aligned} F_A &= \frac{m^b v_1 b_1}{m^b v_1 b_1 + (1-m)^b v_2 b_2} \\ F_J &= \frac{s^g k_1 a_1}{s^g k_1 a_1 + (1-s)^g k_2 a_2} \\ D_f &= 1 - \left|F_A - F_J\right| \end{aligned} \tag{5}$$

The mean phenotypic traits, the number of phenotypes, the plant community state were then averaged on the 50 replicates for each combination of juvenile and adult mutation rates.

Analysis of an extended version of the model

Note that the previous model does not include direct competition (e.g. for nutrient or space) among the two plant species. This allows us to focus our discussion on the effects of the interacting species and its larvae/adult structure. This simplicity also allows us to get a mathematical analysis of ecological and evolutionary dynamics that is not possible in more complex settings. However, in Supplementary material Appendix 4, we carry an analysis of extended version of our initial simple model, in which the two plants directly compete. We then compare numerically or semi-analytically obtained results of this extended model to the analytical results of the simple linear model presented in the main body. Overall, the conclusions we get for the simple model are robust to the inclusion of plant competition. Especially, our conclusions regarding the conditions for coexistence, as well as the evolutionary predictions we propose below concerning the evolution of diet specialization and overlap are unaltered by such modifications.

Results

Ecological dynamics: how do diet specialization and niche overlap of the two insect stages affect plant coexistence?

We first assume that the traits are fixed and present some key aspects of the ecological dynamics of the community. There are four possible states of the community at equilibrium: extinction of the three species (equilibrium 0), one plant only and the insect (equilibrium *i* with plant P_i) and coexistence of the three species (equilibrium 3). Two additional one-plant–insect equilibria mathematically exist but are never feasible (densities being negative) so we discard them from the rest of the analysis. Here we focus mainly on the study of the coexistence equilibrium. We present the detailed analytical study of one-plant equilibria in the Supplementary Material Appendix 2.

While we described indirect ecological effects between juveniles and adults, the two stages are also linked directly, through maturation and reproduction. The first step of the ecological analysis is then to investigate the direct, indirect and total effects between the different sub-populations at equilibrium. We demonstrate through the study of the negative inverse Jacobian matrix for the one-plant equilibrium that coupling the adult and juvenile population does not change the qualitative indirect effects predicted initially: through the plant, the juvenile stage has a negative indirect effect on the adult growth rate, while the adult stage has a positive effect on the juvenile growth rate (see details in Supplementary material Appendix 2).

Given the feasibility and local stability of equilibrium 1 (detailed in Supplementary material Appendix 2), we consider the stability against the invasion of a second plant, that could lead to coexistence of the two plants. P_2 can invade in the insect-P_1 system only if the per capita growth rate of a very small density of P_2, at equilibrium 1, is positive. This condition can be written:

$$r_2 > (1-s)^g a_2 J^*_{(1)} - (1-m)^h w_2 b_2 A^*_{(1)} \tag{6}$$

The invasion of P_2 is possible if P_1 supports a high enough adult equilibrium density compared to the juvenile density, and if P_2 is weakly consumed by the juveniles or highly pollinated by the adults. The invasion of a plant that could not persist alone ($r_2 < 0$) may happen due to the presence of the insect and P_1. In such instances, a facilitation of plant P_2 by P_1 occurs, through their interactions with the insect (Bruno et al. 2003). Under certain conditions, we observe bistability of the two one-plant equilibriums (Fig. A2.1 in Supplementary material Appendix 2).

The coexistence of the two plants and the insect (Eq. 3) leads to the following populations:

$$\begin{cases} P_1^*{}_{(3)} = \dfrac{d_A b_2 (1-m)^h v_2 A^*{}_{(3)}{}^2 - a_2 k_2 (1-s)^g J^*{}_{(3)} \left(d_A A^*{}_{(3)} + d_J J^*{}_{(3)}\right)}{A^*{}_{(3)} J^*{}_{(3)} \left(a_1 k_1 s^g b_2 v_2 (1-m)^h - a_2 k_2 (1-s)^g b_1 v_1 m^h\right)} \\ P_2^*{}_{(3)} = \dfrac{a_1 k_1 s^g J^*{}_{(3)} \left(d_A A^*{}_{(3)} + d_J J^*{}_{(3)}\right) - d_A b_1 v_1 m^h A^{*2}_{(3)}}{A^*{}_{(3)} J^*{}_{(3)} \left(a_1 k_1 s^g b_2 v_2 (1-m)^h - a_2 k_2 (1-s)^g b_1 v_1 m^h\right)} \\ A^*{}_{(3)} = \dfrac{a_1 s^g r_2 - a_2 (1-s)^g r_1}{a_2 (1-s)^g b_1 w_1 m^h - a_1 s^g b_2 w_2 (1-m)^h} = \dfrac{\dfrac{r_2}{a_2 (1-s)^g} - \dfrac{r_1}{a_1 s^g}}{\dfrac{b_1 w_1 m^h}{a_1 s^g} - \dfrac{b_2 w_2 (1-m)^h}{a_2 (1-s)^g}} \\ J^*{}_{(3)} = \dfrac{b_1 w_1 m^h r_2 - b_2 w_2 (1-m)^h r_1}{a_2 (1-s)^g b_1 w_1 m^h - a_1 s^g b_2 w_2 (1-m)^h} = \dfrac{\dfrac{r_2}{b_2 w_2 (1-m)^h} - \dfrac{r_1}{b_1 w_1 m^h}}{\dfrac{b_1 w_1 m^h}{a_1 s^g} - \dfrac{b_2 w_2 (1-m)^h}{a_2 (1-s)^g}} \end{cases} \tag{7}$$

