

Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies

K. Del-Claro¹ · V. Rico-Gray² · H. M. Torezan-Silingardi¹ · E. Alves-Silva¹ · R. Fagundes¹ · D. Lange⁵ · W. Dáttilo⁴ · A. A. Vilela¹ · A. Aguirre³ · D. Rodriguez-Morales³

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Abstract All mutualistic plant–animal interactions are mediated by costs and benefits in relationships where resources (from plants) are exchanged by services (from animals). The most common trading coin that plants offer to pay for animal services is nectar; the main servers are hymenopterans. Extrafloral nectar (EFN) is produced in almost all aboveground plant parts not directly related with pollination, and their true function has long been an issue of discussion among naturalists and will be our main subject. The protective function of extrafloral nectaries (EFNs) is reviewed and considered with an alternative hypothesis, presenting not only ants, but also spiders and wasps as potential and effective agents in these protective interactions. Despite their likely relevance, the phenological variation (mainly sequential flowering and resprouting) of host plants mediating these interactions have been generally ignored. We discuss how the outcomes of each ant–EFN bearing plant interaction vary depending on physical and

biotic changes in interacting organisms (internal factors such as phenology and species identity) as well as in their environments (external factors such as climatic variation), all of which may modify the character of each interaction. We propose that ant–EFN bearing plant interactions serve an excellent and unique model to test the “Geographic Mosaic Theory” of coevolution providing us a more clear view of how evolution has structured these plant–animal ecological networks.

Keywords Ants · Ecological networks · Herbivory · Myrmecophily · Mutualism · Predators

“I would prefer even to fail with honor than win by cheating”

Sophocles

In the natural world there is never an option to fail; to win the game of survival and reproduction is essential. Plant–animal interactions are among the most ancient group of species relationships on Earth, where despite the existence of some fidelity, lies, exploitation, and cheating are commonplace. These relationships shaped terrestrial biodiversity through creation, extinction, and coevolution of interactions mediated by a balance of loss and gains (Thompson 2013). In a current perspective, biodiversity must embrace the enormous richness present in plant–animal interactions, considering the life histories, biology and behavior of related species (Price 2002). So, we must accept that the outcomes of each interaction vary depending on physical and biotic changes as in related organisms (internal factors) as in their environments (external factors) which may modify the character of each interaction (Del-Claro

✉ K. Del-Claro
delclaro@ufu.br

¹ Instituto de Biologia, LECI (Laboratório de Ecologia Comportamental e de Interações), Pós-graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, CP 38400-902, Uberlândia, MG, Brazil

² Instituto de Neuroetología-Universidad Veracruzana, 91190 Xalapa, Veracruz, Mexico

³ Instituto de Ecología A.C., Red de Interacciones Multitróficas, Carretera antigua a Coatepec 351, El Haya, CP 91070, Xalapa, Veracruz, Mexico

⁴ Red de Ecoetología, Instituto de Ecología A.C., Carretera antigua a Coatepec 351, El Haya, CP 91070, Xalapa, Veracruz, Mexico

⁵ Universidade Tecnológica Federal do Paraná, Campus Santa Helena, Santa Helena, PR, Brazil

et al. 2013a; Del-Claro and Marquis 2015). A mutualism will never be unconditionally a mutualism; in fact, the same is valid for any relationship, because over time (either slowly or quickly), evolutionary changes will modify the results and direction of interactions (Bronstein 1998; Del-Claro and Torezan-Silingardi 2012; Thompson 2013). All mutualistic plant–animal interactions are mediated by costs and benefits, in relationships where resources (from plants) are exchanged by services (from animals). Sometimes the costs for the plants are high and resources are the plant's own tissues when used by herbivores. Other times the benefits are high and plants receive protection against herbivores from a third partner species. The most common reward that plants offer to pay for animal services is nectar.

The nectar

Nectar is an aqueous solution that can be secreted on virtually all aboveground structures of plants (Elias 1983; Díaz-Castelazo et al. 2005). This liquid may be very rich in carbohydrates (mainly sucrose and/or fructose), with diluted compounds of lipids, enzymes, amino acids, phenols, alkaloids and volatile organic compounds (Koptur 1994; Blüthgen et al. 2004; González-Teuber and Heil 2009). Floral nectar is the most commonly studied nectar and is clearly associated with the beneficial plant–animal interaction of pollination (Faegri and Van der Pijl 1976; Torezan-Silingardi 2012). On the other hand, extrafloral nectar (EFN) is secreted on both vegetative and reproductive plant parts (e.g., spike, pedicel, bud, calyx, leaves, shoots, petioles, bracts, and stems) but without any direct relation with pollination (Fig. 1). Indeed, EFN attracts ants that may repel pollinators from visiting flowers (Ness 2006; Assunção et al. 2014). Since their discovery, extrafloral nectaries (EFNs) and their true function to plants have been the issue of discussion among naturalists and will be the focus of this review.

Extrafloral nectaries: what are they for?

Physiologists argued that plants secrete EFN to get rid of excess carbohydrates, where protectionists promoted their ecological defensive function (see reviews in Bentley 1977a, Heil 2015). In the defensive function, EFNs will attract mainly ants that will feed on its nectar and in counterpart prey on or chase away herbivores benefitting the plant (Bronstein 1998; Rico-Gray and Oliveira 2007). After more than 100 years of debate initiated by Belt (1874), the majority of empirical studies and reviews have demonstrated undoubtedly that ants benefit the plant through the reduction of herbivory (Oliveira and Freitas 2004; Rosumek

et al. 2009; Zhang et al. 2015; Fig. 2). Despite ant–EFN bearing plant studies assume a positive benefit to ants, very few of them were dedicated to prove ant benefits in these relationships (Lach et al. 2009). One of them clearly shows that nectar from EFNs is a valuable resource to ants, increasing individual and also colony growth rate and survivorship (Byk and Del-Claro 2011). This confirms the mutualistic character of these relationships.

