

Ant aggression and evolutionary stability in plant–ant and plant–pollinator mutualistic interactions

L. OÑA & M. LACHMANN

Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Keywords:

herbivory;
plants;
pollination;
theory.

Abstract

Mutualistic partners derive a benefit from their interaction, but this benefit can come at a cost. This is the case for plant–ant and plant–pollinator mutualistic associations. In exchange for protection from herbivores provided by the resident ants, plants supply various kinds of resources or nests to the ants. Most ant–myrmecophyte mutualisms are horizontally transmitted, and therefore, partners share an interest in growth but not in reproduction. This lack of alignment in fitness interests between plants and ants drives a conflict between them: ants can attack pollinators that cross-fertilize the host plants. Using a mathematical model, we define a threshold in ant aggressiveness determining pollinator survival or elimination on the host plant. In our model we observed that, all else being equal, facultative interactions result in pollinator extinction for lower levels of ant aggressiveness than obligatory interactions. We propose that the capacity to discriminate pollinators from herbivores should not often evolve in ants, and when it does it will be when the plants exhibit limited dispersal in an environment that is not seed saturated so that each seed produced can effectively generate a new offspring or if ants acquire an extra benefit from pollination (e.g. if ants eat fruit). We suggest specific mutualism examples where these hypotheses can be tested empirically.

Introduction

Mutualistic interactions between two species have been widely studied and have permitted the analysis of the potential ecological and evolutionary factors responsible for mutualism breakdown. A possible disruptive factor in two species interaction systems is the emergence of cheaters or exploiters (Ferriere *et al.*, 2002). But even without cheaters and exploiters, the fact that the partners of the interaction do not share the same evolutionary future causes a conflict, especially with respect to their reproduction.

In this study, we discuss an evolutionary conflict between mutualists brought to light through an interaction with a third partner. Such evolutionary conflicts between mutualists are common, because in mutualistic

associations it is rarely the case that all components of fitness are aligned between mutualistic partners (Herre *et al.*, 1999; Wilkinson & Sherratt, 2001). Some examples where mutualism is horizontally transmitted include mycorrhizae and plants, rhizobia and luminescent bacteria in fish and cephalopods (Kato & Yamamura, 1999). The inclusion of a third species places the conflict in an ecological context by analysing its effects on the other ecological partner. This is important because mutualisms are shown to have a crucial role in the structure of the ecological community as it has been shown for plant–pollinator networks (Bastolla *et al.*, 2009) and for plant–mycorrhizae symbionts (Klironomos *et al.*, 2000). The mechanisms for reduction of the conflict discussed here are general. These include vertical transmission and ‘bribes’ through which the benefit gained can be shared between partners.

A well-studied mutualism is the one present between plants and ants conferring biotic defence against herbivores. Many myrmecophytes are pollinated by insects (Rico-Gray & Oliveira, 2007). Examples of plants

Correspondence: Leonardo Oña, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
Tel.: +49 341 3550 769; fax: +49 341 3550 555;
e-mail: leonardo_bubach@eva.mpg.de

associated with protective ants and insect pollinators are highly common and geographically widespread, involving different species of ants, plants and pollinators (Table 1). Ants provide their host plant with protection from herbivores such as beetles; and in turn, plants provide the ants with several kinds of resources ranging from extrafloral nectar, food bodies (e.g. Pearl Bodies, Beltian bodies in *Acacia*, Mullerian bodies in *Cecropia*, Beccarian bodies in *Macaranga*) to nesting sites (e.g. domatia, thorns, etc.). In many associations, a combination of resources is provided and differences in specialization and specificity may be resource based (Rico-Gray & Oliveira, 2007).

The most thoroughly studied cases among ant–myrmecophyte associations include the swollen-thorn *Acacia cornigera* (Fabaceae) and its ant inhabitant *Pseudomyrmex ferrugineus* (Pseudomyrmecinae) in eastern Mexico, studied in the classic works by Janzen (1966, 1967a,b, 1969, 1973). *Acacia* species are distributed worldwide and ant-inhabited acacias seem to have evolved separately in the tropics of America and Africa (Abrahamson, 1989).

Janzen observed several characteristic traits in both acacia and ants that suggest the mutualism had evolved over a long period of time [in table I of (Janzen, 1966)]. There is an important variation in the level of aggressiveness in these ants (Janzen, 1966). Ant inhabitants include obligate, highly adapted *Pseudomyrmex* species that strongly protect the plant; obligate or facultative *Pseudomyrmex* species that provide less effective or no defense at all and species from other genera such as *Camponotus* and *Crematogaster* that never protect the plant (Ward, 1999; Raine *et al.*, 2004). The same patterns of aggressiveness exist in other ant–plant mutualisms (see some examples in Table 1). It has been suggested that aggressiveness could evolve rapidly with little selective pressure (Janzen, 1966). A second mutualism in the system involves the interaction between the plant and its pollinators. The plant provides the pollinators with nectar and/or pollen, and pollinators enable plant outcrossing with other plants. A conflict emerges between plants and ants because ants are aggressive against any disturbance to the plant, but for the plant, preventing pollinator

Table 1 Examples of plant–ant and plant–pollinator mutualistic interactions.

Plant genus	Ant genus (cite interaction)	Resource interchange	Obligate/ Facultative	Pollinators [cite interaction]	Distribution
<i>Acacia</i> sp. (Fabaceae)	<i>Pseudomyrmex</i> sp., <i>Crematogaster</i> sp Janzen (1966), p. 530	Throlls and/ or nectar, pollen, Beltian bodies	From facultative to strongly obligate	Bees (Fam. <i>Megachilidae</i> , <i>Halictidae</i>), wasp, flies, butterflies, birds Willmer & Stone (1997), p. 710, Solomon-Raju & Purnachandra-Rao (2002), p. 701	Worldwide, New (more obligate) and Old (more facultative) World
<i>Macaranga</i> sp. (Euphorbiaceae)	<i>Crematogaster</i> sp. <i>Camponotus</i> sp. Smith (1903), p. 700, Itioka <i>et al.</i> (2000), p318, Federle <i>et al.</i> (1998), p1, Feldhaar <i>et al.</i> (2003), p327, Fiala <i>et al.</i> (1989), p429, Fiala & Maschwitz (1991), p430, Fiala & Maschwitz (1992), p431, Fiala <i>et al.</i> (1994), p432, Fiala <i>et al.</i> (1999), p. 433	Food bodies, extrafloral Nectaries, Nest	From facultative to strongly obligate	Thrips (<i>Frankliniella occidentalis</i>) Moog <i>et al.</i> (2002), p. 629	Tropics of southeast Asia
<i>Piper</i> sp. (Piperaceae)	<i>Pheidole</i> sp. Rickson & Risch (1984), p. 694, Risch <i>et al.</i> (1977), p. 697, Tepe <i>et al.</i> (2007), p. 702	Nest, food bodies	From facultative to strongly obligate	Hymenoptera and diptera (mainly bees genus <i>Megachile</i> and stingless bees (Apidae)) Kikuchi <i>et al.</i> (2007), p. 624	Tropical rain forest of costa rica
<i>Tachigali</i> sp. (Caesalpinaceae)	<i>Pseudomyrmex</i> sp. Fonseca (1994), p. 492, Ward (1999), p. 709	Domatia	From facultative to strongly obligate	Bees, nocturn bees (<i>Megalopta</i>) Odegaard & Frame (2007), p. 696, Wolda & Roubik (1986), p. 711	Amazonia
<i>Hirtella</i> sp. (Chrysobalanaceae)	<i>Allomerus</i> sp. Izzo & Vasconcelos (2002), p. 529	Domatia	Obligate	Butterflies Arista <i>et al.</i> (1997), p. 109	Amazonia

access would be detrimental (Willmer & Stone, 1997). Plants are selected to produce offspring through pollination, whereas for the ants only the survival of the individual plant on which they live is important. Thus, plants are selected to be pollinated, whereas ants are indifferent to pollination and are selected to be aggressive to herbivores.

