CHAPTER FIVE

Eco-Evolutionary Dynamics of Plant–Insect Communities Facing Disturbances: Implications for Community Maintenance and Agricultural Management

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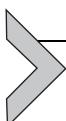
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Abstract

Understanding the response of natural communities to current global changes is crucial for the conservation and management of ecosystems. While the ecological and evolutionary responses of antagonistic or mutualistic systems have been studied separately, few studies investigate the eco-evolutionary response of systems combining different interaction types. We build an evolutionary model of a plant–pollinator–herbivore community, where both pollinators and herbivores are confronted with the same external disturbance, insecticide use. Pollinators' and herbivores' response to disturbances is controlled by a trait (e.g. sensitivity trait) that incurs a cost in reproduction. Using Adaptive Dynamics Theory, we find that herbivore evolution lowers densities of species and may

drive pollinators to extinction while pollinator evolution increases densities and enhances community maintenance. We then show that coevolution, by constraining the variability of coevolving species, produces qualitative dynamics that cannot be predicted from the mere addition of single-species evolution scenarios.

1. INTRODUCTION

Human activities generate disturbances that affect both the ecological and evolutionary dynamics of communities and ecosystems (Palumbi, 2001; Vitousek, 1997). Several examples of trait evolution in response to anthropogenic disturbances, as well as their consequences for the maintenance of populations and ecosystem services have been reported (Dieckmann and Ferrière, 2004). Fisheries, for example, lead to maturation of fishes at earlier age and smaller size (Olsen et al., 2004). These changes in phenotypic traits affect the growth rate of populations and compromise fish stocks (Olsen et al., 2004). In agricultural landscapes, evolution of resistances to pesticides has been often reported (Rex Consortium, 2013). The emergence of pesticide resistance reduces the efficacy of pest control measures, along with side effects of pesticides on natural populations, which compromises the durability of agricultural systems (Potts et al., 2010). These changes in life-history traits can affect population growth rates (Coltman et al., 2003; Olsen et al., 2004) by generating positive ("Evolutionary Rescue"; Gomulkiewicz and Holt, 1995) or negative effects ("Evolutionary Deterioration" and "Evolutionary Suicide"; Dieckmann and Ferrière, 2004; Gyllenberg and Parvinen, 2001; Matsuda and Abrams, 1994) on population survival. These kind of processes have been named eco-evolutionary effects (Fussmann et al., 2007; Pelletier et al., 2009; Schoener, 2011). Drops in fish densities associated with evolution of earlier maturation (i.e. a case of "Evolutionary Deterioration") for instance, compromise the durability of fisheries (Olsen et al., 2004). These evolution-driven changes in ecological densities (or eco-evolutionary effects) may then propagate to the community level through ecological indirect effects (sensu Wootton, 1994).

Unfortunately, models studying eco-evolutionary dynamics and species extinction in the face of disturbances usually account for just one species (e.g. Gomulkiewicz and Holt, 1995) or one interaction type (e.g. antagonistic interactions; Matsuda and Abrams, 1994). Recently, several studies have emphasized the importance of the interplay between antagonistic and mutualistic interactions for natural communities, because they produce

density-dependent effects of different signs on species growth rates (Fontaine et al., 2011; Georgelin and Loeuille, 2014). In fact, mutualistic interactions affect positively the growth rates of partner species while antagonistic interactions affect negatively these growth rates. When the interplay between the two interaction types is accounted for, the sign of the emergent indirect effects between antagonistic and mutualistic species sharing a resource is highly constrained by population traits and abundances (Georgelin and Loeuille, 2014). Evolutionary dynamics of traits can also change the signs of these indirect effects. Evolution of traits in antagonistic interactions may lead to an increase in densities of the species (i.e. a case of "Hydra Effect"; Abrams and Matsuda, 2005), while in mutualistic interactions, it can lead to a decrease in densities and even extinctions (Bronstein et al., 2004).

Agricultural landscapes are confronted with insect pests (antagonistic interactions) and rely on pollination services (mutualistic interactions). The joint objective of pest control and pollination service therefore needs models that consider the two interaction types. Particularly, given that pesticides are often used to limit pests, eco-evolutionary dynamics associated with such a disturbance have to be understood within the complete system, to provide an integrative understanding of the propagation of indirect effects within the agricultural system. The interplay of phenotypic changes and ecological dynamics may affect these communities through two mechanisms. First, some phenotypic traits are simultaneously involved in antagonistic and mutualistic interactions (Fontaine et al., 2011). An obvious example is the existence of floral signals in plants that are detected not only by pollinators but also by herbivores (Strauss, 1997). Secondary metabolites that repel herbivores of plants can also affect interactions with mutualists, for example by changing the attractiveness to pollinator (Strauss et al., 1999). Second, antagonistic and mutualistic species may be linked through indirect density-dependent effects via a third species (Georgelin and Loeuille, 2014; Wootton, 1994). For instance, pollinators and herbivores are linked through the density of plants. Hence, changes in herbivore density due to either direct effects of disturbances (ecological effects) or associated evolutionary responses (eco-evolutionary effects) will change pollinator density and vice versa. In this work, we will focus on this second mechanism, how an evolutionary response to disturbance in pollinator and herbivore populations will affect the community dynamics through this indirect density-dependent effect. We model the eco-evolutionary consequences of pesticide application on plant–pollinator–herbivore communities in agricultural landscapes.

The use of pesticides in agricultural landscapes affects both herbivores and pollinators (Rex Consortium, 2013). From an ecological point of view, an important concern posed by pesticides is the threat to pollination services. Declines in pollinator density and diversity put the crop yields at risks, reducing agricultural sustainability (Klein et al., 2007). From an evolutionary perspective, several examples of pesticide resistance have now been reported, often in a few generations (Mallet, 1989; Rex Consortium, 2013). To date, most evolutionary studies have been interested in designing strategies that manage or delay the onset of resistance in pests (Rex Consortium, 2013). While these studies are crucial for the maintenance of crop yields, we still have little information on the consequences of pesticide uses for eco-evolutionary dynamics of communities and for the simultaneous management of pests and pollination services (Loeuille et al., 2013).