The classic demonstrations of protective hypothesis are ant exclusion experiments which evaluate the effects of ant presence or absence on plant fitness, mainly leaf area loss and/or fruit set production (Bentley 1977a, b; Horvitz and Schemske 1984). However, there are studies showing neutral or negative effects of ant visitation on EFNs bearing plants (e.g. Rashbrook et al. 1992). For example, Byk and Del-Claro (2010) tested in the Brazilian savanna the protective action of a very common and abundant EFN visiting ant, *Cephalotes pusillus* on the EFN-bearing tree *Ouratea spectabilis* (Ochnaceae). Results showed that besides providing no benefit to the plants, pollen consumption by *C. pusillus* may reduce flower fertilization. Variation in the effects of EFN-gathering ants on plants has been reported for various ant–plant systems (Bronstein 1998; Rico-Gray and Oliveira 2007; and references therein). Differences in capabilities among ant species to inhibit herbivore activity are a possible cause for these variable outcomes. For example, ant–herbivorous thrips relationships occurring in EFN-bearing tropical plants are common but largely unexplored. Should thrips be deterred by ants, a positive effect of ants on plant fitness might be expected. Alves-Silva and Del-Claro (2015) investigated the influence of the ant *Camponotus blandus* on thrips, *Pseudophilothrips obscuricornis*, abundance and herbivory in three extrafloral nectaried species: *Banisteriopsis malifolia*, *B. laevifolia* and *B. stellaris*. Thrips abundance and herbivory were higher on ant-present stems of *B. malifolia* and *B. laevifolia*, where thrips managed to escape from ants by hiding in between clusters of flower buds (thymotaxis behaviour). In *B. stellaris* the results were the opposite, as flower bud clusters did not offer hiding places, so thrips were unable to hide from ants; thus both thrips abundance and herbivory were lower on ant-present stems. Thrips herbivory had no significant effect on flower and fruit set, but samaras (V-shaped winged fruits of Malpighiaceae) attacked by thrips presented severe distortions and asymmetries. This caused damaged fruits to be dispersed closer to the mother plant, whereas uninjured fruits were dispersed further away. This study is evidence that ant–plant–herbivore systems have variable outcomes depending on the species involved, their behavior and the plant structure under consideration. This type of complex and ambiguous results stimulated alternative hypotheses for the function of EFNs.

Fig. 1 Different types of extrafloral nectaries (EFNs) and visitors: **a** *Solenopsis* sp. visting an EFN on a stem of *Passiflora sexocellata* (Passifloraceae); **b** *Ectatomma tuberculatum* over EFNs at the base of a leaf of *Qualea multiflora* (Vochysiaceae); **c** *Camponotus crassus* sucking nectar from a bracteal EFN of *Orotea spectabilis* (Ochnaceae); **d** *Camponotus planatus* feeding on EFNs on the underside of a leaf blade of *Hibiscus tiliaceus* (Malvaceae); **e** *Oxyopes macroscelides* (Oxyopidae) feeding on EFN on a leaf petiole of *Banisteriopsis mallifolia* (Malpighiaceae); **f** *Ectatomma tuberculatum* with mandibles full of nectar collected from the EFN (extra nuptial nectary or pericarpial nectary) present on developing fruits of *Tocoyena formosa* (Rubiaceae)



The main hypothesis

Until the 70s, the function of EFNs was controversial and uncertain (Bentley 1977a; Table 1), yet scientists agreed that EFNs were plant organs unrelated to pollination (Koptur 2005). Much debate occurred because some

ecologists assumed that by attracting predatory insects such as ants, EFNs acted as an indirect mechanism of plant protection against herbivores (protective hypothesis). Another point of view, the exploitation hypothesis, was that sugar secreted by leaves was nothing but by-products of plant metabolism in order to achieve equilibrium of