An extreme case of a similar conflict is known as plant castration (Yu & Pierce, 1998). In plant castration, mutualistic ants protecting the plant from herbivores also destroy flowers, thereby reducing fruit production and subsequent plant reproduction. This also leads to an increase in plant resources for ant domatia (Frederickson, 2009). Whereas plant castration seems to be present in some species (Yu & Pierce, 1998; Frederickson, 2009) and although it has been argued that ant interference in plant reproduction may be directly favoured by natural selection more often than previously thought (Frederickson, 2009), it has also been remarked that in the absence of some external factor, both the plants and plant-castrating ants would probably decline to extinction (Yu & Pierce, 1998; Yu *et al.*, 2001; Frederickson, 2009) (In these references, the external factor is given by another cooperative, noncastrating ant, coexisting in the system favoured by spatial structure). Ants, however, do not always manipulate the resources from the plant. Sometimes the plant itself limits the resources available for ants (Palmer *et al.*, 2008). Therefore, there is no evidence that castration is a generalized mechanism explaining all of the plant–ant conflict on plant reproduction.

The conflict is still present when ants do not castrate the plant but are aggressive to pollinators (Willmer & Stone, 1997; Ghazoul, 2001). Ants can certainly have the physiological capacity to discriminate between different types of insects (Liepert & Dettner, 1993; Schatz *et al.*, 2003). Therefore, one can expect that ants are physiologically able to discriminate pollinators from herbivores. This, however, could be costly for ants because discrimination could bring about mistakes. Ants that have to discriminate herbivores from pollinators could, under some conditions, mistake a herbivore for a pollinator and incur a cost. This is especially true because there is an evolutionary arms race for the herbivores not to be attacked so they could evolve to be mistaken for a pollinator.

It has been proposed that this conflict can be reduced through temporal and spatial separation between ants and pollinators through plant chemicals that act against ants and protect the flowers, thus preventing conflict (Feinsinger & Swarm, 1978; Prys-Jones & Willmer, 1992; Willmer & Stone, 1997). This argument, however, cannot explain why ants do not evolve resistance to floral repellents (Ghazoul, 2001). It has been hypothesized that these chemicals mimic ant alarm pheromones that are necessarily evolutionarily conserved and which are thought to be structurally similar across widely separated ant lineages (Ghazoul, 2001). It has also been

argued that this constraint can be the cause of aggressive behaviour in ants, explaining as well the cases of castration by ants (Ghazoul, 2001). Nevertheless, floral chemical deterrents are not universally repellent to ants (Rico-Gray & Oliveira, 2007), and often, ants and pollinators overlap in their activities (Willmer & Stone, 1997). Moreover, from an evolutionary point of view, these two explanations are not convincing: herbivores could take advantage of areas or times when ants are not present, and ants would then be selected to overlap with pollinators to protect their plant. The question therefore remains: under which conditions will ants be selected to discriminate pollinators from herbivores and direct their aggressiveness only against the latter?

We discuss two mechanisms of conflict reduction, by increasing the alignment of plant and ant fitness benefits. The first is increasing vertical transmission, and the second is providing a fitness benefit to ants from plant pollination.

The first mechanism of reducing conflict is limited dispersal. If a seed that results from pollination generates a plant on which the ant colony or its offsprings can reside on, then ants will protect pollinators to increase their own inclusive fitness. In that case, we will expect to observe ants that discriminate pollinators from herbivores to be present in plants exhibiting limited dispersal. However, we will argue that in plant species living in an environment where the number of plants is not limited by the number of seeds produced, but instead by space (i.e. under the influence of K-selection) the association between plant and ants will be broken, and ants will not evolve to discriminate pollinators unless another benefit is provided.

A second mechanism for reducing the conflict would be if ants receive benefit from the pollination of the plant. This would be the case, for instance, if ants were to eat the fruits produced or the elaiosomes attached to the seeds. Under such conditions, ants would be selected to ensure that their host plant is fertilized.

Such a direct benefit from the action of pollinators can be present in ant gardens, the arboreal nests of several species of ants from which epiphytic angiosperms can grow. It was once believed that the association between ants and plants was highly specific (Ule, 1901), whereas it is now considered as an opportunistic one (Madison, 1979). Plants benefit from the ant protection against herbivores and in some cases from the ant dispersion of seeds and fruits. Ants benefit by taking nectar and elaiosomes from seeds or fruits (without damaging the seeds). Some of these epiphytes interact with pollinators, and the same potential conflict of ants attacking pollinators has been observed (Davidson, 1988). If ants are too aggressive to pollinators, the level of autogamy will be increased (Madison, 1979).

As observed by Janzen (1966), ants tend to be more aggressive when they are in obligatory interactions with their plant hosts than when in facultative interactions.

This pattern might have to do with the fact that, in obligatory interactions, ants depend on the plant for their survival, and the absence of the myrmecophytes would drive them to extinction and vice versa (Janzen, 1966, 1967b). Therefore, the partners devote much more of their resources and services in obligatory interactions than in facultative interactions. However, the ecological consequences that a given degree of ant aggressiveness will have in one or the other case are not clear. Are the ecological consequences of ant aggressiveness on pollinators influenced by the nature – obligatory vs. facultative – of the ant–plant association?

In facultative ant–plant associations, the effect of plant seasonality on the conflict studied here could be variable. But in obligatory interactions, ants and plants require each other for their survival and in absence of one, the other dies. In Acacias, for instance, obligatory interactions are characterized by specialized features. These include traits that are regarded as essential for the ant–plant interaction, such as year-round leaf production, very enlarged foliar nectaries and leaflets with tips modified into Beltian bodies. Instead, in facultative interactions, leaves shed during the dry season, and plants are characterized by compound unmodified leaves (Janzen, 1966).

In this work, we model the interaction between plants, ants and pollinators using models of population dynamics set in an evolutionary context. We define a threshold in ant aggressiveness as determining a pollinator's survival or extinction. A pollinator's extinction can be viewed as actual extinction or as a shift in the plant's interaction from that specialist pollinator to more generalist ones. The model suggests that, under the same conditions, facultative interactions exhibit pollinator extinction for lower levels of ant aggressiveness than obligatory interactions over a broad range of parameter values. We then explore the conditions under which a discriminating ant can invade the population. We find that in the simple model, discrimination can never invade. A brief investigation into the hypothesis of limited dispersal suggests that this mechanism will not work in seed-saturated environments. Finally, we show that the ants can evolve to discriminate pollinators from herbivores when the cost of not attacking herbivores is overcome by an extra benefit that ants could gain from pollination. Figure 1 shows a schematic diagram of interaction between plant, ant and pollinator and the relevant aspects studied.

The model

The interaction between the three species has been described using the structure of the classical model of mutualistic interactions proposed by May (May, 2001). The system has been transformed into a nondimensional equations system (Murray, 2003) (see Supporting Information) given the following general set of differential equations:

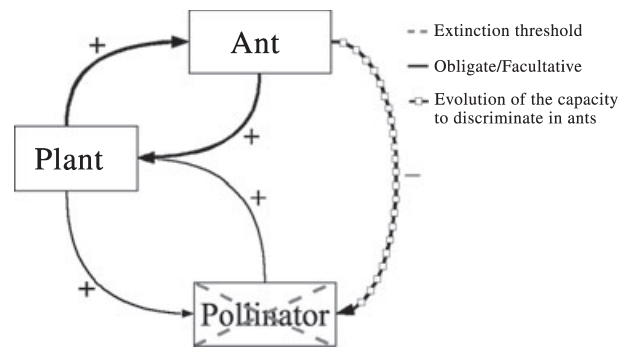


Fig. 1 Diagram of interaction between plant, ant and pollinator and the relevant aspects studied. The first step was to define a threshold in ant aggressiveness determining pollinator survival or extinction. Secondly, we analysed the effect of the nature of the plant–ant interaction (obligatory or facultative) in pollinator response to ant aggressiveness and finally, we studied potential scenarios where the capacity to discriminate pollinators from herbivores could evolve in ants.