Our goal here is to understand how adaptive responses of herbivores and pollinators to pesticides may change the ecological dynamics of these communities in agricultural landscapes. We incorporate evolutionary dynamics in a plant–pollinator–herbivore model we previously used to study consequences of pesticides for ecological dynamics (Georgelin and Loeuille, 2014). We let species sensitivities to pesticides evolve and study the consequences of trait evolution dynamics for the maintenance of the community (species densities and community composition). We study two evolutionary scenarios separately. First, only one species is allowed to evolve (either the pollinators or the herbivores). Second, we tackle the co–evolutionary dynamics of the two sensitivity traits. We focus on three questions:

  (i)   What are the expected evolutionary dynamics of the sensitivity traits and how do selected strategies depend on the intensity of disturbance? Based on direct selective effects, we expect that any increase in disturbance will select for a lower level of sensitivity (higher resistance).

 (ii)   What are the ecological consequences of trait evolution in terms of densities and community composition? We previously showed that ecological dynamics under a low pesticide sensitivity of pollinators enhances the viability of the community (through effects on density, extinction threshold and resilience; Georgelin and Loeuille, 2014). We therefore make the hypothesis that evolution of pollinators towards less sensitivity will help the maintenance of the community. Conversely, we make the opposite prediction for the evolution of herbivores.

(iii)   Can the co–evolutionary dynamics be predicted from the superposition of two previous cases, where only one species evolves? If, as

we predict, antagonist and mutualist adaptive responses have opposite effects on the community, we expect that the consequences of coevolution on the viability of the community will depend on the evolutionary potentials of the two species, as well as on eco-evolutionary effects. Our main results suggest that single antagonistic or mutualistic trait evolution have contrary effects on community structure. While adaptive response of herbivores decreases the densities of the two other species and eventually leads to extinction of pollinators, adaptive response of pollinators can help the herbivores to remain in the system. Thus, contrary to other models (Abrams and Matsuda, 2005; Bronstein et al., 2004), evolution reinforces the consequences of ecological dynamics rather than limiting them. However, when co-evolutionary dynamics are considered, mutation rates heavily constrain the maintenance of the community. Co-evolutionary outcomes cannot be inferred from the simple addition of single-species evolutionary outcomes. We discuss how these results can help explain the current pollination crisis and provide lessons for the future management of agricultural landscapes.

2. MODEL AND METHODS

2.1 Ecological dynamics

The model represents a community of three species, one plant species P, one pollinator species M and one herbivore species H:

$$\frac{dP}{dt} = r_p P\left(1 - \frac{P}{K_P}\right) + k_p\left(\frac{a_m MP}{1 + a_m h_m P}\right) - \left(\frac{a_h HP}{1 + a_h h_h P}\right) \tag{1}$$

$$\frac{dM}{dt} = r_m M\left(1 - \frac{M}{K_m}\right) + k_m(s_m)\left(\frac{a_m MP}{1 + a_m h_m P}\right) - g_m(s_m)lM \tag{2}$$

$$\frac{dH}{dt} = k_h(s_h)\left(\frac{a_h HP}{1 + a_h h_h P}\right) - d_h H - g_h(s_h)lH \tag{3}$$

Variables and parameters are defined in Table 1.

Interspecific interactions are modelled with Holling type II functional responses (Holling, 1959). Hence, herbivores and pollinators consuming plants are constrained by handling times h_h and h_m, respectively. Similar functional responses have been used and discussed extensively both for predator–prey (Oksanen et al., 1981; Rosenzweig and MacArthur, 1963) and for mutualistic interactions (Holland et al., 2002; Jang, 2002; Thébault and Fontaine, 2010; Wright, 1989). Plants and pollinators, in the absence of

Table 1 Definitions and dimensions of variables and parameters
Variable/parameter description (dimension)

P	Plant density (ind m^{-2})
M	Pollinator density (ind m^{-2})
H	Herbivore density (ind m^{-2})
r_p	Plant intrinsic growth rate (t^{-1})
r_m	Pollinator intrinsic growth rate (t^{-1})
K_p	Plant carrying capacity (ind m^{-2})
K_m	Pollinator carrying capacity (ind m^{-2})
a_m	Plant–pollinator encounter rate (ind^{-1} m^2 t^{-1})
a_h	Plant–herbivore encounter rate (ind^{-1} m^2 t^{-1})
h_m	Pollinator handling time (t)
h_h	Herbivore handling time (t)
k_p	Conversion efficiency of pollination by plant (dimensionless)
$k_m(s_m)$	Conversion efficiency function of pollinator (dimensionless)
$k_h(s_h)$	Conversion efficiency function of herbivore (dimensionless)
d_h	Herbivore intrinsic death rate (t^{-1})
l	Mortality rate due to disturbance (t^{-1})
$g_m(s_m)$	Sensitivity function of the pollinator (dimensionless)
$g_h(s_h)$	Sensitivity function of the herbivore (dimensionless)
s_m	Sensitivity trait of the pollinator (dimensionless)
s_h	Sensitivity trait of the herbivore (dimensionless)

interacting species, have independent growths, limited by carrying capacity (K_p and K_m, respectively). In other words, the mutualistic interaction is considered to be facultative: plants partly rely on anemophilous pollination or pollination by non-modelled pollinator species and pollinators rely also on other types of resources, such as non-modelled plant species. On the contrary, we consider herbivores as being specialist of the focal plant species. Herbivores, especially agricultural pests, are often reported to be more specialized than pollinators (Bernays and Graham, 1988; Fontaine et al., 2009). In the absence of plants, herbivore density decays exponentially due to

intrinsic mortality rate d_h. The parameter l expresses the extra-mortality rate due to the disturbance (pesticide use). It expresses the quantity of pesticides that is released and affects both pollinators and herbivores. Organisms show different sensitivities to pesticides (Desneux et al., 2007; Goulson, 2013; Pelosi et al., 2013). Functions g_h and g_m, and their dependency on traits s_m and s_h, account for this variability. Traits s_h and s_m combine all relevant traits that have an impact on the sensitivity of the organisms to insecticides, such as detoxification traits or changes in patch or resource exploitation. In the example of peach–potato aphids, seven types of resistances are described, each associated with a modification of pesticide target enzymes (Bass et al., 2014). Some of these modifications provide resistance synergistically against the same insecticides. Hence, s_h and s_m, can be thought as the combination of these different traits, that modify the overall sensitivity of organisms to pesticides.