In order to have coexistence the mainly pollinated plant must also be the mainly predated plant. This is shown considering the positivity of adult density. The numerator and denominator of $A^*_{(3)}$ Eq. 7 must have the same sign, i.e. if the growth/predation ratio of P_2, $\dfrac{r_2}{a_2 (1-s)^g}$, is higher than the one of P_1, the mutualism/predation ratio of P_1, $\dfrac{b_1 w_1 m^h}{a_1 s^g}$ must be higher than the one of P_2. For a given level of consumption, one plant must have a strong intrinsic growth, while the other must strongly interact with the mutualistic stage. In addition, at the stable equilibrium, the sign of the long-term effect (sensu Vázquez et al. 2015) of P_i on P_j is the opposite sign of r_j (Supplementary material Appendix 2).

In summary, coexistence is favored in a system where the two stages preferentially interact with the same plant, let us say P_1. The effect of this interaction on P_2 is either positive (if P_2 is an obligate mutualist, $r_2 < 0$) or negative (if P_2 is a facultative mutualist, $r_2 > 0$). We illustrate how diet specialization and overlap affect ecological coexistence on Fig. 2 (with the tradeoff scenarios used in the evolution analysis). When $m >> s$, P_1 is more pollinated and less predated than P_2 (above the diagonal) and only P_1 stably subsists in the system. Symmetrically, only P_2 subsists below the diagonal. Coexistence is favored along the diagonal, when pollination on one plant is balanced by predation. This result therefore stresses the importance of juvenile and adult diets overlap for the maintenance of the system.

We do not detail other (cyclic, complex) dynamics, as our adaptive dynamics approach explicitly assumes stable and feasible equilibria. We illustrate such dynamics in Supplementary material Appendix 2 Fig. A2.1 (see as well Revilla and Encinas-Viso 2015).

Evolutionary dynamics: evolution and co-evolution of diet specialization for both stages

We assume for analytical tractability that r_1 and r_2 are positive, which corresponds to a case of facultative mutualism

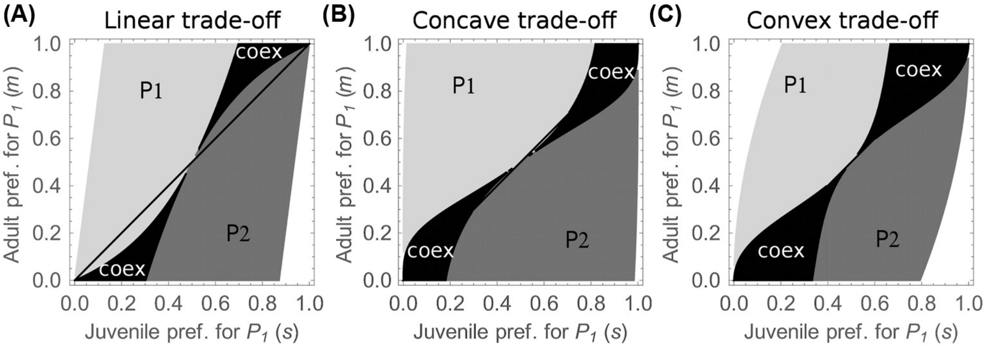

Figure 2. Changes in community structure in the (s, m) space, for three tradeoff structures. The stability and feasibility areas of Eq. 1 (P_1 only), 2 (P_2 only) and Eq. 3 (coexistence of P_1 and P_2) are represented respectively in light gray, gray and black. White areas correspond to unstable dynamics which can lead to extinction. The diet overlap is maximal ($s \sim m$) around the diagonal (solid line). Upper-right and lower-left corners correspond to extreme specializations. (A) $h = g = 1$. (B) $h = 1.5$, $g = 0.5$. (C) $h = 2.5$, $g = 1.3$.

with the adult stage for the plants (e.g. because they interact with other pollinators that we do not model here or because they may reproduce asexually or self-reproduce).

Evolution of the juvenile preference at a fixed adult preference

We determine the fitness $W(s_{mut}, s_{res})$ and fitness gradient $G(s_{mut}, s_{res})$ of a mutant s_{mut} given a resident s_{res}:

$$W\left(s_{mut}, s_{res}\right) = d_J \frac{J_{res}^*}{A_{res}^*} V_{J_{mut}}\left(s_{mut}, s_{res}\right) - d_A d_J$$

$$G\left(s_{mut}, s_{res}\right) = d_J \frac{J_{res}^*}{A_{res}^*} g\Big(a_1 k_1 s_{mut}^{\;g-1} P_1^*\left(s_{res}\right) - a_2 k_2 \left(1 - s_{mut}\right)^{g-1} P_2^*\left(s_{res}\right)\Big) \qquad (8)$$

If a given plant is almost extinct, the gradient tends to be either always positive or always negative: evolution leads to complete specialization on the other plant (the preference trait either increases to 1 or decreases to 0).