$$\dot{p} = p (w - p + j_{pai} F(p, a_i) + j_{px} G(p, x) - k H(p, x, a_i)) \quad (1)$$

$$\dot{x} = k_1 x (1 - x + j_{xp} \Omega(p, x) - j_{xa} \Theta(x, a_i)) \quad (2)$$

$$\dot{a}_i = k_2 a_i (w - a_i + (j_{ap} - c) \Psi(p, a_i) + b \Delta(p, x)) \quad (3)$$

The functions $F(p, a_i)$, $G(p, x)$, $H(p, x, a_i)$, $\Omega(p, x)$, $\Theta(x, a_i)$, $\Psi(p, a_i)$ and $\Delta(p, x)$ are assumed to be either linear or Holling type II (Holling, 1959) p. 385. Here, p , x and a_i describe the population densities of plants, pollinators and ants, respectively. The index ‘i’ refers to either ‘d’ – ants that discriminate pollinators from herbivores – or ‘n’ – do not discriminate. The terms j_{pai} and j_{px} represent the benefit that plants derive from the ants and from the pollinators, respectively; j_{xp} represents the benefit that the pollinators derive from the interaction with plants, and j_{ap} represents the benefit that the ants derive from the interaction with plants. k_1 and k_2 are the reproductive rates of pollinators and ants, respectively – plants have a reproductive ratio of 1, given the transformations for nondimensionality (see Supporting Information). k is the cost that plants pay for the aggressive behaviour of ants to pollinators (reducing the pollination). c is the cost that the nonaggressive ants have to pay to discriminate herbivores from pollinators, and b is the extra benefit the ants that discriminate will obtain from pollination (for example by eating fruits). The parameter w is 1 in facultative (nonobligatory) interactions or is -1 in obligatory interactions. An interesting propriety of this model is that it enables one to evaluate and compare the consequences of the nature of the ant–plant interaction, changing only the parameter w . Finally, j_{xa} represents the negative effect of ant

aggressiveness on pollinators and is expected to have a strong effect on the system dynamics.

Results

Pollinator tolerance threshold in facultative and obligatory ant–plant interactions

The model given by eqns 1–3 has been studied in a simplified version for facultative interaction between ants and plants to obtain an analytical result determining a threshold between pollinator survival and extinction. Then, we compared the consequences of facultative and obligatory interactions by means of a more complex model.

For the simple version of the model, we assumed $w = 1$ (determining a facultative interaction), linear functions defining interaction terms between populations (no Holling type II), and $k = ad = c = b = 0$. Then, the system takes the form:

$$\dot{p} = p(1 - p) + j_{pa}ap + j_{px}xp \quad (4)$$

$$\dot{x} = k_1x(1 - x + j_{xp}p - j_{xa}a) \quad (5)$$

$$\dot{a} = k_2a(1 - a + j_{ap}p) \quad (6)$$

As shown in Fig. 2, when ant aggressiveness against pollinators is above a given threshold, pollinators are driven to extinction. Mathematically, this is represented by a transcritical bifurcation in which two different equilibrium points exchange stability: below a threshold value, the stable equilibrium is the one in which all species coexist (Supporting Information: eqns 8–10), whereas above it, only ants and plants survive (Supporting Information: eqns 11–13). Using j_{xa} (the level of ant aggressiveness against pollinators) as a control parameter, the transcritical bifurcation takes place in the critical value j_{xa}^* :

$$j_{xa}^* = (1 - x^{(1)} + j_{xp}p^{(1)})/a^{(1)} \quad (7)$$

Therefore, pollinators survive for low level of ant aggressiveness, and when ant aggressiveness is above the threshold given by eqn 7, pollinators are driven to extinction. This extinction can be interpreted as real extinction for specialist pollinators or as a shift in partners for generalist pollinators that can interact with other plants associated with less-aggressive ants.

Next, we compared the effect ant aggressiveness has on pollinators in obligatory and facultative interactions. A model that includes a linear response for the interaction terms for obligatory interaction does not have stable equilibria. We therefore followed Wright (Wright, 1989) in modelling both obligatory and facultative interactions using a single model that includes a saturating response (Supporting Information: Holling type II functional response (Holling, 1959) for the interaction terms eqns 38–41). This allowed us to represent both type of interactions between ants and plants changing only the parameter w ($w = 1$ for facultative interactions and $w = -1$ for obligatory interactions). In this model, the analytical expression for the pollinator equilibria at different levels of ant aggressiveness is algebraically too complex. To understand how the equilibria are affected by obligatory or facultative interactions, we simulated the system using different numerical values of parameters. We found that the pollinators are more tolerant to ant aggressiveness in obligatory than in facultative interactions and that this pattern holds for the vast majority of the parameters studied. The results of the simulations for one set of parameters are shown in Fig. 3.

Ants that discriminate pollinators from herbivores

In order to test how the system stability changes with the ant behaviour, we introduced two types of ants: ants that discriminate between herbivores and pollinators,

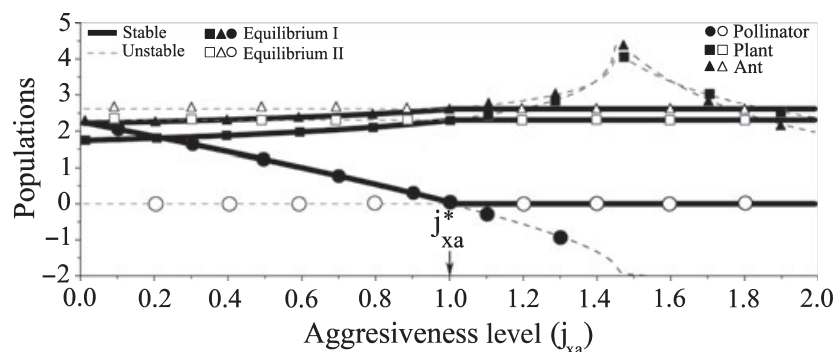


Fig. 2 Plants, pollinators and ants population at equilibrium as a function of the ant aggressiveness against pollinators (j_{xa}). The equilibrium I where the three species coexist loses stability when $j_{xa} = j_{xa}^*$, driving pollinators to extinction by a transcritical bifurcation. The equilibrium I where all species coexist is given by eqns (8–10) in Supporting Information. The system is stable if $j_{xa} < j_{xa}^*$. If $j_{xa} > j_{xa}^*$, the equilibrium II is only stable and is characterized by the survival of ants and plants only. It is given by eqns (11–13) in Supporting Information. The parameters were as follows: $j_{px} = 0.5$, $j_{pa} = 0.5$, $j_{xp} = 0.7$, $j_{ap} = 0.7$, $k_1 = 0.4$, $k_2 = 0.4$, $k = 0.3$.