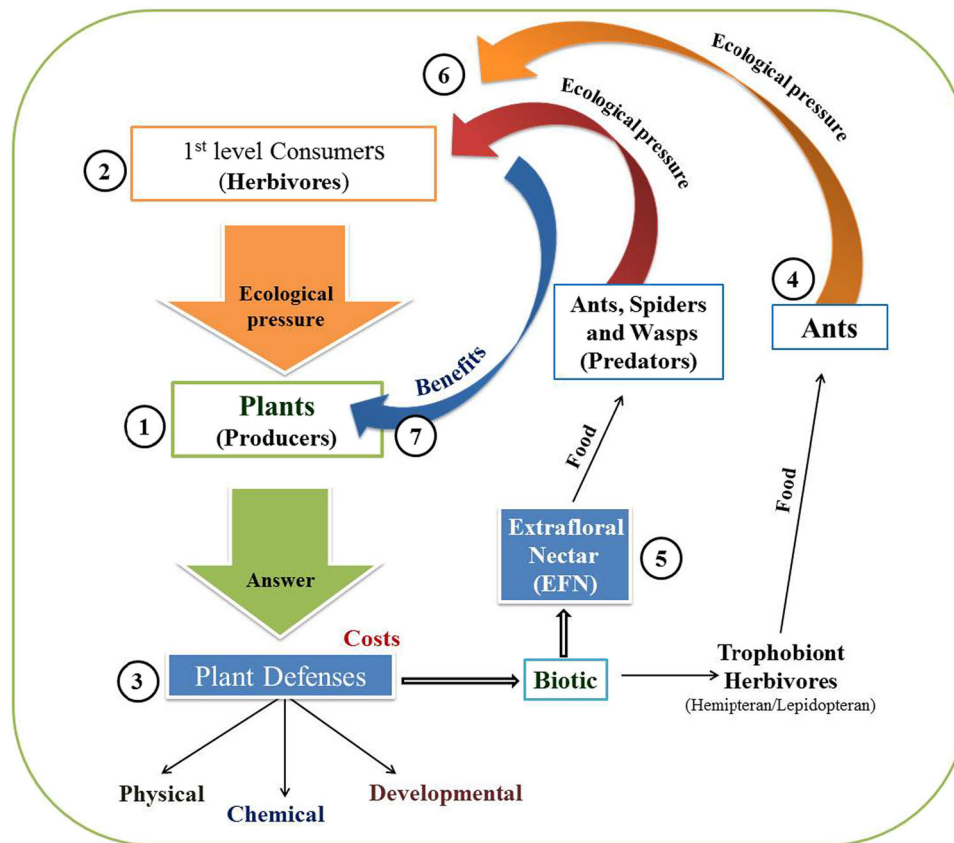


Fig. 2 The “Protective Hypothesis”. Plants (1) are the main food source to herbivores that exert strong ecological pressure (2) on them. Plants developed several distinct defenses (3) against herbivory: (3) for example, the presence of trichomes (i.e. physical), alkaloids (i.e. chemical) and resprouting in dry season (i.e. developmental). In terrestrial environments, the association with a protective animal, mainly ants (but also spiders and wasps), is an important defense (biotic). The biotic defense occurs through an indirect association between the plant and ants, but possible also via herbivores (trophobiont) that produces exudates (like honeydew) that attracts and feed

ants (4). Extrafloral nectar (EFN; mainly produced in leaves or inflorescences) is the main resource (5) plants offer to ants and other predators in exchange for protection. Nectar is an energetic food supply, but ants also need protein and will attack herbivores they find on plants (6) exerting an ecological pressure on the second trophic level that will direct benefit (7) the plants. Trophobiont herbivores (i.e. membracids) may benefit the host plant only when its damages produce fewer costs to the plant than the benefits produced by the ants (4) they associate

Table 1 Brief description of the hypotheses related to the function of extrafloral nectaries (EFNs)

Hypothesis	Brief definition
Protective	EFNs attract predators (mainly ants, but also spiders and wasps) which protect the plant against herbivores (protectionists original hypothesis)
Exploitation	Nectar is secreted as a waste product of excess carbohydrates (physiologists original hypothesis)
Flower-distraction	EFNs distract ants from flowers, where they might affect pollination, scaring away or preying upon pollinators
Ant-distracting	EFNs distract ants from trophobiont (myrmecophilous) insects (i.e. hemipterans) leaving them unattended, reducing their damage to the host plants

carbohydrates and nutrients (Bentley 1977b—A.R.E.S.), but was not supported when investigated (Baker et al. 1978; Koptur 2005). However, extrafloral nectar composition is quite different from phloem-sap (and even floral nectar, Keeler 1977), indicating that it is actively synthesized by specialized cells (Chanam et al. 2015). Nowadays, several instances confirm that EFNs are indeed important structures related to the mutualistic association with predatory/carnivorous arthropods such as ants, spiders, and wasps, that feed on nectar and in turn ward off potential herbivores (Katayama and Suzuki 2011; Koptur et al. 2015; Stefani et al. 2015). In association with ants, EFN-bearing plants experience increased performance (i.e. number of fruits; Cuautle and Rico-Gray 2003; Nascimento and Del-Claro 2010). But that are exceptions (Boecklen 1984; Rashbrook et al. 1992).

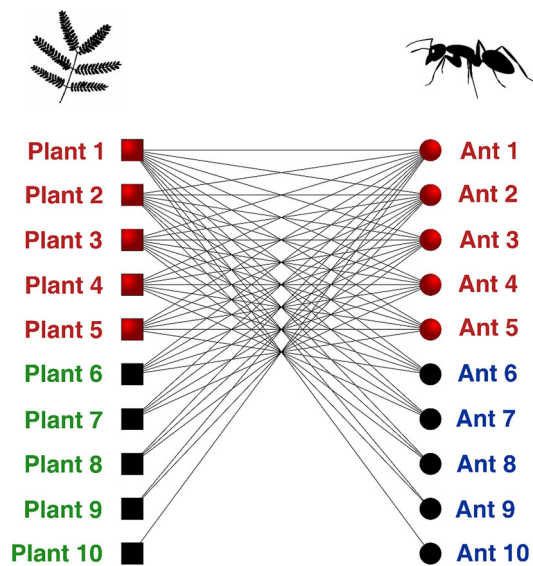


Fig. 3 Ecological network involving EFN-bearing plants (*squares*) and ants (*circles*). Each *node* represents one plant or ant species, and *lines* represent ant–plant interactions. Plants and ants with *red nodes* are those species present in the generalist core of the network, and all other species represent the periphery of the network. This network is ordered according to the nested pattern (see *text* for more information)

The protective hypothesis

In addition to predatory ants, wasps and even spiders feed on EFNs (Figs. 1, 3) and are effective plant-guards (Ruhren and Handel 1999; Cuautle and Rico-Gray 2003; Nahas et al. 2012; Alves-Silva et al. 2013; Stefani et al. 2015); parasitoids of plant herbivores also increased action in plants with EFNs (Bächtold et al. 2014). However, in general, ants are usually pointed out as the main plant-partners (Koptur 2005; Byk and Del-Claro 2011; Cuautle et al. 2015). The protective hypothesis should also consider the interactions between ants and myrmecophilous (trophobiont) insects, as these also provide ants with sugary food resources (honeydew; Del-Claro and Oliveira 1999) and in turn experience protection from natural enemies (Stadler et al. 2003; Weeks 2003; Fagundes et al. 2013), that can be extended to the host plant (Moreira and Del-Claro 2005; Oliveira and Del-Claro 2005). Similarly to ant–EFN bearing plants, ant-derived protection against natural enemies of honeydew-producing hemipterans was demonstrated to vary with factors such as tending ant species, developmental stage of hemipterans and natural enemies abundance (Del-Claro and Oliveira 2000; Stadler et al. 2003; Fagundes et al. 2013), as well as competition among hemipteran aggregations for the services provided by ants (Cushman and Addicott 1989).