We now consider that the two plants coexist at the resident equilibrium. A singular strategy s^* is defined by the Eq. 9, with plants densities being at equilibrium 3 cf. (Eq. 7); and cannot be expressed analytically:

$$a_1 k_1 \left(s^*\right)^{g-1} P_1{}^*_{(3)}\left(s^*\right) - a_2 k_2 \left(1 - s^*\right)^{g-1} P_2{}^*_{(3)}\left(s^*\right) = 0 \qquad (9)$$

Given that:

$$\left.\frac{\partial G\left(s_{mut}, s_{res}\right)}{\partial s_{mut}}\right|_{s_{mut} \to s_{res} \to s^*} < 0 \Leftrightarrow \qquad (10)$$

$$d_J \frac{J_{res}^*}{A_{res}^*}(g-1) g\left(a_1 k_1 \left(s^*\right)^{g-2} P_1\left(s^*\right) + a_2 k_2 \left(1 - s^*\right)^{g-2} P_2\left(s^*\right)\right) < 0$$

the singular strategy is non-invasible if and only if $g < 1$, i.e. the tradeoff is concave (specialization is costlier than generalism).

It is convergent if (Eq. 11):

$$C\left(s^*\right) = g - 1 + \left(1 - s^*\right) s^* \left(\frac{1}{P_1^*} \left.\frac{\partial P_1}{\partial s_{res}}\right|_{s_{res} \to s^*} - \frac{1}{P_2^*} \left.\frac{\partial P_2}{\partial s_{res}}\right|_{s_{res} \to s^*}\right) < 0 \qquad (11)$$

We demonstrate that, at the singular strategy, $\left.\frac{\partial P_2}{\partial s_{res}}\right|_{s_{res} \to s^*} > 0$ and $\left.\frac{\partial P_1}{\partial s_{res}}\right|_{s_{res} \to s^*} < 0$ (see Supplementary material Appendix 3 for proof).

Then, if $g < 1$, the singular strategy is both evolutionary and convergent-stable (continuously stable strategy, or CSS), i.e. it is the endpoint of evolution (Fig. 3A–B). If $g > 1$ and $C(s^*) < 0$, the singular strategy is an evolutionary branching point (EBP): evolution converges to it, then phenotypic diversification occurs due to disruptive selection (Fig. 3C–D). If $g > 1$ and $C(s^*) > 0$, the singular strategy is a repellor. In such instances, evolution pushes toward the specialization on either plant, depending on the initial trait value.

Consequences for community structure may be far-reaching. For instance, in the CSS scenario on Fig. 3A, the singular strategy lies in the coexistence area (in black). If the two plants coexist in the initial community, evolution reinforces the maintenance of the community by pushing it away from extinction boundaries. Also, evolution starting from a one plant community (light and dark gray areas) brings the specialization trait in the coexistence area, facilitating the invasion of the other plant. On Fig. 3B, we present two possible evolutionary dynamics converging to the CSS, from an initial state of coexistence ($s = 0.9$) or non-coexistence ($s = 0.3$). Evolution may not only maintain or facilitate the coexistence of the community, but also increase its functional diversity. For instance, on Fig. 3C, an evolutionary branching point leads to a stable dimorphism in the juvenile class (Fig. 3D).