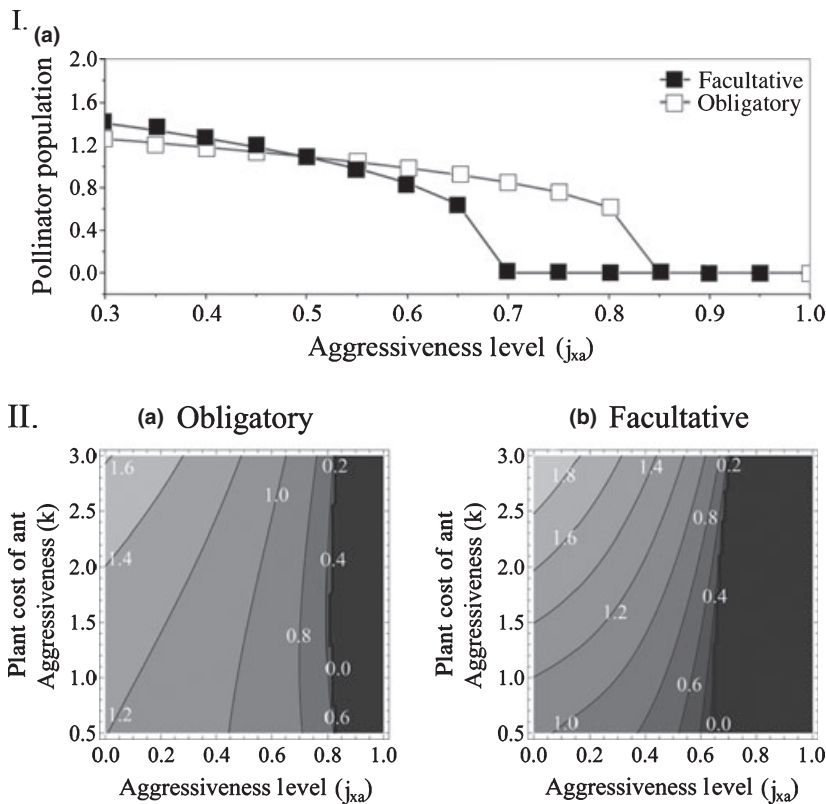


Fig. 3 Pollinator extinctions in facultative interactions compared to obligatory interactions. I. (a) Here, we show the response of pollinator populations to different levels of ant aggressiveness (j_{xa}) using the extended model given by eqns (38–41) in Supporting Information. II. (a and b) Combined effect of parameter j_{xa} with parameter k on pollinator population. The parameter values were as follows: $\vartheta = 0.04$, $j_{pan} = 1.85$, $j_{px} = 1.3$, $k_1 = 1.4$, $k_2 = 2.4$, $j_{xp} = 0.7$, $j_{ap} = 1.35$, with $w = 1$ in facultative case and $w = -1$ in obligatory case. The initial conditions were $P = 0.5$, $x = 1$ and $a = 1$. [in (a) $k = 1.2$].

therefore are aggressive to both pollinators and herbivores, and ants that discriminate between them, therefore do not attack pollinators. The ants that discriminate are symbolized by a_d , and the nondiscriminating ants are given by a_n . From a game theory perspective, this can be interpreted as different strategies played by the ants. One group of ants plays the strategy ‘discriminate’, whereas the other group plays the strategy ‘don’t discriminate’.

The model is given by the following equations:

$$\dot{p} = p(1 - p + j_{pan} a_n + j_{pad} a_d + j_{px} x - kx a_n) \quad (8)$$

$$\dot{x} = k_1 x(1 - x + j_{xp} p - j_{xan} a_n) \quad (9)$$

$$\dot{a}_n = k_2 a_n(1 - (a_n + a_d) + j_{ap} p) \quad (10)$$

$$\dot{a}_d = k_2 a_d(1 - (a_n + a_d) + (j_{ap} - c) p) \quad (11)$$

Here, we have assumed that there are no differences between the two ant groups except in the terms influenced by the capacity to discriminate. These include the parameters j_{pan} and j_{pad} , which represent the efficiency that each group of ants has to reduce the action of herbivores on the plant (the subscripts n and d refer to nondiscriminating and discriminating ants, respectively). Ants that discriminate are expected to commit some mistakes not attacking the herbivores, which would reduce the benefit that they offer to the plant, thus

$j_{pan} > j_{pad}$. Moreover, a consequence of not attacking herbivores is a reduction in the plant size and with it a reduction in the domatia available for the ants to expand their colony. We therefore included a cost term c that modifies the benefit the discriminating ants gain from the plant. Although aggressiveness can itself be physiologically costly, we assumed that the benefit of decreasing aggressiveness is smaller than the cost paid by increased herbivory.

We found that the two types of ants cannot coexist for any positive cost ($c > 0$). In that case, $\dot{a}_n > \dot{a}_d$ and the nondiscriminating ants can invade an equilibrium with the discriminating ant, but not vice versa (Supporting Information: Fig. S1).

Vertical transmission of mutualism through plant limited dispersal

In other horizontally transmitted mutualisms, such as mycorrhize (Wilkinson, 1997) and rhizobium (Bever & Simms, 2000), spatial limited dispersion has been proposed to mitigate the conflict between partners over reproduction.

Limited dispersal of plants could bring about associations between ant and plant progeny similar to true vertical transmission. In this case, ants will gain a benefit from pollination – the production of plant offspring on which the offspring of the ant colony can later reside. The

factors that influence the benefit that ants can reap are the following:

- Average spread distance of plant seeds. The further the seeds are dispersed, the more the benefit of increased seed production is spread among the colonies' neighbours, and thus the less benefit the colony that lives on the plant acquires.
- Average spread distance of offspring of an ant colony. The larger the range, the more neighbouring colonies a colony has, and again benefits to the hosts are spread to many other colonies.
- Density of ant colonies. Again, the larger the density the more neighbours a colony has.
- The increase in the number of plants in a certain area as a result of increasing the number of seeds.

If the plant increases its seed production in an area A_p , the ant colony has an area of dispersal A_a and the density of ants per unit area is ρ , then the colony will share the benefit that this plant provides with $(A_p + A_a)/\rho$ of its neighbours. This last factor has a strong influence on the benefit to the colony: if the host plant increases its seed production by a certain amount, by how much does the plant density in the area around the host increase? If the plant population is at an equilibrium, increasing the number of seeds will not increase the number of plants in the next generation and thus will not give a fitness benefit to the ant colony.

The connection between the number of neighbours with which the colony shares the benefit and the chance for a genotype to invade is complex and deserves a more detailed analysis. Because this is a tangential subject here, we will make a simplifying assumption that from time to time the population undergoes global mixing, so that we do not need to take into account the increased density of the parent genotype in a certain area. In this case, a colony that shares a fitness benefit of $(1 + s)$ with n of its neighbours in a globally competing population of N ants has a benefit of approximately $[1 + (1 - \frac{n}{N})s]$ compared with the average fitness of an individual in the population, for small s . Combining the previous formulas, the benefit the ant colony receives can be expressed as $[1 + (1 - (\frac{A_p + A_a}{\rho N})) \frac{df}{dx} dx]$, where $\frac{df}{dx}$ is the derivative of the additional plants produced in an area as a function of the increased fertilization of the host plant, and dx is the number of additional seeds produced.

When the dispersion area of ants and plants is much smaller than the total population size of ants, the expression $[1 - (\frac{A_p + A_a}{\rho N})]$ will be approximately 1. In that case, the main factor to the amount of benefit the colony receives is $\frac{df}{dx}$ – this means that in a nonseed-saturated environment, the benefit to the colony can be significant, whereas in a seed-saturated environment, the ants will not evolve to discriminate pollinators from herbivores unless another benefit is provided.

Extra benefit and the ability to discriminate

In horizontally transmitted mutualisms, conflicts can arise because of the mutualists' lack of interest in each other's reproduction. This lack of interest, and with it the conflict, can be reduced if the benefit received by the partner is conditional on the production of offspring by the host. Examples where a potential conflict over reproduction is reduced by this mechanism include cases of seed predation such as the one present in yucca–moths interactions (Pellmyr & Huth, 1994) and in wasp figs–wasp interactions (Bronstein, 1992). In these mutualistic associations, one of the partners acquires a benefit conditional on the reproduction of the other one, aligning their reproductive interests. This mechanism is also present in the association between plants and their dispersers, where the benefit that the dispersers acquire is the fruit containing seeds that are the product of plant reproduction (Herre *et al.*, 1999).

The conflict over reproduction in ant–plant interactions take place when ants mistake a pollinator for a herbivore. Therefore, we were interested in the conditions that favour the evolution of the capacity to discriminate between herbivores and pollinators in ants. To reduce the evolutionary conflict between ants and plants, we introduced a benefit to the ants that depends on the pollination rate. One alternative to balance the cost of discrimination is to acquire an extra benefit from fruit production. This takes the form of an additional term $[k_2 b(a_d p x)]$ in the equation for the growth rate of the ants. This term expresses that ants will benefit from a pollination event (proportional to the population of plants, ants and pollinators) that will eventually generate a fruit (or a seed with elaiosomes). We will explore two regimes. In the first, we check whether the additional benefit gained from additional pollination will enable discriminating ants that do not attack pollinators to invade and persist in a population of nondiscriminating ants. In a second analysis, we use a population of ants that gain a benefit from pollination and can discriminate and allow the parameter that determines aggressiveness to pollinators to change. We ask whether a mutant with higher or lower aggressiveness to pollinators would invade.