The ecological dynamics of this system and the impacts of disturbances on the structure of the community are detailed in Georgelin and Loeuille (2014). At the coexistence equilibrium, plant density is only dependent on herbivore parameters (top-down control) while pollinator and herbivore densities depend on both species parameters:

$$P^0 = \frac{d_h + g_h(s_h)l}{a_h(k_h(s_h) - h_h(d_h + g_h(s_h)l))} \tag{4}$$

$$M^0 = \frac{K_m(r_m - g_m(s_m)l + a_mP^0(k_m(s_m) + h_m(r_m - g_m(s_m)l)))}{r_m + a_mh_mP^0r_m} \tag{5}$$

$$H^0 = \frac{(1 + a_hh_hP^0)((K_p - P^0)(1 + a_mh_mP^0)r_m + a_mK_pM^0k_p)}{a_hK_p(1 + a_mh_mP^0)} \tag{6}$$

2.2 Evolutionary dynamics

To study the adaptive responses of both pollinators and herbivores to the disturbance, we first study how sensitivity traits affect the growth rates of each species. Low sensitivity to disturbance, for instance via detoxification mechanisms (Cresswell et al., 2012; Després et al., 2007), often incur allocation costs, reducing growth or reproduction (Carrière et al., 1994; Rex Consortium, 2013). To account for this trade-off, we assume that sensitivity traits negatively affect the conversion efficiency functions, $k_h(s_h)$ and $k_m(s_m)$. While allocation costs are documented, we have no information on the shape of the trade-off functions, which are crucial for evolutionary dynamics

(de Mazancourt and Dieckmann, 2004). To investigate a wide range of evolutionary possibilities, we use exponential functions for k_m, k_h, g_m and g_h:

$$k_m(s_m) = k_{m_0} \exp(c_m s_m) \text{ and } k_h(s_h) = k_{h_0} \exp(c_h s_h)$$
$$g_m(s_m) = g_{m_0} \exp(z_m s_m) \text{ and } g_h(s_h) = g_{h_0} \exp(z_h s_h)$$

This formulation allows sensitivity traits s_h and s_m to take any real value. For an evolving species i, parameters c_i and z_i permit to control the shape of the g_i versus k_i trade-off. If $c_i > z_i$, the trade-off between reproduction and survival is convex, while when $c_i < z_i$, the trade-off is concave. Figure 1 depicts the functioning of this trade-off, based on the different values of c_i and z_i.

We use Adaptive Dynamics methods to analyse the eco-evolutionary dynamics of the community confronted with disturbances (Dieckmann and Law, 1996; Geritz et al., 1998; Metz et al., 1992). We first study the case when only one species evolves (pollinators or herbivores) then we study the coevolution of the two species. When only one species evolves, variations of sensitivity trait can be expressed by the following equations:

$$\frac{ds_h}{dt} = C_H \mu_H \sigma_H^2 H^0(s_h) \left(\frac{\partial \omega_{H_{mut}}(s_{h_{mut}}, s_h)}{\partial s_{h_{mut}}} \right)_{s_{h_{mut}} \to s_h} \tag{7}$$

for herbivores and

$$\frac{ds_m}{dt} = C_M \mu_M \sigma_M^2 M^0(s_m) \left(\frac{\partial \omega_{M_{mut}}(s_{m_{mut}}, s_m)}{\partial s_{m_{mut}}} \right)_{s_{m_{mut}} \to s_m} \tag{8}$$
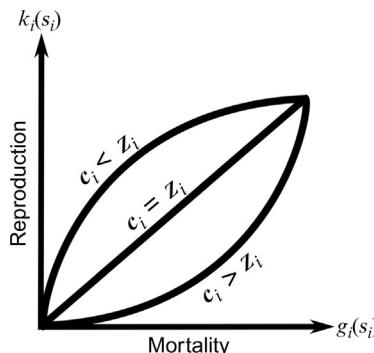
Figure 1 Schematic representation of the different trade-off shapes, based on the relative values of z_i and c_i (i being either h or m). An increase in reproduction due to an increase in s_h or s_m entails an increase in mortality (or a decrease in survival). According to z_i and c_i, the trade-off can be convex, concave or linear.

for pollinators, where C_i (i being either H for herbivores or M for pollinators) is a scaling parameter, μ_i is the per individual mutation rate, σ_i^2 is the variance of mutation effects on the sensitivity traits s_m or s_h. H^0 and M^0 are the herbivore and pollinator population densities at the ecological equilibrium (Eqs. 4–6) and the fitness gradient term corresponds to the selective pressures acting on the trait (Dieckmann and Law, 1996). Equations (7) and (8) imply that the phenotypic change is the product of two terms: (i) the phenotypic variability produced by mutations (products $\mu_H \sigma_H^2 H^0(s_h)$ and $\mu_M \sigma_M^2 M^0(s_m)$ in Eqs. 7 and 8, respectively), hereafter referred to as "evolutionary potential" and (ii) a term that embodies the natural selection process acting on this evolutionary potential. The fitness of a mutant is defined by its growth rate when rare in the environment set by the resident populations (Geritz et al., 1998; Metz et al., 1992). Invasion fitness equation, in the case of herbivores, is expressed by:

$$\omega_{H_{mut}}(s_{h_{mut}}, s_h) = k_h(s_{h_{mut}}) \frac{a_h P^0(s_h)}{1 + a_h h_h P^0(s_h)} - d_h - g_h(s_{h_{mut}})l \qquad (9)$$

and in the case of pollinators by:

$$\omega_{M_{mut}}(s_{m_{mut}}, s_m) = r_m \left(1 - \frac{M^0(s_m)}{K_m}\right) + k_m(s_{m_{mut}}) \frac{a_m P^0(s_h)}{1 + a_m h_m P^0(s_h)}$$
$$- g_m(s_{m_{mut}})l \qquad (10)$$

Evolution ends when the fitness gradient vanishes (Eqs. 7 and 8). Such points are called singular strategies (Geritz et al., 1998). Singular strategies can be classified according to two stability properties: invasibility and convergence. A singular strategy is non-invasible when no mutant can invade such a strategy (Maynard Smith, 1982). A singular strategy is convergent if only mutants with closer trait value to the singular strategy can invade (Christiansen, 1991; Eshel, 1983). Convergence and invasibility criteria can be studied by differentiating fitness functions twice according to sensitivity traits s_h or s_m (Geritz et al. 1998 and see Supplementary material on https://www.dropbox.com/s/qa7g6usf3hpsejr/appendix_georgelin_aer.pdf?dl=0).