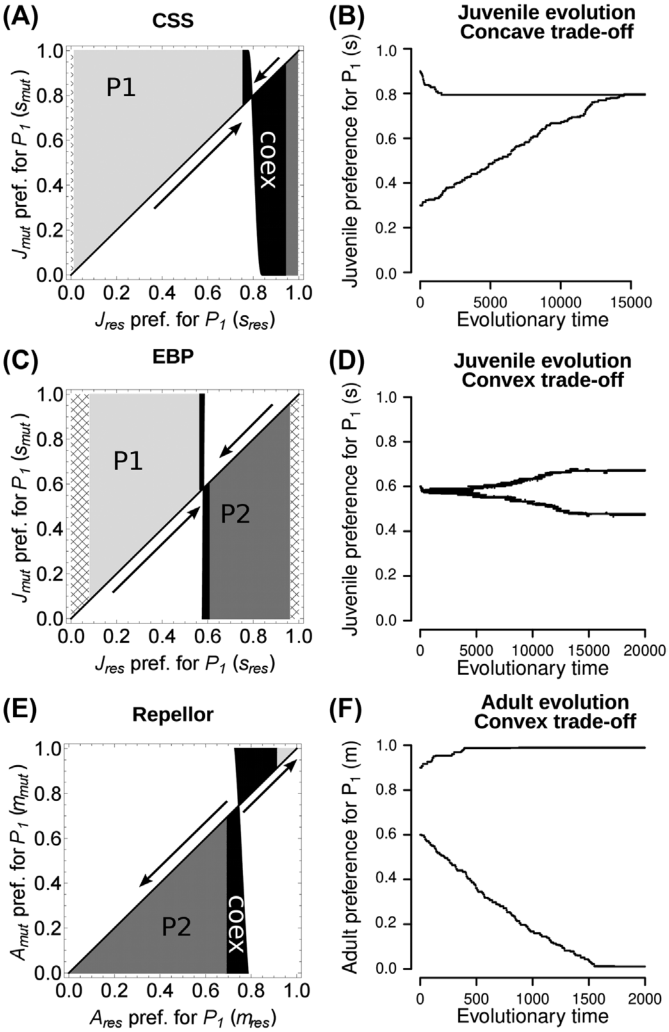

Figure 3. Evolutionary dynamics of one stage preference. In each PIP (A, C, E), in white areas the mutant fitness is negative while it is positive in black, light and dark gray areas. Light gray, dark gray and black, correspond to ecological Eq. 1, 2 and 3 respectively. Hatching indicates unstable states. The black points indicate the phenotypic composition of the population in the corresponding simulations (B, D and F). (A) continuously stable strategy (CSS) ($h = 1.5$, $g = 0.5$, $m = 0.8$) for the juvenile preference, illustrated by two evolutionary dynamics that converge to the CSS (B). (C) evolutionary branching point (EBP) ($h = 2.5$, $g = 1.3$, $m = 0.85$), leading to stable dimorphism of juvenile preference (D). (E) Repellor for the adult preference ($h = 1.5$, $g = 0.5$, $s = 0.8$), leading to full specialization on P_2 or P_1 according to the initial preference (F).

Evolution of the adult preference at a fixed juvenile preference

Similarly, the fitness and fitness gradient of a mutant m_{mut} given a resident m_{res} are:

$$W(m_{mut}, m_{res}) = -d_A\left(V_{J_{res}}(m_{res}) + d_J\right) + V_{A_{mut}}(m_{mut}, m_{res})V_{J_{res}}$$

$$G(m_{mut}, m_{res}) = hV_{J_{res}}(m_{res})(b_1 m_{mut}{}^{h-1} v_1 P_1(m_{res}) - b_2(1-m_{mut})^{h-1} v_2 P_2(m_{res}) \quad (12)$$

A singular strategy is defined by:

$$b_1(m^*)^{h-1} v_1 P_1(m^*) - b_2(1-m^*)^{h-1} v_2 P_2(m^*) = 0 \quad (13)$$

If only one plant persists at the resident equilibrium, evolution again leads to specialization of the adult stage on this plant. We focus on the coexistence equilibrium (Eq. 7). Using the evolutionary stability condition (Eq. 14), we show that the singular strategy for the adult preference is non invasible if the tradeoff on adult specialization is concave, ie when being a specialist is costlier than generalism ($h < 1$).

$$\left.\frac{\partial G(m_{mut}, m_{res})}{\partial m_{mut}}\right|_{m_{mut} \to m_{res} \to m^*} < 0 \Leftrightarrow \quad (14)$$
$$h(h-1)V_{J_{res}}(m_{res})\left(m^{*h-2} b_1 v_1 P_1(m^*) + (1-m^*)^{h-2} b_2 v_2 P_2(m^*)\right) < 0$$

Table 1. Evolutionary dynamics of the adult and the juvenile preference, depending on the tradeoff constraining specialization for each stage.

	Concave tradeoff ($g < 1$ or $h < 1$)	Convex tradeoff ($g > 1$ or $h > 1$)
Evolution of the juvenile preference at a fixed adult preference	CSS Promotes the coexistence of the plants (generalist juvenile)	EBP or repellor (not observed numerically) Promotes community diversity (coexistence and diversification in the juvenile trait)
Evolution of the adult preference at a fixed juvenile preference	Garden of Eden or CSS (not observed numerically) Decreases coexistence of the plants, evolutionary murder of one plant (specialist adult)	Repellor Decreases coexistence of the plants: evolutionary murder of one plant (specialist adult)

The convergence criterion of the singular strategy is:

$$C(m^*) = h - 1 + (1 - m^*)m^* \left(\frac{1}{P_1^*} \frac{\partial P_1}{\partial m_{res}} \bigg|_{m_{res} \to m^*} - \frac{1}{P_2^*} \frac{\partial P_2}{\partial m_{res}} \bigg|_{m_{res} \to m^*} \right) \qquad (15)$$

We show that $\left.\frac{\partial P_1}{\partial m_{res}}\right|_{m_{res} \to m^*} > 0$ and $\left.\frac{\partial P_2}{\partial m_{res}}\right|_{m_{res} \to m^*} < 0$

Therefore, if $h > 1$, the singularity is both divergent and evolutionarily unstable: it is a repellor (Fig. 3E–F). If $h < 1$, the singularity is a CSS (if $C(m^*) < 0$) or a Garden of Eden ($C(m^*) > 0$), which means that the singular point is locally evolutionary stable (non invasible by nearby mutant strategies) but can never be reached starting from a different trait value. Biologically, this situation is equivalent to a repellor. If m^* is a repellor or a Garden of Eden, evolution leads to full specialization, on one plant or the other depending on the initial value of adult preference. CSS were not observed by simulations. Again, evolution has important implications for coexistence. During the specialization that occurs in Garden of Eden or repellor scenarios, the system moves away from the coexistence area: evolution eventually leads to the extinction of one of the two plant species (Fig. 3E–F).