In the first case, the system is given by:

$$\dot{p} = p(1 - p + j_{pan} a_n + j_{pad} a_d + j_{px} x - k x a_n) \quad (12)$$

$$\dot{x} = k_1 x(1 - x + j_{xp} p - j_{xan} a_n) \quad (13)$$

$$\dot{a}_n = k_2 a_n(1 - (a_n + a_d) + j_{ap} p) \quad (14)$$

$$\dot{a}_d = k_2 a_d(1 - (a_n + a_d) + (j_{ap} - c) p + b p x) \quad (15)$$

By analysing these equations, we can study the ecological stability of the system for the two species of ants with different strategies. Among the equilibria of the

system, only two are of biological relevance and correspond either to the survival of the ants that discriminate or to the survival of the other ants (Supporting Information: Appendix S4). Figure 4a shows the parameter ranges in which each ant population is stable. The conditions required for ants to discriminate can only be reached when the extra benefit (b) is above a given value:

$$b > \frac{1 - (a_n^{(1)} + a_d(0))}{p^{(1)}x^{(1)}} + \frac{j_{ap} - c}{x^{(1)}} \quad (16)$$

where the superscript 1 refers to the equilibrium in which $a_d^{(1)} = 0$, $a_d(0)$ is the initial population of a_d and by definition $\dot{a}_d = 0$. This demonstrates that for some parameter values, the outcome depends on the initial conditions of the system (given by the ant population size). Using a model that includes a Holling type II saturation response for the interaction terms instead of a linear model, the results are the same except that the two ant species coexist in the region that depends on the initial conditions in the model stated above (Fig. 4c).

Equation 16 can be simplified when a_n is at equilibrium ($\dot{a}_n = 0$) and introducing a small number of the ant a_d (i.e. $a_d(0) \rightarrow 0$):

$$\frac{b}{c} > \frac{1}{x^{(1)}} \quad (17)$$

If this condition is fulfilled, ants can evolve the capacity to discriminate pollinators from herbivores. From eqn 17, we can observe that the ratio between the benefit and the cost can be very small for high pollinator population at the equilibria ($x^{(1)}$). This has been obtained assuming that the benefit is proportional to the pollinator population. It could also be assumed that the cost depends on the proportion of herbivores to pollinators (i, for instance, the herbivores are proportionally more numerous than pollinators, the probability that the ants mistake a pollinator for a herbivore will be higher). In this case, the term $(-c k_2 a_d p)$ in eqn 15 would be multiplied by $\left(\frac{H^*}{x^{(1)}}\right)$. Then, the capacity of ants to discriminate could only evolve if $\frac{b}{c} > \frac{H^*}{(x^{(1)})^2}$, assuming

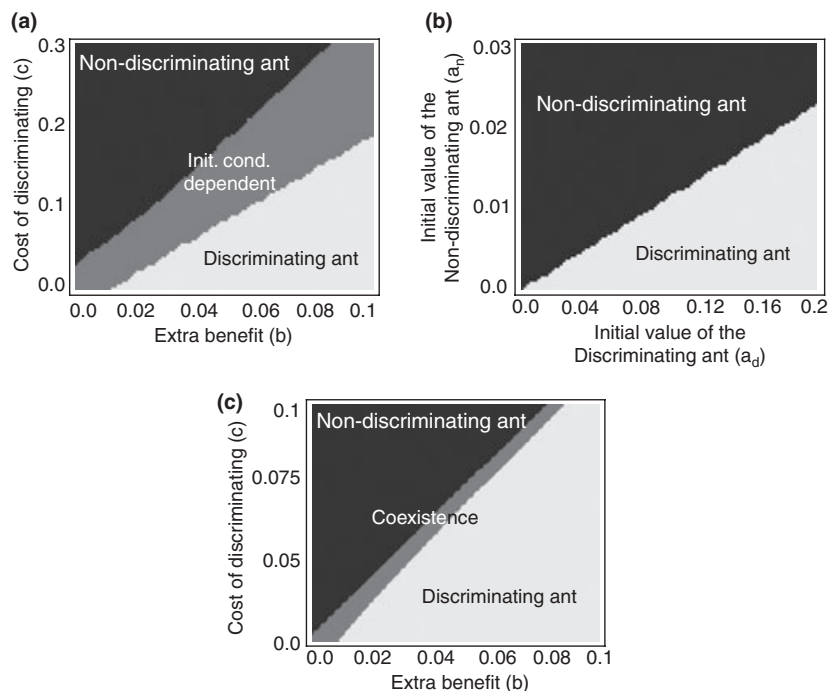


Fig. 4 Strategy dominance in facultative interactions (obligatory is similar). In (a), there are three possible outcomes: the nondiscriminative ant wins, the discriminative ant wins or the outcome depends on the initial conditions. The outcome in all cases depends on the values of the cost to discriminate (c), and benefit of fertilization (b). In (b), we take $c = 0.22$ and $b = 0.07$, in the region where the output depends on the initial conditions. Here, we used the model given by eqns (25–28) in Supporting Information. The parameter values were: $j_{pad} = 0.35$, $j_{pan} = 0.5$, $j_{px} = 0.5$, $k_1 = 0.4$, $k_2 = 0.2$, $k_3 = 0.2$, $j_{xp} = 0.7$, $j_{xan} = 0.3$, $j_{ap} = 0.35$, $k = 0.2$. In (c), we use the model given by eqns (38–41) in Supporting Information. In this case there are three possible outcomes: the nondiscriminative ant wins, the discriminative ant wins or both coexist, the outcome in all cases depends on the values of the cost of discrimination (c), and the extra benefit from pollination (b). The parameter values were as follows: $\vartheta = 0.04$, $j_{pad} = 1.35$, $j_{pan} = 1.5$, $j_{px} = 1.3$, $k_1 = 1.4$, $k_2 = 1.2$, $k = 1.2$, $j_{xa} = 0.5$, $j_{xp} = 0.7$, $j_{ap} = 1.35$, $w = 1$.

the population of herbivores is roughly constant and equal to H^* .

In the previous analysis, we studied the evolutionary dynamics of the system (12–15) for two species of ants with different strategies: discriminating pollinators and those that treat pollinators just like herbivores. This was carried out assuming that ants do not attack herbivores at all.

In the following, we let the aggressiveness level towards pollinators evolve. We assume that ants can discriminate pollinator from herbivore, at a cost, and ask which aggressiveness level to pollinators will adopt. We look at the dynamics of invading mutants for the aggressiveness parameter (j_{xa}) using adaptive dynamics (Ferriere *et al.*, 2004). Under this framework, mutations would generate strategies in a continuum space that could invade the whole ant population. Moreover, we assumed that the detrimental effect of ant aggressive behaviour on plants (k), the cost of discriminating (c) and also the extra benefit (b) depends on the level of aggressiveness (j_{xa}). We also assumed that the interaction terms follow a Holling type II response – a saturating function – through the results were similar for a linear response. In this case, the system is given by:

$$\dot{p} = p \left(w - p + j_{pan} \frac{a}{p + \vartheta} + j_{px} \frac{x}{p + \vartheta} - k j_{xa} \frac{x a}{p + \vartheta} \right) \quad (18)$$

$$\dot{x} = k_1 x \left(1 - x + j_{xp} \frac{p}{x + \vartheta} - j_{xa} \frac{a}{x + \vartheta} \right) \quad (19)$$

$$\dot{a} = k_2 a \left(w - a + (j_{ap} - c e^{-j_{xa}}) \frac{p}{a + \vartheta} + b e^{-j_{xa}} x \frac{p}{a + \vartheta} \right) \quad (20)$$

Figure 5a shows three examples of pairwise invasibility plots (PIP) of one aggressiveness level to pollinators vs. a second one, all done for different numerical combinations of the cost and benefit parameters c and b to show the possible types of behaviour that can emerge. According to the values of parameters c and b , a more aggressive ant mutant can either always invade (Fig. 5aI) or never invade (Fig. 5aIII) or invade only if the mutation generates an aggressive individual with a j_{xa} above the repeller point (Fig. 5aII). Figure 5b summarizes the different behaviours of the PIPs for different combinations of parameter values c and b . This includes a region where the aggressiveness j_{xa} will always increase – and ants will not discriminate – a region where it will always decrease – and ants will discriminate – and a repeller point. The regions where aggressiveness will always invade or will never invade are represented by a repeller point equal to 0 and by a repeller point that tends to infinity, respectively.