The scientific support for the protective hypothesis (i.e. extrafloral nectar mediated ant–plant mutualism), as well as the importance of trophobiont exudates (i.e. hemipteran honeydew) to ants is extensive. Herbivore damage may

elicit a physiological response from plants, resulting in increased production of extrafloral nectar with consequent higher ant recruitment. In this case EFN acts as an inducible defense (Koptur 1989; Grasso et al. 2015; Heil 2015; Jones and Koptur 2015). One additional point potentiating EFN as an indirect and inducible defense is the nectar composition. After sugars, amino acids are the most abundant chemical element in nectar, however, 100 times or less concentrated than sugars. The unbalanced carbon-to-nitrogen (C/N) ratio of EFN may increase ants' desire for N-rich protein and hence stimulated their interest in prey herbivorous insects on these plants (Ness et al. 2009). Ants preferentially visit plants with larger nectaries that produce more nectar (Baker-Méio and Marquis 2012). Ant abundance at EFNs is positively related to nectar concentration, which is reflected in lower herbivory rates (Alves-Silva and Del-Claro 2013). EFN activity follows the ontogeny of plant herbivores (Tilman 1978), maximizing the chance of ants finding and deterring herbivores (Vilela et al. 2014).

Ants may feed on extrafloral nectar produced on or around flowers, and extend their protective behavior to plants' reproductive structures (Rico-Gray 1989; Del-Claro and Marquis 2015). Many arboreal and ground-dwelling ant species obtain a significant part of their demand for carbon and nitrogen from both, nectar and honeydew (Blüthgen et al. 2003; Fiedler et al. 2007; Lach et al. 2009). These resources contain most of the nutrients required for the growth of ant larvae, adult metabolism and colony survivorship (Byk and Del-Claro 2011). Therefore, nectar from floral and extrafloral nectaries, the honeydew excreted by sap-sucking herbivores (e.g. hemipterans), and sugary secretions of lepidopteran larvae indeed attract ants, intensifying its forage on vegetation (Davidson et al. 2003; Blüthgen et al. 2003, 2004). Wilder et al. (2011) showed a great positive impact of a diet rich in carbohydrates (provided by artificial EFNs) to the invasive carnivorous ant *Solenopsis invicta*. These authors proposed that the strong, positive effects of carbohydrates on colony growth and the low cost of producing this macronutrient for plants and hemipterans may have aided the evolution of food-for-protection mutualisms and help explain why these interactions are so common in ants. In addition, greater access to plant-based resources in the introduced range of *S. invicta* may help to explain the high densities achieved by this species throughout the southeastern United States.

Can extrafloral nectaries distract ants from flowers?

An interesting hypothesis brought up in the nineteenth century, but rarely tested empirically until recently (Wagner and Kay 2002), was the role of EFNs as ant distractors from

flowers with nectaries (flower-distraction hypothesis; Table 1). As sugar sources are vital to ant nutrition and colony survivorship (Lach et al. 2009; Byk and Del-Claro 2011), it is expected that ants also forage on flowers to obtain nectar (Rico-Gray 1993; Santos et al. 2014). Nonetheless, ant visitation on flowers might be detrimental to plant reproduction, especially because pollinators might be deterred, expelled, and/or preyed upon by flower-visiting ants, which also reduces the amount of nectar available to effective pollinators (Assunção et al. 2014). Small but also larger bees, like bumblebees, may avoid flowers visited by ants, reducing the pollination (Ness 2006). In a manipulative field experiment, Assunção et al. (2014) using plastic ants, showed that just the ant shape on a flower can significantly reduce the visit of pollinators, a dramatic indirect cost of a mutualism. These authors argue that multitrophic interaction studies must consider these indirect costs of mutualisms to provide a more realistic view of these systems as a whole.

In this context, some studies have examined the flower-distraction hypothesis. The extrafloral nectar quality, secretion, and timing can indeed substantially distract ants from flowers (Wagner and Kay 2002). Nonetheless, some specific floral volatile compounds are also responsible for driving away ants from flowers. Junker et al. (2007) showed that ants were repelled by flowers of nine tropical species; palatable floral nectar may be hidden from ants in unpalatable corollas (Haber et al. 1981). Detailed analyses revealed that flower chemicals, rather than nectar, were responsible to deter ants from visiting flowers (Junker and Blüthgen 2008), demonstrating that the same floral compounds might both deter ants and attract pollinators (e.g. linalool). Although there are cases of ant pollination (Gómez and Zamora 1992), they appear to be rare events (Beattie et al. 1984) and more often than not, ants inflict physical damage to plant reproductive structures (Byk and Del-Claro 2010). Therefore, plants experience eventual gains in fitness when ants are kept off flowers and foraging is concentrated on vegetative structures only (Rico-Gray 1980; Stephenson 1982; Ness 2006; Assunção et al. 2014).

Are extrafloral nectaries a defense against ant–hemipteran associations?