We summarize the possible evolutionary dynamics of the adult and juvenile preference in Table 1.

Effect of the non-evolving stage preference value on the evolution of the other stage preference

Based on indirect effects, we predicted that the evolution of juvenile preference leads to diet overlap while the evolution of adult preference leads to niche separation. We numerically test this hypothesis (Fig. 4). For increasing (fixed) adult preferences, evolution leads to higher juvenile preferences (Fig. 4A): the selective pressures on the juvenile stage lead to a diet overlap. While we also show a positive correlation between the juvenile preference and the adult singular strategy (Fig. 4B), the latter is divergent: the adult strategy evolves away from the juvenile preference. Evolution then leads to niche separation.

Co-evolution of the two stage preferences

We now let the two traits evolve simultaneously. For the juvenile phenotype, we consider tradeoff scenarios leading previously to CSS (Fig. 3A–B) or EBP (Fig. 3C–D), while for the adult phenotype, we arbitrarily consider a convex tradeoff leading to a repellor (Fig. 3E–F) (as the tradeoff shape does not affect the evolutionary outcome for the adult trait evolution, qualitatively leading to evolutionary bistability either through repellors or garden of Eden). If run until evolutionary equilibrium, the simulations lead to the same qualitative result: the adult stage fully specializes on one plant and its evolution stops. The juvenile trait follows the adult trait and either stabilizes at a CSS or diversifies into two branches (EBP point). This leads to a high diet overlap allowing the coexistence of the two plants. We however expect the transient dynamics and stability of the evolutionary dynamics to depend on the relative speed of the juvenile and adult evolution (Fig. 5). This speed not only depends on the selection process (the gradient of fitness), but also on the two phenotypes variability (here manipulated through variations in the mutation rates). The system is far from complete niche separation. Maximum niche separation is observed for cases of rapid evolution of the adult and slow evolution of the juvenile (Fig. 5A–B). The evolution of the insect then kills one of the two plants, by favoring mutualistic specialization on the other (evolutionary murder sensu Dercole et al. 2006). Fast evolution of both stages favors coexistence (Fig. 5C–D) and even leads to diversification in the juvenile preference (stable polymorphism) in EBP scenarios (Fig. 5D, hatched area).

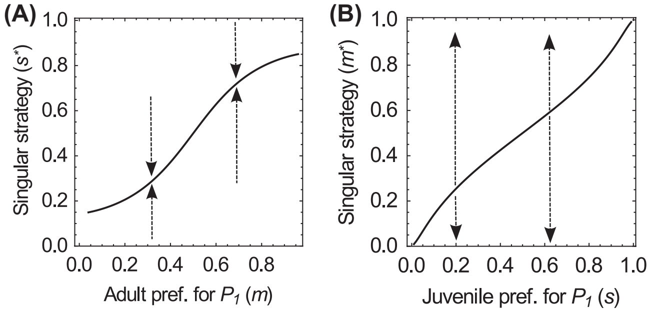

Figure 4. Correlation between the singular strategy for the evolution of the preference of one stage and depending on the fixed preference of the other, non-evolving, stage. In (A), we observe a positive correlation between the selected juvenile preference and the fixed adult preference, because the singular strategy is convergent. In (B), we observe a negative correlation between the evolution of adult preference and the fixed juvenile preference, because the strategy is divergent. Evolutionary directions are indicated by dashed arrows.