The results obtained in this case are qualitatively similar to the ones explored by the ecological dynamics. In both cases, the emergence of ants that discriminate herbivores from pollinators is favoured by high

benefit from pollination and low cost of mistaking herbivores.

Discussion

The mechanisms to reduce the evolutionary conflict between partners described in this study do not operate only on a subset of plant–ant interactions, but apply as well to other horizontally transmitted mutualisms. Among other mechanisms to reduce conflict (e.g. partner choice and punishment), spatial effects have been proposed to have a role in horizontally transmitted mutualisms such as mycorrhize (Wilkinson, 1997) and rhizobium (Bever & Simms, 2000). Similarly, the presence of a conditional incentive may have decreased conflict over reproduction in other horizontally transmitted mutualisms where reproduction of the host is necessary to obtain reward, such as in wasp figs–wasp interaction (Bronstein, 1992), yucca–moths interaction (Pellmyr & Huth, 1994) or the interaction of plants and seed dispersers (Herre *et al.*, 1999). Therefore, both our results that seed saturation in the environment will restrict the effect that spatial structure has in reducing conflict and the idea that a conditional reward can potentially reduce conflict can be applied to other horizontally transmitted mutualisms.

We have chosen the well-studied case of the conflict over reproduction present in ant–plant associations. In these cases, there are several ways in which ants can interfere or disrupt plant reproduction (Wagner, 2000; Yu *et al.*, 2001; Frederickson, 2009). Plant reproduction can be disrupted by plant castration where ants manipulate plant reproduction to increase the resources that plants devote to ants (Yu *et al.*, 2001; Frederickson, 2009). Ants can reduce the frequency of pollinator visits behaving aggressively or by taking nectar from the flowers (Willmer & Stone, 1997; Wagner, 2000; Ghazoul, 2001; Wagner & Kay, 2002). Different hypotheses have been proposed to understand the conflict generated by ants on plant reproduction. For instance, extrafloral nectaries and similar structures could have evolved to deter the ants from moving on to the flowers (Keeler, 2000; Wagner & Kay, 2002). Also, plants could use chemical deterrents against ants to generate spatial and temporal separation between ants and pollinators. However, one could expect that ants could evolve resistance to the floral repellent (Ghazoul, 2001). Nevertheless, it has been proposed that chemical repellents mimic ants alarm pheromones that are evolutionary conserved (Ghazoul, 2001). Moreover, chemical deterrents are not universally repellent to ants (Rico-Gray & Oliveira, 2007) and often, ants and pollinators overlap in their activities (Willmer & Stone, 1997), so it is less likely that this strategy can solve the conflict in all cases. In this work, we have studied different potential mechanisms that can operate to avoid such conflict as well as its ecological and evolutionary consequences.

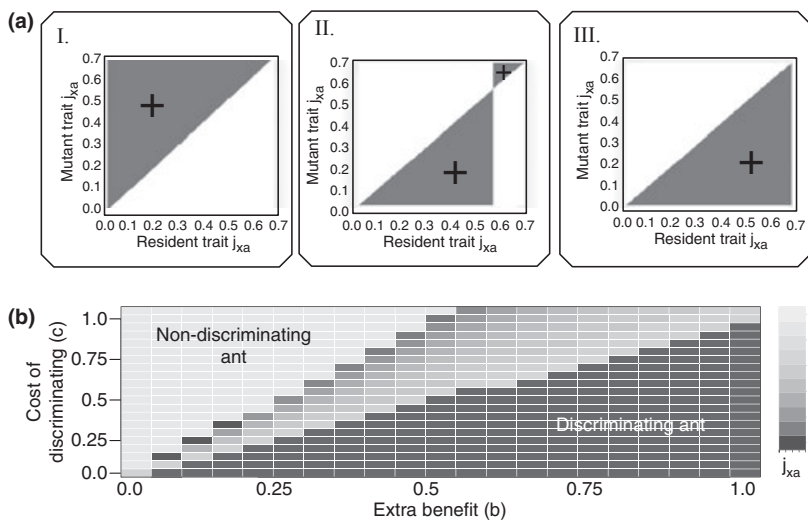


Fig. 5 (a) Pairwise invasibility plots (PIP). Grey areas indicates positive invasibility. (b) Summary of the different PIP: In the lighter area only nondiscriminative ants invade, in the darker area only discriminative ants invade. In the region in between, the scenario is as in the panel (a) II from the middle: a repeller is present, in this case the grey level represents the value of j_{xa} at the repeller point. The parameters were: $\vartheta = 0.04$, $j_{pa} = 1.35$, $j_{px} = 1.3$, $k_1 = 1.4$, $k_2 = 1.2$, $k = 1.2$, $j_{xp} = 0.7$, $j_{ap} = 1.35$. PIP from (a) from left to right ($c = 1$, $b = 0.0$, $c = 0.6$, $b = 0.5$, $c = 0$, $b = 1$).

We briefly analysed the ecological consequences that a given degree of ant aggressiveness will have in facultative compared to obligatory plant–ant interactions. Extensive simulations of our model across a wide set of parameters suggest that pollinators will be more tolerant to ant aggressiveness in obligatory than in facultative interactions. It should be noticed that, in two-species mutualistic systems, obligatory interactions are evolutionarily less stable than facultative ones, as one species depends more tightly on the second. Interestingly, we have shown that the ecological effect on a third associated species (the pollinator) is less strong when the interaction ant–plant is obligatory.

A host plant benefits from pollinator visitation and would therefore have increased fitness if ants discriminated pollinator from herbivore and avoided attacking the first. Discrimination, however, can lead to mistakes and let some of the herbivores eat the plant, thus reducing the benefits that the ants acquire from the plant. Therefore, in a system composed by two types of ants, a discriminating and a nondiscriminating one, we would predict that the first type will be out-competed by the second. We observed that unless ants acquire an additional benefit, discrimination should not evolve. Then, we have analysed the conditions in which the capacity to discriminate could evolve in ants.

One possible process that we briefly studied and could generate associations between ants and plants progeny is limited dispersal. We found that in a seed-saturated environment, where the number of plants around the host plant will not increase as a result of additional pollination events, ants will not evolve to discriminate pollinators from herbivores. However, this process should be studied more deeply in a future work considering explicit spatial effects.

In this work, we have shown that if ants derive a benefit from pollination, they can evolve the capacity to

discriminate pollinators from herbivores. We have demonstrated that, if the ratio between the benefits from pollination and the cost of not attacking herbivores by mistaking them for pollinators is high enough, the discriminating ants will be resistant to invasions from mutants of their own species as well as to other ant species that are aggressive to pollinators and that have not evolved to eat fruit. The ‘fruit’ considered here can be any reward that emerges from pollination. Different structures can be added to the seeds to attract ants: these include the general structure called elaiosomes that can have different origins in different species but are morphologically and chemically similar (Rico-Gray & Oliveira, 2007), and include aril, caruncle, funiculus and pericarp.

The potential scenarios for the resolution of the conflict, either by limited seed dispersal or by an extra benefit from pollination for the ant, will be possible in plant species where the flowers are hermaphrodites, or in female plants from dioecious species. Because they will produce neither seeds nor fruits, male flowers from dioecious and monoecious plant species would be attacked by ants. If ants are too aggressive, the level of autogamy is expected to be high in hermaphrodite plants, as mentioned occurs for some cases on the ant–plant associations found in ant gardens. This suggests that the conflict of ants over plant reproduction will be more pronounced in dioecious and monoecious plant species because male flowers could be prevented from pollinator visits (if enough sexual dimorphism exists so that it can be perceived by ants), reducing the amount of pollen that can be interchanged. The same conflict will limit the pollen transport and thus reduce the seed set in self-incompatible species. In self-compatible species, offspring generated from self-fertilization are often less fit than the offspring of unrelated individuals, as recognized since Darwin (Darwin, 1876). This inferiority of inbred prog-

eny compared to outbred progeny, known as inbreeding depression, is because of the expression of deleterious recessive mutations in homozygous inbred progeny (Eckert *et al.*, 2009).