In the case of coevolution, the trait variation depends on the traits of both resident populations (pollinators and herbivores):

$$\frac{ds_h}{dt} = C_H \mu_H \sigma_H^2 H^0(s_h, s_m) \left(\frac{\partial \omega_{H_{mut}}(s_{h_{mut}}, s_h)}{\partial s_{h_{mut}}}\right)_{s_{h_{mut}} \to s_h} \qquad (11)$$

$$\frac{ds_m}{dt} = C_M \mu_M \sigma_M^2 M^0(s_h, s_m) \left(\frac{\partial \omega_{M_{mut}}(s_{m_{mut}}, s_h, s_m)}{\partial s_{m_{mut}}} \right)_{s_{m_{mut}} \to s_m} \tag{12}$$

The two fitness equations become:
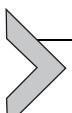
$$\omega_{H_{m_{mut}}}(s_{h_{mut}}, s_h) = k_h(s_{h_{mut}}) \frac{a_h P^0(s_h)}{1 + a_h h_h P^0(s_h)} - d_h - g_h(s_{h_{mut}})l \tag{13}$$

$$\omega_{M_{m_{mut}}}(s_{m_{mut}}, s_m, s_h) = r_m \left(1 - \frac{M^0(s_m, s_h)}{K_m} \right) + k_m(s_{m_{mut}}) \frac{a_m P^0(s_h)}{1 + a_m h_m P^0(s_h)}$$
$$- g_m(s_{m_{mut}})l$$

$$\tag{14}$$

Sets of strategies (s_m^*, s_h^*) that make fitness Eqs. (13) and (14) vanishing are called Singular Coalitions. Invasibility and convergence criteria of such coalitions can again be studied by differentiating fitness functions (Kisdi, 2006).

2.3 Numerical simulations of eco-evolutionary dynamics

Analytical tools of Adaptive Dynamics (Eqs. 7–10) were used when possible. In addition to this mathematical analysis, we undertake extensive numerical simulations, for two reasons. First, the analytical tools of Adaptive Dynamics are based on restrictive hypotheses (stable ecological equilibrium, rare mutations with weak phenotypic effects and clonal reproduction) (Dieckmann and Law, 1996; Geritz et al. 1998; Metz et al., 1992). Numerical simulations allow us to relax these hypotheses. Second, in the case of coevolution, only sufficient (but not necessary) conditions of convergence can be obtained analytically (Kisdi, 2006). When such conditions are violated, it cannot be guaranteed whether the system will converge towards the coalition or not. Details on the simulation procedures can be found in Supplementary material on https://www.dropbox.com/s/qa7g6usf3hpsejr/appendix_georgelin_aer.pdf?dl=0.

3. RESULTS

Below, we summarize the main results of our analysis. Full details of the mathematical computations and numerical simulations as well as details on the dynamics of plant–herbivore and plant–pollinator subsystems can be found in Supplementary material on https://www.dropbox.com/s/qa7g6usf3hpsejr/appendix_georgelin_aer.pdf?dl=0.

3.1 Evolution of herbivore sensitivity trait only

Depending on the trade-off shape, two qualitative dynamics are possible. For a convex or linear trade-off ($z_h \leq c_h$), the fitness gradient is always positive and then, ever-increasing sensitivities are selected (Fig. 2A). For a concave trade-off ($z_h > c_h$), sensitivity will reach a Continuously Stable Strategy (CSS), a singular strategy that is convergent and non-invasible. Evolution
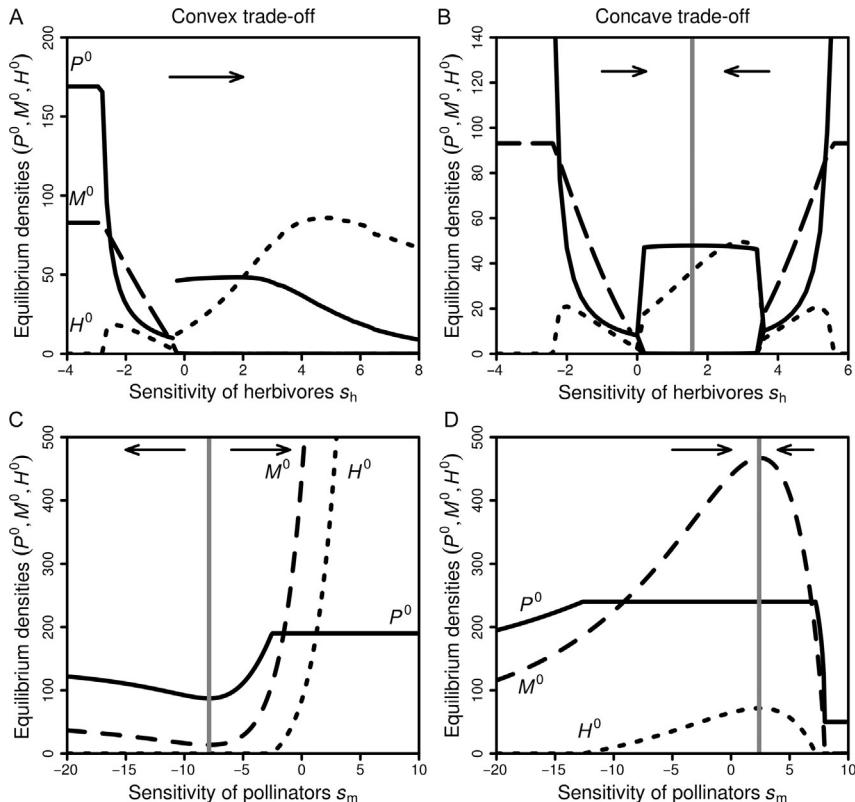
Figure 2 Density variations of plants (continuous lines), pollinators (long-dashed lines) and herbivores (dashed lines) at the ecological equilibrium during the evolution of herbivores (A and B) or of pollinators (C and D). Two types of trade-offs are depicted, convex (A and C) and concave (B and D). Vertical lines correspond to the sensitivity singular strategies s_h^* or s_m^* and arrows depict the direction of evolution. Parameters values are $r_p = 0.5\ t^{-1}$; $r_m = 0.5\ t^{-1}$; $K_p = 50$ ind m^{-2}; $K_m = 50$ ind m^{-2}; $a_m = 1$ ind^{-1} m^2 t^{-1}; $a_h = 1$ ind^{-1} m^2 t^{-1}; $h_m = 0.2$ t; $h_h = 0.1$ t; $k_p = 0.5$; $d_h = 3.5\ t^{-1}$; $l = 1\ t^{-1}$; $k_{m_0} = 1$; $g_{m_0} = 1$; $k_{h_0} = 1$; $g_{h_0} = 1$; $s_m = 2$ in graphs (A) and (B); $s_h = 1.25$ in graphs (C) and (D); $c_h = 0.3$ and $z_h = 0.2$ in (A); $c_h = 0.4$ and $z_h = 0.8$ in (B); $c_m = 0.5$ and $z_m = 0.1$ in (C); $c_m = 0.1$ and $z_m = 0.3$ in (D).