The interaction between sap-sucking hemipterans and ants (trophobiosis) is based on the exchange of honeydew for ant protection, and this mutualism ranges from facultative to obligatory (Way 1963; Cushman and Addicott 1989; Del-Claro 2004; Fagundes et al. 2013). Honeydew is an exudate rich in sugars and its composition is similar to extrafloral nectar, but honeydew may also contain amino acids, minerals and secondary compounds from the host

plant (Blüthgen et al. 2004). Among the honeydew components, ants show a marked preference for sucrose and melezitose (Del-Claro and Oliveira 1993; Cornelius et al. 1996). The association between ants and hemipterans provides a concrete benefit for both parties (Fig. 2). Ants obtain compounds rich in carbohydrates while tending and constantly patrolling the hemipteran's colonies (Cushman and Addicott 1989; Zvereva et al. 2010). Ants can control the amount of excreted honeydew by touching the hemipterans with its antennas, what eventually strengthens the mutualistic interaction (Del-Claro and Oliveira 1996; Stadler and Dixon 2005). In association with ants, hemipterans are protected from predators (Muller and Godfray 1999) and the colonies experience increased survivorship and fecundity (Del-Claro and Oliveira 2000; Fagundes et al. 2013).

Becerra and Venable (1989) speculated that EFNs may act to lure away tending ants from myrmecophilous hemipterans (e.g. aphids, membracids, pseudococcids and coccids), the ant-distracting hypothesis (Table 1). In short, according to Becerra and Venable (1989), “the main fitness benefit of EFN's is the reduction of homopteran damage”. Hemipterans are sap-sucking herbivores and can inject harmful substance and pathogens in the plant (Bach 1991; Delabie 2001), affecting the physiological and morphological development of the hosts (Bach 1991). For instance, hemipterans can modify the shape of plant organs (Oliveira and Isaias 2010), reduce plant growth (Dixon 1971; Del-Claro and Mound 1996; Oliveira and Del-Claro 2005), photosynthetic rates (Hawkins et al. 1987) and nitrogen compounds (Dixon 1971). The ant-distracting hypothesis could be extended to other myrmecophilous insects such as butterfly larvae (Lycaenidae and Riodinidae) that also engage in mutualistic associations with ants (Pierce et al. 2002; Bächtold et al. 2014). From the plant's point of view, associations between ants and trophobiont insects are not beneficial because trophobionts are herbivores. For instance, riodinid larvae may remove up to 38 % of leaf area of their hosts (DeVries 1989) and lycaenid larvae may feed on flowers and buds (Oliveira and Del-Claro 2005; Bächtold et al. 2013).

Experimental fieldwork conducted by scientists worldwide indicated that the ant-distracting hypothesis is highly conditional (Moya-Raygoza and Larsen 2001). Indeed, it works only in facultative ant–hemipteran associations, and/or when extrafloral nectar provides more benefits to ants, in terms of nutritional resources, than honeydew (Chanam et al. 2015). Fiala (1990) criticized this hypothesis questioning the supposed superiority of extrafloral nectar to honeydew in being highly predictable in space, time and quality (as viewed by Becerra and Venable 1989). Other studies shown that when given a choice, ants predominantly tend hemipterans over EFNs (Katayama et al. 2013) and

might even monopolize the honeydew-producing insects (Blüthgen et al. 2000; Campos and Camacho 2014; Zhang et al. 2012). In addition, laboratory observations showed that threatened myrmecophilous insects produce more nectar-like liquids and recruit more ants than that not threatened, what might maximize the mutualistic interaction (Agrawal and Fordyce 2000). Field experimental work showed that in plants lacking EFNs, but infested by hemipteran aggregations, the introduction of an alternative sugar source (artificial EFNs), increased the abundance of ants climbing onto the plant. The hemipterans, being more ant tended increased the production of droplets of honeydew and soon the two resource sources were full of ants, the distraction was ineffective (Del-Claro and Oliveira 1993; see also Zhang et al. 2012).

Perhaps the greatest criticism concerning the ant-distracting hypothesis is that myrmecophilous insects are not always detrimental for plant performance. Benefits may occur when ants extend their foraging behavior and patrol the whole plant, acting as effective plant-guards even tending hemipterans in non-extrafloral nectaried plants (Moreira and Del-Claro 2005). It occurs because tending ants may be aggressive and not only deters the natural enemies of their insect partners, but also plant's herbivores, thus rendering an effective plant protection (Bach 1991; Gaume et al. 1998). In this scenario, the positive effect of ants on plants (i.e. reduced herbivory rates) outweighs the hemipterans' (or other myrmecophile group) herbivory (Styrsky and Eubanks 2007). The evidence for plant protection incurring from ant–hemipteran associations includes: greater branch growth (Room 1972; Messina 1981), lower leaf area loss (Moreira and Del-Claro 2005), reduced damage on meristems (Del-Claro et al. 2006), higher flower and seed production (Messina 1981), reduced leaf mortality by fungi (Bach 1991; Queiroz and Oliveira 2001), removal of eggs of non-hemipteran herbivores (Bach 1991) and pruning of branches of nearby competing plants (Yumoto and Maruhashi 1999).

In general, plants supporting ant–hemipteran associations can experience neutral, positive, or negative effects (Snow and Staton 1988; Rico-Gray and Castro 1996; Del-Claro 2004). According to Rico-Gray and Oliveira (2007), three criteria determine how beneficial the trophobiosis is for the host plant: the trophobiont herbivore should not be the main herbivore; it cannot reach high population density; and tending ants must deter much of the plant herbivores. Given the high abundance and diversity of ants and myrmecophilous insects (Blüthgen et al. 2000, 2004), further detailed studies might shed light on the costs and benefits to plants in supporting ants and their distinct myrmecophilous partners (e.g. Del-Claro and Torezan-Silingardi 2009).