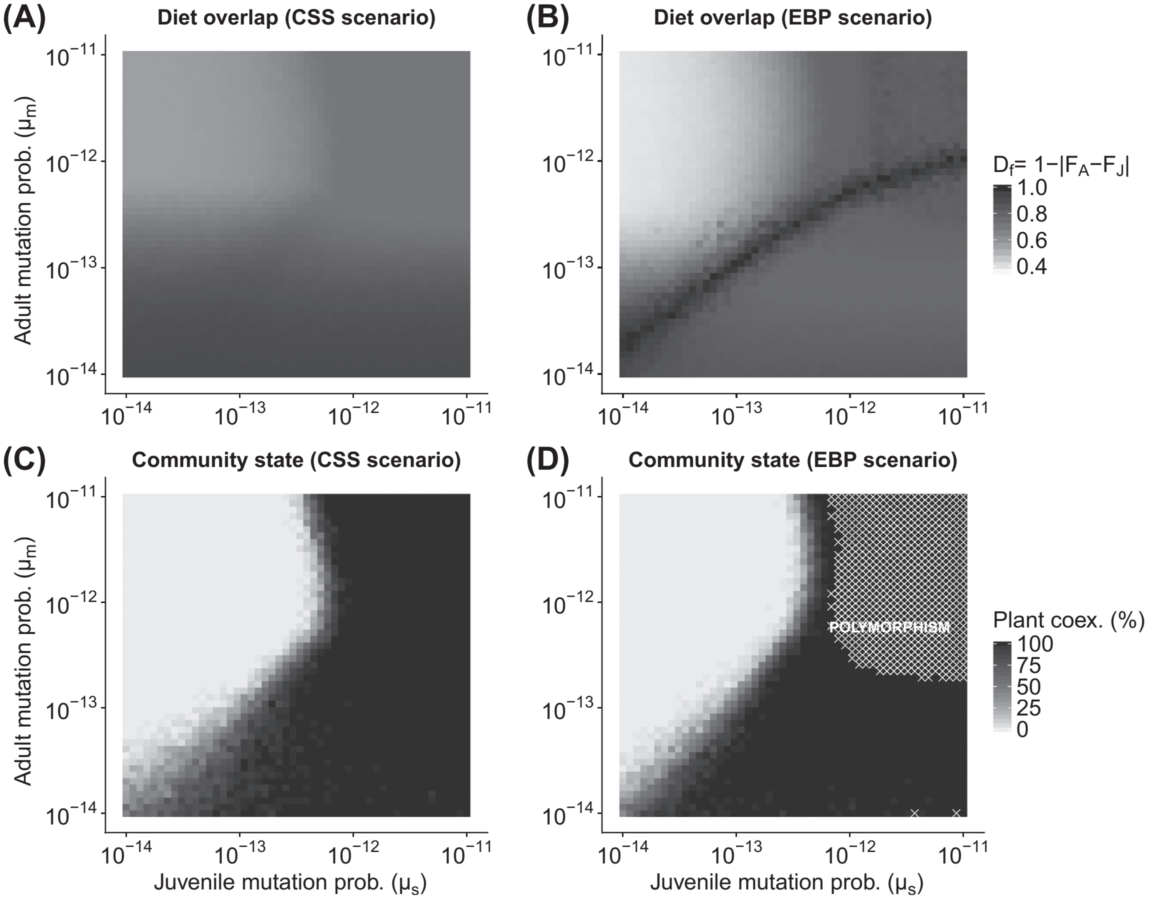

Figure 5. Co-evolution of adult and juvenile preferences. (A) and (B) correspond to a concave tradeoff for juvenile specialization, that is being a specialist is costlier than being a generalist ($g=0.5$, $h=1.5$, $s_i=0.65$; $m_i=0.6$, $\sigma_m=\sigma_s=0.01$), while (C) and (D) correspond to a convex tradeoff for juvenile specialization, that is being a generalist is costlier than being a specialist ($g=1.3$, $h=2.5$, $s_i=0.6$; $m_i=0.6$, $\sigma_m=\sigma_s=0.01$). Each point of the grid represents the average result of 50 replicates. In (A) and (C), we represent the mean diet overlap D_f at the end of the simulation. In (B) and (D), we represent the final ecological state of the community, indicated by the percentage of simulations that end with the coexistence of the plants. In (D), the hatched area corresponds to the occurrence of polymorphism of the juvenile trait in more than 50% of the replicates.

Discussion

The motivation for our study was to investigate the positive correlation between adult and juvenile diet specializations observed in empirical data (Altermatt and Pearse 2011), and its consequences for ecological communities. We show that the ecological coexistence of the two plants requires a balance between predation and pollination, therefore some diet overlap between adult and juvenile specializations. As predicted from the indirect effects occurring between the two stages, juveniles evolve toward generalism and to maximize diet overlap, thereby favoring plant coexistence when the tradeoff on specialization is concave that is being a specialist is costlier than being a generalist. For convex tradeoffs (generalism is costlier than specialism), evolution leads to the coexistence of specialist and generalist strategies due to disruptive selection. The evolution of adult preference results in full specialization, thus minimizing diet overlap, and leading to evolutionary murder of one plant. The outcome of coevolution strongly depends on how the two traits are constrained. If juvenile preference is allowed to evolve faster, a high degree of diet overlap is attained, leading to the coexistence of the two plants or even diversification of strategies. Otherwise, evolution leads to niche separation and to the evolutionary murder of one plant. We discuss our results in the light of the three questions addressed in the introduction.

Effect of the structure of the insect population on the ecological dynamics

Without evolution, the interplay of antagonistic and mutualistic interactions due to the insect population structure creates non-intuitive indirect effects between the two plants. By studying the one plant system, we show that such effects are stabilizing for the maintenance of diversity. Indeed, considering a community assembly approach where a propagule invades a one-plant–insect system, if this incoming species is locally favored (i.e. its intrinsic growth rate is positive), then it receives a negative indirect effect from the resident plant. On the contrary, when the incoming species would be counterselected (i.e. its intrinsic growth rate is negative), then it receives a positive effect from the resident plant. Therefore, our stage-structured insect species creates negative feedbacks that can help to build diversity and to regulate invasions. The presence of the native plant can facilitate the invasion of a colonizer that would not have subsisted alone, by maintaining a high enough mutualistic effect, and reduced antagonistic effects. The indirect effect of the colonizer on the resident is negative, while the indirect effect of the resident on the colonizer is positive: rather than facilitation (Bruno et al. 2003), the interaction is an apparent antagonism (+,–) (Sauve et al. 2015).