ceases at this point (Fig. 2B). The singular strategy is described by the following analytical formula:

$$s_h = \frac{1}{z_h}\left(\ln\frac{c_h}{g_{h_0}(z_h - c_h)} + \ln\frac{d_h}{l}\right) \tag{15}$$

Equation (15) is composed of two terms. The first term represents the evolutionary constraints associated with the trade-off shape (relative values of c_h and z_h). The second part stresses the importance of ecological conditions, represented by the ratio of natural mortality (d_h) to pesticide-driven mortality (l). Adaptive response to disturbance therefore strongly depends on background mortality. A low (high) level of natural mortality yields a low (high) equilibrium sensitivity.

Regardless of the trade-off shape, evolution of herbivore sensitivity always leads to a decrease in the densities of both plants and pollinators, as long as all species are present (Fig. 2A and B). Herbivore sensitivity evolution affects negatively the density of plants by increasing top-down pressures. Consequently, pollinator density decreases as well and given a high sensitivity to disturbance (high sensitivity s_m), pollinator population may even go extinct (Fig. 2A and B). In such instances, the disturbance leads to an Evolutionary Murder of pollinators. Once pollinators disappear, plant and herbivore densities may display cyclic dynamics (Fig. 2B). When pollinator sensitivity is sufficiently low to avoid extinction, however, herbivore evolution leads to an eco-evolutionary equilibrium where the three species coexist at reduced densities.

3.2 Evolution of pollinator sensitivity trait only

When only pollinators evolve, the existence of a singular strategy s_m^* is constrained by the trade-off shape. When the trade-off is linear ($z_m = c_m$), no such singularity exists. In this case, pollinators evolve towards ever-decreasing sensitivities when disturbance intensity parameter l is high and towards ever-increasing sensitivities when l is low. When the trade-off is not linear, a singular strategy exists, described by the following analytical formula:

$$s_m = \frac{1}{c_m - z_m}\left(\ln\left(\frac{z_m g_{m_0}}{c_m k_{m_0}}\right) + \ln\left(\frac{l}{(a_m P^0(s_h))/(1 + a_m h_m P^0(s_h))}\right)\right) \tag{16}$$

Similar to the evolution of herbivores, the properties of the singularity depend on the trade-off shape. For a convex trade-off ($z_m < c_m$), the singular strategy is invasible and non-convergent (i.e. a Repeller; Fig. 2C).

Conversely, for a concave trade-off ($z_m > c_m$), the singular strategy is a CSS (Fig. 2D). Yet, the equilibrium value s_m^* is dependent not only on the trade-off shape (first term of Eq. 16) but also on the ecological conditions (second term of Eq. 16), in specific, the ratio of mortality due to pesticide to resource benefits stemming from plants. Therefore, a higher density of plants will typically reduce the evolved sensitivity of pollinators.

Evolution of pollinator sensitivity, in the absence of herbivores, always leads to an increase in the densities of plants and pollinators (Fig. 2C and D). Eventually, plant density becomes sufficiently high for the herbivore to invade the system in spite of the disturbance. We call this phenomenon Evolutionary Facilitation: the evolution of pollinator sensitivity creates the conditions for herbivores to establish in the community. Once herbivores are present pollinator and herbivore densities increase with pollinator sensitivity evolution while plant density remains constant, due to the top-down control exerted by herbivores (Eqs. 4–6).

3.3 Coevolution

Regarding the coevolution of pollinators and herbivores, we find that if the two trade-offs are concave, the Singular Coalition is convergent and non-invasible (Absolute Convergence Stability; Kisdi, 2006). Coevolution therefore ends at this point. In the three other cases (when one or both of the trade-offs are convex), numerical simulations are necessary to determine the behaviour of the Singular Coalitions (see Supplementary material on https://www.dropbox.com/s/qa7g6usf3hpsejr/appendix_georgelin_aer.pdf?dl=0).