Optimal defense theory

Based on EFN-bearing plants phenological variation studies (e.g. Heil et al. 2000; Wäckers et al. 2001; Lange et al. 2013; Vilela et al. 2014), followed by manipulative field experiments (e.g. Nahas et al. 2012; Alves-Silva et al. 2014; Koptur et al. 2015) recent studies have pointed out that EFN is secreted in a phenotypically plastic manner according to the predictions of the Optimal Defense Theory. In general, the 'Optimal Defense Theory (ODT)' predicts that plant investment is directly proportional to the tissue value and the likelihood of it being successfully damaged by herbivores (McKey 1979; Rhoades 1979). For EFN-bearing plants, ODT also holds that plants should secrete more nectar on the most valuable organs (e.g. youngest leaves) and in periods when herbivore pressure is higher (Falcão et al. 2014; Calixto et al. 2015; Del-Claro and Marquis 2015). Because nectar secretion is directly related to protection of ants against herbivores (Rico-Gray and Oliveira 2007), different factors may influence the phenotypic plasticity of a plant species to optimize its trade-off between nectar secretion and defensive benefits (Holland et al. 2009; Vilela et al. 2014; Heil 2015). Indeed, EFN is one of several plant defenses against herbivores that may be temporally adjusted. Distinct plant defenses can be physiologically compatible or the pressure and selection exerted by herbivores on distinct plants can direct them to different defenses, one at time (Agrawal and Fishbein 2006; Zhang et al. 2015). In a recent study in the tropics, Calixto et al. (2015) determined that three defenses (trichomes, EFNs and leaf toughness) vary in effectiveness during leaf development in a same plant species. The number of trichomes was higher during initial leaf development, toughness at the end, and EFNs were actives during the middle period. Their results indicated that this tree species synchronizes its foliar defenses in order to optimize performance in anti-herbivory protection over time. Additionally, due to the fact that EFNs are most actives on young leaves and reproductive plant parts (Holland et al. 2009; Rosumek et al. 2009; Del-Claro et al. 2013b), these authors suggest that EFN act mainly to attract predators as an indirect defense (see also Heil 2015; Zhang et al. 2015).

Plant phenology, herbivore synchronization, and ants

The pressure that herbivores exert over plant development and fitness leads plants to develop numerous defensive strategies (Fig. 2). While some defenses are constitutive, others like EFN are induced only upon the perception of attack to allow for optimal resource allocation (Karban and

Baldwin 1997; Campbell and Kessler 2013). Increased EFN secretion is commonly induced after wounding, likely owing to a jasmonic acid-induced cell wall invertase, and is limited by phloem sucrose availability (Heil et al. 2001). Nevertheless, one effective plant trait to avoid herbivory is resprouting or blooming during a season when the main herbivores are less common (Coley and Barone 1996). From a consumer-resource perspective, sequential flowering may represent a plant defensive strategy against floral herbivores (Marquis and Lill 2010; Vilela et al. 2014). Ant–plant–herbivore interactions occur within multitrophic systems whose outcomes are strongly influenced by plant phenology (Lange et al. 2013). Studies comparing conditional outcomes in ant–plant–herbivore interactions mediated by temporal variation in host-plant phenology are of great relevance to the ecology of interactions and the conservation of natural communities. However, such studies are recent and rare (Rosumek et al. 2009; Lange and Del-Claro 2014; Calixto et al. 2015; Zhang et al. 2015). For example, the Brazilian Cerrado savanna has a community of Malpighiaceae shrubs that possess EFNs which are effectively tended by protective ants (Torezan-Silingardi 2011; Alves-Silva et al. 2014; Ferreira and Torezan-Silingardi 2013). Vilela et al. (2014) hypothesized that the sequential flowering of these related Malpighiaceae plants may result in a shared herbivore guild over time that may be quite harmful to plant species, making the association with ants critical to the plants reproductive success. Indeed, authors confirmed the hypothesis. The shrubs studied bloom in succession, producing floral rewards throughout the year, generating the conditions needed to maintain a sustainable population of pollinators and other floral visitors (e.g. Gentry 1974; Newstrom et al. 1994; Sigrist and Sazima 2004; Costa et al. 2006). Vilela et al. (2014) showed that the sequential resprouting and flowering of these four distinct EFN-bearing plants, studied in a same location, also provided an uninterrupted food supply to a diverse herbivore guild, including EFN to ants. In Malpighiaceae, immature structures (e.g., young leaves, buds and flowers) generally have low structural resistance to physical damage, making the shoots and inflorescences especially attractive to chewing and sucking insects (Del-Claro et al. 1997; Torezan-Silingardi 2011). The shared herbivore guild may be quite harmful to these members of Malpighiaceae, making the association with ants decisive to plant optimal development. Thus, the sequential flowering of species studied by Vilela et al. (2014) favored the use of these plants by a similar herbivore guild over time. Herbivores moved from plant species to plant species following the sequential resprouting and flowering (resource offer), and ants did the same, following EFN sequential production among plants. The interaction with ants were important to plants to reduce the abundance of sharing herbivores and foliar herbivory.

The strength of positive effects on reproductive structures was affected by the variation in the morphological and behavioral characteristics of certain herbivore groups and ants associated with particular host plants. Thus, in this example the association with ants was critical to the optimal development of a group of plant species that present sequential flowering and association with EFN visiting ants.