As predicted, a strong overlap of diet specializations ensures plant coexistence by creating a balance of positive and negative effects, modulating intrinsic growth rates. Such coexistence conditions recall vulnerability–competitive ability tradeoff involved in the maintenance of competing species sharing predators (Paine 1966, Holt et al. 1994, Leibold 1996). While in these works, coexistence is based on the fact that the best competitor for resources is more vulnerable to predation, in our case, coexistence is made possible if the species that exploit best the mutualistic interaction is more affected by the antagonistic stage. Indeed, coexistence is stable if P_1 benefits more from mutualism (compared to predation), so that the insect has a higher pollination/predation ratio on P_1. This result is also in agreement with former results showing that pollinator preference should not be too biased for plants to coexist (Revilla and Krivan 2016).

Evolution of specialization and diet overlap

Evolution towards specialist or generalist strategies strongly depends on how preferences for the two plants are traded off. Consistent with many previous works on the evolution of specialization as well as with the biological significance of the tradeoff shape (reviewed by Ravigné et al. 2009), we find that concave tradeoffs usually lead to generalist juveniles, while convex tradeoffs favor more specialist juveniles (branching points). Regarding adult strategies, evolution most often lead to specialization, regardless of the tradeoff shape. Hence, the sole shape of the tradeoff is not sufficient to explain the difference between adult evolution and juvenile evolution. This difference may be explained by the nature of the feedback generated by the plant–adult or plant–juvenile interaction. In the juvenile evolution case, the antagonistic interaction generates a negative feedback between plant abundance and the juvenile preference. Considering adult evolution, the increased level of specialization may be explained by the synergy between two different feedbacks. One positive feedback is linked to the ecological dynamics, between plant abundance and the adult abundance, due to the mutualistic interaction. This in turn leads to a second positive feedback due to evolutionary dynamics, as increased plant abundances select higher adult preference which further increases the ecological feedback. While the evolutionary negative feedback (juvenile herbivory) regulates and stabilizes the system, the adult mutualistic interaction may destabilize the system and favor infinite growth. A possible way to avoid this would be to consider resource limitation more explicitly (Revilla and Krivan 2016), for instance by modeling nectar availability. We predict that if adults were to compete for plant resources (e.g. nectar competition), generalism would be selected for more often in our model: the evolutionary feedback between plant abundance and adult preference would become negative, as adults would be more constrained in their specialization. Our results are therefore more likely to apply to situations in which resource competition is much more important at the larval stage than the adult stage, for instance because the juvenile stage is much more numerous and/or because juveniles invest mostly in resource consumption to sustain large individual growth.

In the vast majority of cases, for a fixed adult preference, the evolution of juvenile preference leads to a positive correlation between adult and juvenile diet traits, maximizing diet overlap, in agreement with both our prediction and the observation of Altermatt and Pearse (2011). Conversely, for a fixed juvenile preference, adult preference evolution minimizes diet overlap and leads to diet separation in agreement with our predictions, but contrary to Altermatt and Pearse (2011) observation. Hence, we characterize an interstage evolutionary conflict, creating divergent selective pressures on the diet overlap.

In this work, the evolution of adult and juvenile preferences depends on plants profitability, mediated by their abundances. It would be insightful to include trait variation in partner quality (such as nectar quality), to consider the coevolution of insect preference and nectar quality. Partner discrimination is often considered to prevent the invasion of “low-quality” partners (cheaters) in the evolution of mutualism (Heath and Stinchcombe 2013). In our perspective, considering trait variation in nectar quality could prevent extreme specialization of adults since the nectar quality of a given plant species is expected to be selected against, thus selecting for generalism in the adult preference.

The coevolution simulations illustrate this selective conflict between the evolution of juvenile preference and adult preference. The juvenile preference follows the evolution of the adult preference, while the latter escapes the juvenile’s niche until it is fully specialized on one plant and cannot go further. This brings new insights into the results of Altermatt and Pearse (2011): once the juvenile mutation rate is high enough, the coevolution of both preferences always leads to diet overlap. The coevolutionary outcome depends of the traits evolution speed, previous results showing how relative speeds affect transient dynamics and stability (Loeuille et al. 2002, Georgelin et al. 2015). The diet correlation found in the meta-analysis of Altermatt and Pearse (2011) is significant but shows variability: 54% of the studied species include the juvenile host plant in the adult diet. In addition to this statistical variability, we also note that the results obtained by Altermatt and Pearse (2011) were collected in a large region and during a long time period, so that their statistical conclusions may be the result of data aggregation and not necessarily contradict our model predictions. According to our model, a possible explanation for this variability stems from different evolutionary constraints on the juvenile and adult preferences based on the density-dependent indirect effect asymmetry. Physiological constraints may also differ between the two stages: we can assume that larval diets are constrained because of the tight coevolution between the plant physical and chemical defenses and the herbivores. In the case of Lepidotera, the mobility of the two stages are also different. Many larvae develop on the plant where they hatched (evolution in a coarse grained environment). Such a spatial context may reinforce the cost of generalism for larvae diets. Conversely, adults are more mobile and likely experience a higher plant diversity (evolution in a fine grained environment). Studying this influence of spatial mismatch on diet coevolution would require a spatially explicit framework and would be a logical next step for the present work.