The outcomes of co-evolutionary dynamics, however, are also highly dependent on the evolutionary potentials of species. In Fig. 3A, we study the case where the coalition is convergent and non-invasible. We choose one initial point (triangle in Fig. 3A) and then run three simulation scenarios. In one scenario, pollinators and herbivores have the same mutation rates, while in the other two, herbivores evolve faster or slower than pollinators. For each scenario, we run 10 simulations and calculate the mean trajectories of sensitivity traits and population densities. When pollinators evolve faster or when both species evolve at the same speed, evolution ends at a Singular Coalition, as expected (dashed and dotted lines, Fig. 3B1, 3B2, 3C1 and 3C2). However, during the co-evolutionary dynamics, trait values and densities largely depend on these relative mutation rates. The interplay between pollinator and herbivore evolutionary dynamics also affects the direction of density variations. Densities first increase then decrease, when pollinators
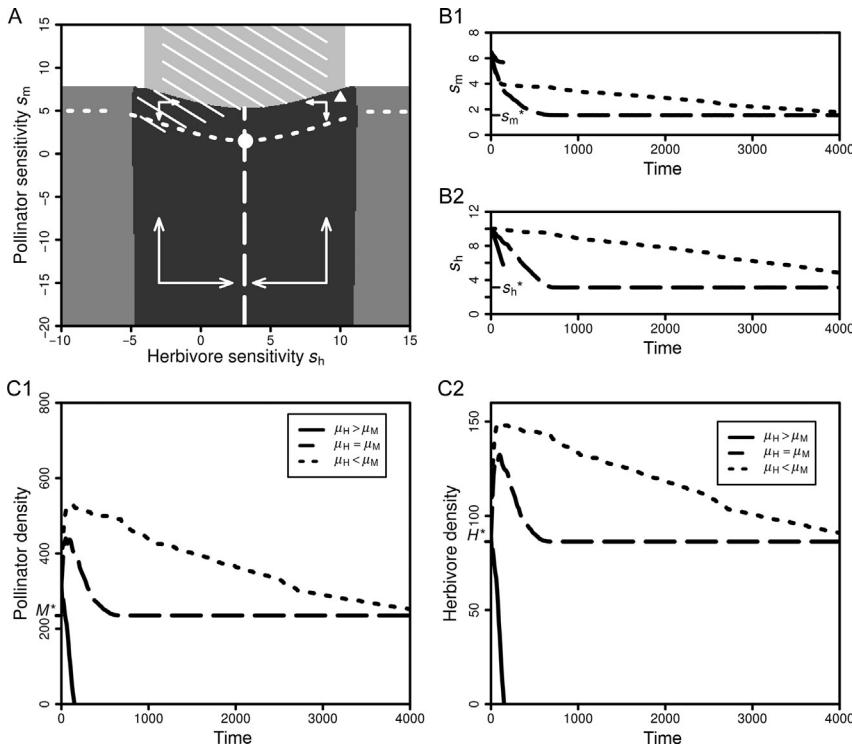
Figure 3 Numerical simulations of the eco-evolutionary dynamics of the community when the two trade-offs are concave and for different evolutionary potentials of the two species. (A) Community composition and evolutionary dynamics. Colours depict community composition. The dark region stands for the coexistence of the three species, dark grey for plant–pollinator community, light grey for plant–herbivore community and white for plant only. White hatching represents regions of cyclic dynamics. The dotted line depicts the singular strategy isocline of pollinators and the long-dashed line depicts the herbivore isocline. Arrows show the direction of evolution of sensitivity traits. Dot depicts the eco-evolutionary singularity. Triangle depicts the start of the simulations. (B) Sensitivity of pollinators (1) and herbivores (2) during the eco-evolutionary dynamics for the three different scenarios of evolutionary potentials. The two evolutionary equilibriums that are theoretically predicted (s_h^* and s_m^*) are depicted on the y-axis. (C) Density of pollinators (1) and herbivores (2) for the three same scenarios (μ_m is the pollinator mutation rate and μ_h is the herbivore one). Densities theoretically predicted at the eco-evolutionary equilibrium (H^* and M^*) are depicted on the y-axis. Parameters values are $r_p = 0.5\ \mathrm{t}^{-1}$; $r_m = 0.5\ \mathrm{t}^{-1}$; $K_p = 50\ \mathrm{ind\ m}^{-2}$; $K_m = 50\ \mathrm{ind\ m}^{-2}$; $a_m = 1\ \mathrm{ind}^{-1}\ \mathrm{m}^2\ \mathrm{t}^{-1}$; $a_h = 1\ \mathrm{ind}^{-1}\ \mathrm{m}^2\ \mathrm{t}^{-1}$; $h_m = 0.2\ \mathrm{t}$; $h_h = 0.1\ \mathrm{t}$; $k_p = 0.5$; $d_h = 3.5\ \mathrm{t}^{-1}$; $l = 1\ \mathrm{t}^{-1}$; $k_{m_0} = 1$; $g_{m_0} = 1$; $k_{h_0} = 1$; $g_{h_0} = 1$; $c_m = 0.2$; $c_h = 0.2$; $z_m = 0.4$; $z_h = 0.4$; $\mu_m = 10^{-6}\ \mathrm{ind}^{-1}$ and $\mu_h = 10^{-5}$, 10^{-6} or $10^{-7}\ \mathrm{ind}^{-1}$.

evolve faster or at the same pace (Fig. 3C1 and 3C2). By contrast, when herbivores evolve faster than pollinators, densities always decrease and Evolutionary Murder of pollinators is observed (plain lines, Fig. 3C1 and 3C2). Subsequently, the community collapses, as cyclic dynamics confine plants and herbivores to low populations. In this case, pollinator evolution is too slow to rescue the community from collapsing.

The evolutionary potential of species is however not simply defined by mutation rates μ_i or mutation amplitudes σ_i^2. In Eqs. (7) and (8), evolutionary potentials are also dependent on H^0 and M^0, respectively, the population densities of herbivores and pollinators. Therefore, because we have observed that the evolution of one partner can strongly influence the density of the other, we expect that co-evolutionary dynamics can create strong density-dependent effects constraining the evolutionary potentials of the two species. In Fig. 4, we depict the case of a convex trade-off for herbivores
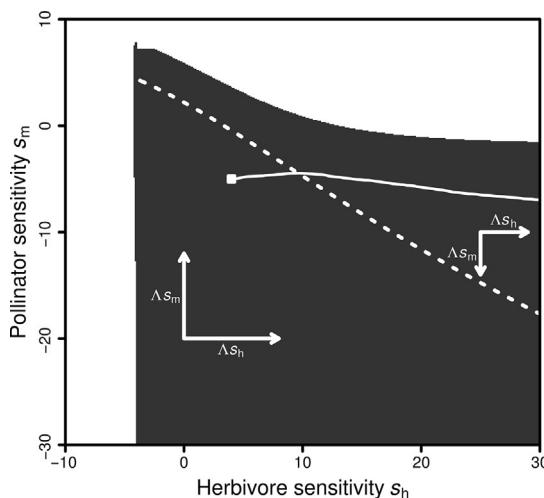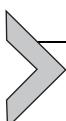
Figure 4 Eco-evolutionary dynamics of the community when the trade-off of herbivores is convex and trade-off of pollinators is concave. The dark zone depicts the coexistence of the three species. The dotted line represents the evolutionary isocline of pollinators. There is no herbivore isocline, since the trade-off is convex so that their sensitivity trait increases continuously. Arrows show the direction of evolution of sensitivity traits. In this case, herbivore sensitivity s_h always increases, while pollinator sensitivity s_m theoretically converges towards the isocline. The continuous line shows a co-evolutionary trajectory, in a scenario where herbivores evolve faster than pollinators. The white square depicts the beginning of the simulation. Parameter values are: $r_p = 0.5$ t^{-1}; $r_m = 0.5$ t^{-1}; $K_p = 50$ ind m^{-2}; $K_m = 50$ ind m^{-2}; $a_m = 1$; $a_h = 1$; $h_m = 0.2$; $h_h = 0.1$; $k_p = 0.5$; $d_h = 3.5$ t^{-1}; $I = 1$ t^{-1}; $k_{m_0} = 1$; $g_{m_0} = 1$; $k_{h_0} = 1$; $g_{h_0} = 1$; $c_m = 0.2$; $c_h = 0.2$; $z_m = 0.4$; $z_h = 0.1$; $\mu_m = 10^{-6}$ ind^{-1} and $\mu_h = 10^{-5}$ ind^{-1}.