Phenological synchronization between herbivores and their host plants frequently determines the quantity and quality of food resources and abundance of herbivores, directly impacting populations and communities (Kerslake and Hartley 1997; Yukawa 2000). Many plant species have been exhibiting phenological shifts in the timing of their life-history events which can affect the requirements for effective biotic defense by ants according to variations in distribution and abundance of herbivores (Amsellem and McKey 2006). Therefore, shifts in plant phenology and disruption of interactions between species are able to affect ant–plant mutualisms, influencing their strength, duration, and final outcomes (Memmott et al. 2007; Both et al. 2009; Singer and Parmesan 2010; Yang and Rudolf 2010). Therewith, the accumulation of phenological data and its influence on associated species will be necessary to assess the effects of global warming on the synchronization of herbivores with host-plant phenology (e.g. Yukawa 2000). This can be essential not only to the preservation of nature in a nearby future but also to maintain a good productivity in agricultural systems. Unfortunately, few entomologists record detailed phenological data on host plants. Such data will give us a better understanding of the interactions between ants, plants, and their herbivores influenced by the plants phenological development within dynamic and complex multitrophic networks (e.g., Dáttilo et al. 2015).

Considering that ant–plant interactions are dynamic and exhibit temporal variation in their structure (Vilela et al. 2014). This variation can influence the outcomes of mutualism, interfering within the effectiveness of ants as biotic control agents of plants against herbivory. This thought highlights the importance of considering the effects of variation in species composition, as well as their characteristics (i.e. natural history, morphology and behavior) in evolutionary ecology, which attempts to understand the patterns behind the topological features and functional structure of mutualistic networks (Lange and Del-Claro 2014).

Ant–plant interactions in a network perspective: the graph theory

Recent studies have used tools derived from graph theory to investigate the organization of ecological interactions in different ecosystems around the world. Metrics such as

connectance, nestedness, specialization, asymmetry, modularity, and species degree, among others (see Bascompte and Jordano 2013) enable conclusions to be drawn about structure, specialization, stability and robustness of interactions involving two or more groups of organisms. These analyses are useful descriptors of ecological systems that can show the composition of the interactions among multiple and complex elements of a system (Bascompte 2009), forming an essential ingredient in studies of natural communities (Hagen et al. 2012).

Within a natural environment different ant and EFN-plant species can interact with each other, generating complex ecological networks of interactions. Using a network approach several studies have described the structure of interactions between ants and plants with EFNs (Guimarães et al. 2006, 2007; Díaz-Castelazo et al. 2010; Sugiura 2010; Dáttilo et al. 2013a, 2014b; Lange and Del-Claro 2014). A nonrandom pattern, nestedness, is often found in these ant–plant networks, predicting that within an ant–plant interaction network there is a central core of highly interacting species with many interactions among themselves. Peripheral species with few interactions interact with a proper subset of the central core of generalists with the most interactions (Fig. 3). Once this central core is virtually connected with all species in an environment, these species have the capacity to influence the ecological and evolutionary dynamics of the whole system.

Several factors have been proposed to explain the origin and maintenance of structural patterns in ant–plant networks including both abiotic and biotic factors, such as temperature and precipitation (Rico-Gray et al. 2012), soil and vegetation features (Dáttilo et al. 2013b), body size of ant species (Chamberlain and Holland 2009), plant phenology (Lange et al. 2013) and ant dominance hierarchy (Dáttilo et al. 2014b). All these factors influence somehow the structure of ant–plant networks. However, the nested pattern is present in all cases. This finding indicates that independent of the local and landscape environmental factors, the nonrandom pattern of these interacting assemblages does not change, and therefore, this cohesive structure appears to be the key for biodiversity and community maintenance (Díaz-Castelazo et al. 2013). Additionally, other studies show that the central core of highly interacting ant species is stable over long time periods (Lange et al. 2013) and spatial scales (Dáttilo et al. 2013a), even after the disturbances generated by tropical hurricanes (Sánchez-Galván et al. 2012). So, why is this central core of ant species so stable? Perhaps because the ant species found in the generalist core are competitively superior, showing massive recruitment and resource domination, compared with peripheral species with fewer interactions (Dáttilo et al. 2014a). A possible biological consequence of the generalist core formed by competitively superior species is that most plant species

found within ant–plant networks could be better protected against herbivory by these dominant ant species (Del-Claro and Marquis 2015), since the number of ants on the host plant is associated with effectiveness in defense against herbivores (Lange and Del-Claro 2014).

The variation in outcome of mutualism between ants and EFN-bearing plants is widely recognized (see Rico-Gray and Oliveira 2007; Rosumek et al. 2009). In ecological networks, knowing the outcomes of interactions among pairwise associates is imperative to draw valid conclusions about the functionality of these networks. In this sense, a recent study conducted by Lange and Del-Claro (2014) evaluated the ant–EFNs bearing plants interaction using two tools: network analysis and experimental manipulation. This study showed that the general structure of the network was maintained over time, but internal changes (species degree, connectance, and ant abundance) influenced the protection effectiveness of plants by ants. This study showed that ant–plant interaction dynamics affected both the network and the outcomes of the mutualism.

Despite the recent increase of knowledge about ant–plant networks, ants also interact with other system elements, such as trophobiont herbivores and lepidopteran larvae (e.g. Bächtold et al. 2013). It is still a considerable challenge and remains an open question about the structure of interaction networks involving plants, trophobiont herbivores, and ants within natural environments. An important future direction is to evaluate the role of each partner within these multi-trophic networks in order to understand the ecological and evolutionary dynamics of interactive communities rich in species and interactions. Are these systems results of coevolutionary process?

Can ant–EFN bearing plant interactions serve as model to test the “Geographic Mosaic Theory”?