Ants deriving benefits from seeds or fruits have been identified and are invariably associated either with antagonistic interactions, where ants eat some of the seeds, or with mutualistic ones, where ants disperse the seeds and take only elaiosomes or similar structures without damaging the seeds. In the latter case, the quality of the dispersers has been seen to be variable (Rico-Gray & Oliveira, 2007). We suggest that the presence of low-quality dispersers that take elaiosomes but do not travel long distances could have evolved to reduce the conflict analysed here. Supporting this notion, it has been observed that ants that are strong defenders of plants against herbivory are not, in general, good dispersers [(Rico-Gray & Oliveira, 2007): Table 3.2]. For example, in the neotropical plant *Turnera ulmifolia*, the associated ant *Camponotus atriceps* is a good defender of plants against herbivory but just an average disperser.

The scenario of a mutualistic interaction between plants, pollinators and ants that also eat fruits has been reported to take place in ant gardens (Davidson, 1988). Some of the epiphytes involved in the mutualism between ants and plants known as ant gardens are associated with pollinators, and the same conflict has been observed (ants attack pollinators) (Davidson, 1988). If ants are too aggressive against pollinators, this will increase the level of autogamy (Madison, 1979). However, if the reward that ants obtain from the fruits produced by the action of pollinators is high enough, then the capacity to discriminate pollinators from herbivores will be able to evolve in ants.

Another example where the proposed scenario to solve the conflict could be present is in the case of *Mentzelia nuda* (Loasaceae). This plant has floral nectar that attracts pollinators favouring plant outcrossing, as well as extra-floral nectaries attracting ants whose activity decrease herbivory. In this case, instead of an elaiosome, the plant produces post-floral nectar on the developing fruits that attract ants whose presence significantly enhances seed set (Keeler, 2000).

We propose a plausible and empirically testable scenario for the evolution of the capacity to discriminate in ants. In fact, little has been explained about the origin of the ability to discriminate that ants have in similar types of association. For example, we believe that in the *Ficus* species (Schatz *et al.*, 2006), it is unclear what the benefit is to an ant that has to discriminate different types of wasps – a mutualistic and a parasitic wasp – and favour the wasp that pollinates [although another study shows the opposite pattern (Schatz *et al.*, 2003)]. Although the ants have a benefit from the plant (nest), they cannot see the effect that the parasitic wasp will have in the long term. The same conflict is present in our case. In the symbiotic interaction between ants and plants a conflict

exists: plants are selected to produce offspring through pollination, whereas for the ants, only the survival of the individual on which they live is important. Ants are indifferent to pollination and are selected to be aggressive to herbivores, whereas plants require pollinators for their reproduction. Our work suggests that a solution would exist if ants acquire a benefit from pollination. In that case, the capacity to discriminate should evolve in ants.

More empirical research would be needed to test our hypothesis. A decrease in ant attack on pollinators has only been analysed in the context of chemical deterrents (Willmer & Stone, 1997; Raine *et al.*, 2002; Ness, 2006). In a similar way, as performed in these studies, ant discrimination could be measured as a reduction of the rate of pollinator attack vs. herbivore attack. The relationship between ant discrimination and several of the concepts that could play an important role in the evolution of ant discrimination (as pseudo-vertical transmission and the fact that ants can benefit from fruits) mentioned here can then be tested empirically. Eventually, this would enable us to understand whether ant discrimination is ecologically correlated to these concepts.

Acknowledgments

L.O. thank Frederick Delfin, Aurelia Chenu, Rolf Kummerli, Susan Ptak and Adam Wilkins for helpful comments on previous versions of this manuscript, and the Max Planck Society for financial support.

References

- Abrahamson, W.G. 1989. *Plant–Animal Interactions*. McGraw-Hill, New York, NY, USA.
- Arista, M., Oliveira, P., Gibbs, P. & Talavera, S. 1997. Pollination and breeding system of two co-occurring *Hirtella* species (Chrysobalanaceae) in Central Brazil. *Bot. Acta* **110**: 496–502.
- Bastolla, U., Fortuna, M., Pascual-Garca, A., Ferrera, A., Luque, B. & Bascompte, J. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**: 1018–1020.
- Bever, J. & Simms, E. 2000. Evolution of nitrogen fixation in spatially structured populations of *Rhizobium*. *Heredity* **85**: 366–372.
- Bronstein, J.L. 1992. Seed predators as mutualists: ecology and evolution of the fig/pollinator interaction. In: *Plant–Insect Interactions*, Vol. 4 (E.A. Bernays, ed.), pp. 1–47. CRC Press, Boca Raton, Florida.
- Darwin, C. 1876. *The Effect of Cross and Self-Fertilization in the Vegetable Kingdom*. John Murray, London.
- Davidson, D. 1988. Ecological studies of neotropical ant gardens. *Ecology* **69**: 1138–1152.
- Eckert, C., Kalisz, S., Geber, M., Sargent, R., Elle, E., Cheptou, P. *et al.* 2009. Plant mating systems in a changing world. *Trends Ecol. Evol.* **25**: 35–43.
- Federle, W., Maschwitz, U. & Fiala, B. 1998. The two-partner ant–plant system of *Camponotus (Colobopsis)* sp. 1 and *Macaranga*