and concave trade-off for pollinators. In this case, we expect that sensitivity trait of herbivores will always increase while trait of pollinators will stick to the isocline. However, when herbivores evolve faster than pollinators, herbivore evolution is sufficiently fast for pollinator sensitivity to cross its isocline, then to be brought further and further from it, therefore causing a large maladaptation in the pollinator population. Indeed, herbivore evolution strongly decreases the density of pollinators, thereby deteriorating their evolutionary potential. Evolution of pollinators towards their isocline is therefore very slow (Fig. 4). Coevolution here, and differences in evolutionary potentials, makes pollinator populations constantly maladapted to the disturbance.

4. DISCUSSION

Ecological dynamics of mixed antagonistic and mutualistic interactions create complex density-dependent effects (Georgelin and Loeuille, 2014). We show here that such indirect effects constrain the evolutionary and co-evolutionary dynamics that can be observed in such systems. These eco-evolutionary dynamics and their consequences for community composition and structure may have profound implications for the simultaneous management of pollination service and pest control in agricultural landscapes.

When only herbivore sensitivity evolves, we find that herbivore adaptive response is detrimental to the maintenance of the whole community. Here, we observe that herbivore evolution (1) lowers its own density and (2) also lowers the densities of the other species (plants and pollinators). Effect (1) is consistent with other theoretical works suggesting that adaptive response of a given population should not be expected to lead systematically to higher population levels (Dieckmann and Ferrière, 2004), and can even lead to population extinction (Evolutionary Suicide; Gyllenberg and Parvinen, 2001). In our case, evolution lowers the herbivore population making it vulnerable to demographic stochasticity (Evolutionary Deterioration; Matsuda and Abrams, 1994). We also note that such deteriorating effects are hierarchical. In the simulations we made, pollinators disappear first during antagonistic evolution. Jones et al. (2009), in a model of antagonistic–mutualistic evolving community, show that evolution of antagonists can lead the whole community to extinction. Their model assumes that the mutualism is obligatory and antagonists need the presence of mutualists to survive (Jones et al., 2009). Such obligatory links facilitate the propagation of deteriorating

evolutionary effects in their community. Our results confirm the idea that mutualists may suffer from antagonistic evolution and are prone to extinction, even in the absence of obligatory links among species.

The evolutionary responses of herbivores to disturbances have large implications for the conservation and management of agricultural communities. In agricultural landscapes, direct mortality due to pesticides or habitat changes is often proposed to explain the decrease of pollinator densities or their extinctions (González-Varo et al., 2013; Potts et al., 2010). Our model suggests that the (often observed) adaptive response of herbivores to pesticides may create indirect ecological effects that decrease pollinator populations and therefore contribute to the loss of pollination services and to the destabilization of communities. While the occurrence of such effects needs to be tested, they illustrate the importance of an evolutionary perspective for the management of agricultural systems (Loeuille et al., 2013).

Contrary to herbivore evolution, we find that pollinator adaptive response to disturbance is beneficial to the community maintenance. Pollinator evolution increases plant density. This creates indirect bottom-up effects that enhance pollinator and herbivore densities. Also, pollinator evolution can ultimately create and maintain the conditions of the establishment and survival of herbivores in the system (a phenomenon we name Evolutionary Facilitation). A recent surge of interest exists in co-evolutionary models of mutualisms (Ferrière et al., 2002; Gomulkiewicz et al., 2003; Guimarães et al., 2011; Nuismer et al., 2012; Zhang et al., 2011), including in antagonistic–mutualistic systems (Jones et al., 2009). These models focus on the role of cheaters or exploiters in mutualistic interactions. Considering the evolution of birth rate, Jones et al. (2009) find that mutualism evolution can lead to an Evolutionary Purging (i.e. Evolutionary Murder of the exploiter by the mutualist), which contradicts our results. Jones et al. (2009) focus on mutualists that are pollinating seed parasites (as it is found in fig and yucca systems for example). Hence, under some conditions (weak intraspecific competition of mutualists and antagonists), the density of pollinating seed parasites is high and creates high parasitism pressure on host plants. This reduces plant density and the availability of non-parasited seeds that are necessary for antagonist survival. By contrast, mutualists, in our model, always have a positive effect on plant growth rate, which explains the discrepancy between the result generated by our and Jones' models. Positive effects of evolution on community structure have already been shown in other mutualistic network models. Evolution and coevolution between

partners can lead to nestedness in mutualistic networks (Zhang et al., 2011), an architecture that increases the maintenance and resilience of such communities (Bascompte et al., 2006; Thébault and Fontaine, 2010). We note also that the possibility of Evolutionary Facilitation we observe here is not restricted to the evolution of mutualistic interactions and can also be observed in a food web context. Evolutionary changes in foraging behaviour of predators can thereby favour the maintenance of community diversity (Loeuille and Loreau, 2009; Urban, 2013).