Coevolution has a variety of definitions (e.g. Roughgarden 1979; Janzen 1980; Ricklefs 1984), and the term has on many occasions been incorrectly used or defined. Thompson (1994) defined it as the “reciprocal evolutionary change between interacting species, in which both of them exhibit specific evolutionary changes as an outcome of the interaction”. Thompson (1999, 2005) later brought one of the best and intriguing discussions to a modern comprehension of the coevolutionary process, the Geographic Mosaic Theory (GMT) of coevolution. This theory suggests that much of the dynamics of coevolution involving pairs or groups of species often occurs at a geographic scale above the level of local populations and below the level of the fixed traits of interacting species. According to Thompson (1999, 2005), it has three ecological bases: (1) species are groups of genetically differentiated populations; (2)

outcomes of interactions vary among communities and time; and (3) interacting species differ in their geographic ranges. These assumptions, if accepted, hypothesize that to shape the coevolutionary process: (1) there is a selection mosaic among populations, favoring distinct evolutionary trajectories to interactions in different populations; (2) there are coevolutionary hotspots, which are the subset of communities in which much of the coevolutionary change occurs; and (3) there is a continual population remixing of the range of coevolving traits, resulting from the selection mosaic, coevolutionary hotspots, gene flow, random genetic drift, and local extinction of populations (see also Thompson 2013). Thus, the GMT predicts that populations will differ in the traits shaped by the interactions, traits of interacting species will be well-matched in some localities and mismatched in others, and there will be few species-level coevolved traits, because few traits will be globally favored (Thompson 1994, 1997, 1999).

Despite being very interesting and clearly presented, the GMT has rarely been tested and the few published papers (Nogueira et al. 2015) suggest that ant–plant–herbivore interactions are good models to test the theory in natural conditions. Animal partners might influence plant evolution in some communities (i.e., plant evolutionary hotspots in which interactions lead to significant selection on plant traits) but not in others (i.e., plant evolutionary coldspots in which no significant selection mediated by animals occur due to different non-adaptive processes; see Thompson 2013; Nogueira et al. 2015). This observation is reinforced by a network overview, previously discussed. We pointed out that the nested pattern observed in all cases of ant–EFNs bearing plant interactions indicate that independent of the local and landscape environmental factors, and the non-random pattern of these interacting assemblages does not change. Thus, this cohesive structure appears to be the key for biodiversity and community maintenance (Díaz-Castelazo et al. 2013; Lange and Del-Claro 2014).

In ant–EFN plant interactions, from one community to others, the same plant species presents variation in internal (i.e. nutrition, phenology, nectar production and quality) and external factors (i.e. variations in meteorological and soil conditions) that direct influence the outcomes of each interaction (see Dáttilo et al. 2014b). Following these variations, and considering that animal species (ants and herbivores) vary in their dispersive capabilities, the core of associated species in each community can vary dramatically, even in the same ecosystem. If, independent of these variations the final character of each interaction is maintained, and ants continue benefitting a plant species in different communities at the same evolutionary time, the GMT will receive positive confirmation. Indeed, it will also confirm that in the evolutionary process the “actors” (related species) can be replaced by the time (i.e. extinction

and speciation), but independent of the actors the “theatrical play” (the interactions) continues.

Perspectives

Plants with EFNs are represented by a great diversity of taxa around the world; these glands evidently occur in approximately 25 % of angiosperms, comprising more than 100 families and 300 genera (Zimmermann 1932; Elias 1983). One recent study showed that EFNs are present in at least 3941 species distributed in 108 families of plants (Weber and Keeler 2013). The percent mean cover of plants with EFNs in different locations worldwide varied greatly, ranging from 0 % at some temperate sites in the USA to 80 % at tropical dry forest hillsides in Costa Rica (Koptur 1992b); tropical biomes contain more EFNs plants than temperate ones (Koptur 1992a; Oliveira and Freitas 2004; Rico-Gray and Oliveira 2007). Despite this immense diversity and distribution among almost all terrestrial landscapes, we still have much to study about interactions mediated by EFNs.

Heil (2015) calls to our attention the lack of information on the quantitative effect of EFN secretion at the ecosystem level. Additionally, this author suggests that one promising research avenue to explore is the genetic and physiological mechanisms that control EFN (and also floral nectar) secretion. Grasso et al. (2015) suggest to direct efforts to study the importance of the control exerted by plants on ant behavior in their multifaceted interactions focusing on the extrafloral nectar (EFN), as EFNs seem to be specially designed to influence and reward ants for their protective services. Indeed, in systems mediated by EFNs bearing plants involving ants, other predators and herbivores present themselves as excellent models for ecologists to test theories involving community structure, diversity, and its maintenance from an evolutionary perspective. How do the outcomes of interactions vary inside ecological networks? What determines the major part of variation in these outcomes? Could it be species identity, phenological variation over time, climatic changes, effects of geographic mosaics, or a combination of factors? These are issues to be explored.

We suggest that seasonally dry tropical forests are particularly important ecosystems in which we can direct efforts searching answers to these questions. Seasonally dry tropical forests (and arid environments in general) are ecosystems where plant phenology has a clear and strong influence of climatic seasonality (Vilela et al. 2014; Del-Claro and Marquis 2015; Dáttilo et al. 2015). In the Americas these ecosystems occur in almost all countries and embrace hundreds of recognized ant–EFNs bearing plants interactions (e.g. Rico-Gray 1993; Rico-Gray and Oliveira 2007). In North and South America we have established

research groups working in plant–animal interactions that could work in a more collaborative manner to do, for example, typical ant-exclusion experiments at a community level (e.g. Lange and Del-Claro 2014), on the same or related plant species in distant and distinct localities, simultaneously. These experiments could corroborate one of more important GMT predicts, that populations will differ in the traits shaped by the interactions, that traits of interacting species will be well-matched in some localities and mismatched in others, and there will be few species-level coevolved traits, because few traits will be globally favored (Thompson 1994, 1999). Thus, ant–EFNs bearing plants interactions are an excellent window to look inside the process and outcomes of coevolution.

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