- puncticulata* (Euphorbiaceae): natural history of the exceptional ant partner. *Insect. Soc.* **45**: 1–16.
- Feinsinger, P. & Swarm, L. 1978. How common are ant-repellent nectars? *Biotropica* **10**: 238–239.
- Feldhaar, H., Fiala, B., Hashim, R. & Maschwitz, U. 2003. Patterns of the *Crematogaster*–*Macaranga* association: the ant partner makes the difference. *Insect. Soc.* **50**: 9–19.
- Ferriere, R., Bronstein, J., Rinaldi, S. & Law, R. 2002. Cheating and the evolutionary stability of mutualisms. *Proc. Biol. Sci.* **269**: 773–780.
- Ferriere, R., Dieckmann, U. & Couvet, D. 2004. *Evolutionary Conservation Biology*. Cambridge University Press, Cambridge, UK.
- Fiala, B. & Maschwitz, U. 1991. Extrafloral nectaries in the genus *Macaranga* (Euphorbiaceae) in Malaysia: comparative studies of their possible significance as predispositions for myrmecophytism. *Biol. J. Linn. Soc.* **44**: 287–305.
- Fiala, B. & Maschwitz, U. 1992. Food bodies and their significance for obligate ant-association in the tree genus *Macaranga* (Euphorbiaceae). *Bot. J. Linn. Soc.* **110**: 61–75.
- Fiala, B., Maschwitz, U., Pong, T. & Helbig, A. 1989. Studies on the South East Asian ant–plant association *Crematogaster borneensis*/*Macaranga*: adaptations of the ant partner. *Oecologia* **37**: 212–231.
- Fiala, B., Grunsky, H. & Maschwitz, U. 1994. Diversity of ant–plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. *Oecologia* **97**: 186–192.
- Fiala, B., Jakob, A. & Maschwitz, U. 1999. Diversity, evolutionary specialization and geographic distribution of a mutualistic ant–plant complex: *Macaranga* and *Crematogaster* in South East Asia. *Biol. J. Linn. Soc.* **66**: 305–331.
- Fonseca, C. 1994. Herbivory and the long-lived leaves of an Amazonian ant-tree. *J. Ecol.* **82**: 833–842.
- Frederickson, M. 2009. Conflict over reproduction in an ant-plant symbiosis: why *Allomerus octoarticulatus* ants sterilize *Cordia nodosa* trees. *Am. Nat.* **173**: 675–681.
- Ghazoul, J. 2001. Can floral repellents pre-empt potential ant-plant conflict? *Ecol. Lett.* **4**: 295–299.
- Herre, E., N, K., Mueller, U. & Rehner, S. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* **14**: 49–53.
- Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canad. Entomol.* **91**: 293–320.
- Itioka, T., Nomura, M., Inui, Y., Itino, T. & Inoue, T. 2000. Difference in intensity of ant defense among three species of *Macaranga* myrmecophytes in a Southeast Asian dipterocarp forest. *Biotropica* **32**: 318–326.
- Izzo, T. & Vasconcelos, H. 2002. Cheating the cheater: domatia loss minimizes the effects of ant castration in an Amazonian ant-plant. *Oecologia* **133**: 200–205.
- Janzen, D. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* **20**: 249–275.
- Janzen, D. 1967a. Fire, vegetation structure, and the ant x acacia interaction in central america. *Ecology* **48**: 26–35.
- Janzen, D. 1967b. Interaction of the bulls-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in Eastern Mexico. *University of Kansas Scientific Bulletin* **47**: 315–558.
- Janzen, D. 1969. Birds and the ant x acacia interaction in Central America, with notes on birds and other myrmecophytes. *The Condor* **71**: 240–256.
- Janzen, D. 1973. Evolution of polygynous obligate acacia-ants in Western Mexico. *J. Anim. Ecol.* **42**: 727–750.
- Kato, M.G. & Yamamura, N. 1999. Evolution of mutualistic symbiosis without vertical transmission? *Theor. Popul. Biol.* **55**: 309–323.
- Keeler, K. 2000. Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *Am. J. Bot.* **68**: 295–299.
- Kikuchi, D., Lasso, E., Dalling, J. & Nur, N. 2007. Pollinators and pollen dispersal of *Piper dilatatum* (Piperaceae) on Barro Colorado Island, Panama. *J. Trop. Ecol.* **23**: 603–606.
- Klironomos, J., McCune, J., Hart, M. & Neville, J. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecol. Lett.* **5**: 137–141.
- Liepert, C. & Dettner, K. 1993. Recognition of aphid parasitoids by honeydew-collecting ants: the role of cuticular lipids in a chemical mimicry system. *J. Chem. Ecol.* **19**: 2143–2153.
- Madison, M. 1979. Additional observations on ant-gardens in Amazonas. *Selbyana* **5**: 107–115.
- May, R.M. 2001. *Stability and Complexity in Model Ecosystems*. Princeton Landmarks in Biology, Princeton, NJ.
- Moog, U., Fiala, B., Federle, W. & Maschwitz, U. 2002. Thrips pollination of the dioecious ant plant *Macaranga hullettii* (Euphorbiaceae) in Southeast Asia. *Am. J. Bot.* **89**: 50–59.
- Murray, J.D. 2003. *Mathematical Biology*, 3rd edn. Springer-Verlag, New York.
- Ness, J. 2006. A mutualisms indirect costs: the most aggressive plant bodyguards also deter pollinator. *Oikos* **113**: 506–514.
- Odegaard, F. & Frame, D. 2007. Generalist flowers and phytophagous beetles in two tropical canopy trees: resources for multitudes. *Taxon* **56**: 696–706.
- Palmer, T., Stanton, M., Young, T., Goheen, J., Pringle, R. & Karban, R. 2008. Breakdown of an ant–plant mutualism follows the loss of large herbivores from an African savanna. *Science* **319**: 192–195.
- Pellmyr, O. & Huth, C. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**: 257–260.
- Prys-Jones, O. & Willmer, P. 1992. The biology of alkaline nectar in the purple toothwort (*Lathraea clandestina*): ground level defences. *Biol. J. Linn. Soc.* **45**: 373–388.
- Raine, N., Willmer, P. & Stone, G. 2002. Spatial structuring and floral avoidance behavior prevent ant-pollinator conflict in a Mexican ant-acacia. *Ecology* **83**: 3086–3096.
- Raine, N., Gammans, N., Macfadyen, I., Scrivner, G. & Stone, G. 2004. Guards and thieves: antagonistic interactions between two ant species coexisting on the same ant-plant. *Ecol. Entomol.* **29**: 345–352.
- Rickson, F. & Risch, S. 1984. Anatomical and ultrastructural aspects of the ant-food cell of *Piper cenocladum* C. DC. (Piperaceae). *Am. J. Bot.* **71**: 1268–1274.
- Rico-Gray, V. & Oliveira, P.S. 2007. *The Ecology and Evolution of Ant–Plant Interactions*. The University of Chicago Press, Chicago.
- Risch, S., McClure, M., Vandermeer, J. & Waltz, S. 1977. Mutualism between three species of tropical *Piper* (Piperaceae) and their ant inhabitants. *Am. Midl. Nat.* **98**: 433–444.
- Schatz, B., Anstett, M., Out, W. & McKey, M.H. 2003. Olfactive detection of fig wasps as prey by the ant *Crematogaster scutellaris* (Formicidae; Myrmicinae). *Naturwissenschaften* **90**: 456–459.
- Schatz, B., Proffitt, M., Rakhi, B. & Borges, R. 2006. Complex interactions on fig trees: ants capturing parasitic wasps as possible indirect mutualists of the fig–fig wasp interaction. *Oikos* **113**: 344–352.

- Smith, W. 1903. *Macaranga triloba*: a new myrmecophilous plant. *New Phytol.* **2**: 79–82.
- Solomon-Raju, A. & Purnachandra-Rao, S. 2002. Pollination ecology and fruiting behaviour in *Acacia sinuata* (Lour.) Merr (Mimosaceae), a valuable non-timber forest plant species. *Curr. Sci.* **82**: 1466–1471.
- Tepe, E., Vincent, M. & Watson, L. 2007. The importance of petiole structure on inhabitability by ants in *Piper* sect. *macrostachys* (Piperaceae). *Bot. J. Linn. Soc.* **153**: 181–191.
- Ule, E. 1901. Ameisengarten im Amazonasgebiet. *Engler's Botanische Jahrbucher für Systematik, Beiblatt* **68**: 45–52.
- Wagner, D. 2000. Pollen viability reduction as a potential cost of ant association for *Acacia constricta*. *Am. J. Bot.* **87**: 711–715.
- Wagner, D. & Kay, A. 2002. Do extraoral nectaries distract ants from visiting owers? An experimental test of an overlooked hypothesis. *Evol. Ecol. Res.* **4**: 293–305.
- Ward, P. 1999. Systematics, biogeography and host plant associations of the *Pseudomyrmex viduus* group (Hymenoptera: Formicidae), *Triplaris* and *Tachigali*-inhabiting ants. *Zool. J. Linn. Soc.* **126**: 451–540.
- Wilkinson, D. 1997. The role of seed dispersal in the evolution of Mycorrhizae. *Oikos* **78**: 394–396.
- Wilkinson, D. & Sherratt, T. 2001. Horizontally acquired mutualisms, an unsolved problem in ecology? *Oikos* **92**: 377–384.
- Willmer, P. & Stone, G. 1997. How aggressive ant-guards assist seed-set in *Acacia* flowers. *Nature* **388**: 165–167.
- Wolda, H. & Roubik, D. 1986. Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* **67**: 426–433.
- Wright, D. 1989. A simple, stable model of mutualism incorporating handling time. *Am. Nat.* **134**: 664.
- Yu, D. & Pierce, N. 1998. A castration parasite of an ant–plant mutualism. *Proc. Biol. Sci.* **265**: 375–382.
- Yu, D., Wilson, H. & Pierce, N. 2001. An empirical model of species coexistence in a spatially structured environment. *Ecology* **82**: 1761–1771.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Pollinator tolerance threshold in facultative ant–plant interaction scenario.

Appendix S2 Aggressive ants and ants that discriminate pollinators from herbivores.

Appendix S3 Obligate vs. Facultative ants and the extended model.

Appendix S4 Extra benefit and the ability to discriminate in ants.

Appendix S5 Evolving the ability to discriminate.

Figure S1 Effect of the cost of discriminate in the system stability.

Figure S2 Histogram for the distances in ant aggressive-ness determining pollinator extinctions for facultative vs obligatory interactions.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Received 27 April 2010; revised 6 November 2010; accepted 11 November 2010