Evolutionary Facilitation has important implications for the conservation of natural communities. The current concern about the loss of mutualistic interactions in natural communities needs to integrate such an evolutionary perspective (Kiers et al., 2010). Mutualistic interactions are not only important as a support for the ecosystem functioning or services they provide (e.g. pollination services; Georgelin and Loeuille, 2014; Potts et al., 2010) but also for their positive influence on the evolutionary dynamics of communities. The loss of pollinators may in turn decrease such positive evolutionary effects and threaten the different species of the community through the modification of evolutionary or co-evolutionary trajectories. The occurrence of Evolutionary Facilitation in our model strengthens the idea that pollinators may help the population of herbivores, in the presence of pesticide application. This result is found both on an ecological scale (Georgelin and Loeuille, 2014) and on an evolutionary scale. A pesticide that is highly selective (i.e. that does not affect pollinator populations too much) would not be efficient because, in this case, high pollinator populations will buffer herbivore populations against this disturbance (Georgelin and Loeuille, 2014).

The range of possible dynamics is much larger when coevolution occurs. We find that a combination of positive and negative density-dependent effects arise, respectively, due to mutualistic and antagonistic evolution, and the community outcomes are heavily constrained by the evolutionary potentials of pollinators and herbivores. When herbivores have a higher evolutionary potential, the phenomenon of Evolutionary Murder of pollinators may occur. However, if pollinator evolution is sufficiently fast, it can rescue the community from this Evolutionary Murder. Evolutionary potentials are constrained by several attributes, such as rate and amplitude of mutations, population densities and generation times of organisms (Dawkins and Krebs, 1979; Fisher, 1930). Higher densities lead to higher genetic and phenotypic variabilities in populations, enhancing their responses to environmental changes (Leimu et al., 2006). Also, the rate of appearance of new mutations is thought to be higher in larger populations, which facilitates

adaptation (Lanfear et al., 2013). Considering agricultural landscapes, pests have by definition high densities. Furthermore, pesticide use is a common response to outbreaks when pest densities are even more important (Barbosa and Shultz, 1987). In such circumstances, herbivore pest evolutionary response is likely to be fast compared to pollinators, whose populations may be already deteriorated by other detrimental factors (González-Varo et al., 2013). Consistent with this view, pest resistances to new toxic compounds have been frequently observed, often in a few generations (Mallet, 1989; Rex Consortium, 2013), while the evolutionary responses of pollinators remain largely undocumented (but see Cresswell et al., 2012). In our model, the relative evolutionary potentials of the two species vary during the co-evolutionary dynamics, due to density changes that are evolutionary driven (Fussmann et al., 2007). In the last scenario we investigate, sensitivity of pollinator is maintained far from its optimum and pollinator population remains maladapted, because fast herbivore evolution strongly reduces pollinator density. This result suggests the need for the joined consideration of the community context and the interplay between different interaction types, when studying the evolutionary responses of populations to disturbances (Fussmann et al., 2007; Loeuille et al., 2013). While such an integrative approach is particularly difficult in the field, not accounting for coevolution and evolutionary potentials of the different species may lead to misconceptions about the dynamics of communities in the face of global changes (Dieckmann and Ferrière, 2004; Loeuille et al., 2013).

The question of trade-off is of particular interest, here. We link the evolution of sensitivity to disturbance to decreases in the growth rates of organisms, through allocation costs. We use exponential functions to depict the relationship between these two components. This allows us to model a wide variety of trade-off shapes, convex, concave or linear. We however acknowledge that other shapes are possible (e.g. saturating functions). We show that these shapes are crucial for the evolutionary dynamics of sensitivity traits, constraining the fate of the community. We have few empirical knowledge regarding the shapes of these trade-offs in natural systems, and we believe that describing such trade-offs is an important challenge for future insecticide resistance research. Recent works have stressed the importance of trade-off shapes for other evolutionary scenarios (defence and growth in predator–prey systems) (Kasada et al., 2014), and we hope this kind of work will develop in future years. Another limit is our focus on allocation costs. In some situations, such allocation costs associated to resistance to pesticides have not been found (Lopes et al., 2008). Resistance can even

confer selective advantages in some environments without pesticides (McCart et al., 2005). Instead of direct impacts on reproduction rate, costs can be associated to traits that are difficult to measure, or acting in a different environment or at a different time in the life cycle of organisms (e.g. Gazave et al., 2001). Gazave et al. (2001) found that resistant phenotypes in the mosquito *Culex pipiens* have a lower survival during the wintering phase. Costs of resistance can also happen due to changes in interspecific interactions rather than from changes in life-history traits. Resistance to organophosphates in peach-potato aphids for instance reduces their response to alarm pheromones and may lead to a higher susceptibility to predation (Foster et al., 2003). In such instances, costs of resistance to insecticide can act in a different way than the ones we modelled here, and the analysis of associated evolutionary dynamics goes beyond the scope of the present chapter. Such an understanding of different cost structures is however an important step to fully understand the eco-evolutionary responses of communities to external disturbances.

Here, we discuss our results through the case of plant–pollinator–herbivore communities confronted with pesticides in agricultural landscapes. However, since we have little information on the eco-evolutionary dynamics of antagonistic–mutualistic communities confronted with external disturbances, we keep our model simple. Hence, these results may give insights for many multiple-interaction types communities, that are confronted with external disturbances, like climate changes (Parmesan, 2006), fragmentation and habitat destruction (Georgelin and Loeuille, 2014; González-Varo et al., 2013). The analysis shown here allows a first understanding of eco-evolutionary dynamics of antagonistic–mutualistic ecological communities, in a simple context. Additional complexities like space, or network architecture, would inevitably influence the results we report here. Another fruitful exercise would be to compare how adaptive processes differ from those found in other antagonistic/mutualistic networks. How positive and negative feedbacks (or activation/inhibition mechanisms) affect stability, and adaptation is for instance a current question in gene regulatory networks (Crombach and Hogeweg, 2008; Pinho et al., 2014). Social networks also contain positive and negative relationships, and Structural Balance Theory can then be used to study how the adaptive modification of social relationships can affect group stability (Doreian, 2002; Hummon and Doreian, 2003). Because adaptation is guided by different selective processes acting on units of different scales in social networks, gene networks and ecological networks, the effect of adaptation on stability and

complexity is expected to differ among network types. However, comparing such differences could help us to understand how network dynamics *per se* matters for adaptation, and to establish interdisciplinary links among different scales of organization.

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