Effect of evolution on the ecological dynamics

The juvenile preference evolution has a positive effect on the community diversity, facilitating plant coexistence and diversifying insect strategies. Given a concave tradeoff on juvenile preference (being a specialist is costlier than being a generalist), the initial community of one plant only can be changed to coexistence of two plants. Evolution allows for invasion of a second plant which was not possible in the initial equilibrium: it is a case of "evolutionary facilitation", as defined by Georgelin et al. (2015) and results from ecological negative feedbacks. More juvenile specialization on a given plant favors the invasion of the second one because it suffers less predation. This selects for less specialization on the first plant, evolution ending in generalism and coexistence. If the initial equilibrium is coexistent, then evolution attracts selected phenotypes away from extinction boundaries. When the juvenile preference exhibits a convex tradeoff (that is being a generalist is costlier than being a specialist), evolution diversifies the community. We observe two subpopulations that are more specialized than the original one and a coalition between a specialist and a generalist for the parameters chosen in coevolution simulations. This coalition allows for coexistence: the mean predation pressure on one plant balances mean predation pressure on the other one, relative to their pollination rates. If the juvenile mutation rate is not high enough compared to the adult one, the faster evolution of adult preference can lead to evolutionary murder of one plant (Dieckmann and Ferrière 2004, Dercole et al. 2006), following the adult full specialization on the other plant. As the adult specialization on one plant increases, because of the positive effect of pollination, more specialization on this plant is selected for: the increase of specialization results from a positive feedback between ecological and evolutionary effects.

As often in theoretical analysis, and especially when studying small modules, we make several simplifying assumptions that may be considered unrealistic. We discuss here how relaxing these assumptions may change the outcome of our model. Regarding the ecological dynamics, we assume linear growth and interactions and no plant competition in order to focus on the apparent competition generated with the interaction with the juvenile stage. In a robustness analysis, we include direct plant competition (Supplementary material Appendix 4) and show that our main results hold in this scenario. Regarding the evolutionary dynamics, the main concern of realism is related to the restrictive adaptive dynamics assumptions, for instance the clonal reproduction, monomorphic populations, and separation of time scales. These assumptions can be relaxed by numerical simulations: in the coevolution part of our study (Fig. 5) we consider varying mutation probabilities such that mutation events may happen before the ecological equilibrium is reached. We do not think that rapid evolution should fundamentally alter our predictions, as in our model the ecological feedback loops are consistent with the evolutionary feedback loops: a positive ecological and evolutionary feedback in the adult case, and a negative ecological and evolutionary feedback in the juvenile case, but this assumption is worth testing in further extensions of the model. Accounting for diploid reproduction has been shown to be robust compared to clonal reproduction in diversification scenarios (Geritz and Kisdi 2000). We expect it could matter in our model if we explicitly differentiate behavioural sexual dimorphism in the interaction with the plants (egg laying only by the female for instance). Given that our population already assume ontogenetic stage structure, we think it would be difficult to get analytical results when accounting for sexual structure, but could be investigated with numerical simulations in a future study. Adaptive dynamics as we apply it here provide scenarios where the population becomes non-monomorphic. When it is costlier to be a generalist than a specialist for the juvenile, we obtain an evolutionary branching point with the coexistence of two morphs (coalition): one generalist and one specialist. Thus, while the initial population is monomorphic, our model allows to derive the conditions under which it may become polymorphic.

Our study brings an eco-evolutionary perspective to the diet specialization convergence of a population manifesting an ontogenetic change of role between its stages. We used a simple linear model that displayed complex ecological and evolutionary dynamics. We adapted the non-structured population fitness approach to a two-stage insect population, from which we obtained analytical insight on the selective conflict occurring between the two stages. We hereby keep the model simple to investigate indirect effects and evolutionary dynamics more thoroughly, but present the results of an extended analysis including direct competition for the plants in the Supplementary material Appendix 4. Some of our results may be compared to empirical data. For instance, data on the overlap of juvenile and adult diet were used to set our model and discuss our results. But our model also allows us to link such evolutionary dynamics to the community structure and maintenance. While the observed effects are consistent with the predictions made from indirect effects identification, it remains difficult to link these with natural results dealing with species invasions or biodiversity maintenance. It may thus be interesting to investigate how our results depend on the network context. In particular, we think the trade-off shapes may be important to consider since the network structure is partly determined by the distribution of generalist and specialist interactions (as in nestedness for mutualistic networks). We however hope that this work will open new doors to test the mechanisms we propose and to understand better the interplay of antagonistic and mutualistic effects in ecological networks.

Acknowledgements – We thank François Massol for his advice on using a matrix-based approach to obtain the fitness criteria in a stage-structured population.
Conflict of interest – The authors declare no conflict of interest.
Author contributions – AP, EG and NL designed the model, AP conducted the analysis and wrote the first draft, all authors contributed to discussions and substantial corrections of the manuscript.

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Supplementary material (available online as Appendix oik-05128 at <www.oikosjournal.org/appendix/oik-05128>). Appendix 1–5.