



PROTECTION MUTUALISM: AN OVERVIEW OF ANT-PLANT INTERACTIONS MEDIATED BY EXTRAFLORAL NECTARIES

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Abstract: Ants and plants bearing extrafloral nectaries (EFNs) are among the most abundant interacting organisms in the Neotropics, being considered excellent models for studies of ecological interactions. These mutualisms have been studied for more than 150 years. The first studies on this subject addressed the indirect benefit of the presence of ants on plants, reducing the foliar herbivory in most cases. Recently, the direct and indirect benefits of these interactions for ants and for EFNs-bearing plants survivorship, growth and reproduction, have shown conditionality to spatial and temporal variations. Here, we reviewed how the topic “protection mutualism in ant-plant interactions mediated by EFNs” has been approached more recently. A great number of papers dealing with this theme have been published in the last 30 years and new perspectives have emerged in the last decade. We showed how scientific and academic areas are working to improve the knowledge on protection mutualisms considering ant-plant ecological networks and how they can shape communities. Furthermore, we discuss some aspects related with the EFNs evolutionary hypotheses, the existence of conditionalities in ant-plant protection mutualism mediated by EFNs, and we provide some perspectives to inspire new studies that will help in the understanding of these fascinating ecological interactions.

Keywords: biotic defense; ecological interactions; herbivory; myrmecophilous plants; predators.

INTRODUCTION

Insects, the most abundant organism in terrestrial ecosystems, correspond to more than 50% (about 1 million species) of the total species of living beings described so far (Grimaldi & Engel 2005, but also see May 1988, Stork 1988, Stork *et al.* 2015). They have different life histories, most of which affecting consumers of first trophic levels, but also greatly influencing the adaptive value of plants (Del-Claro & Torezan-Silingardi 2012).

Mainly first level consumers, they are also the food base for the higher trophic levels. As predators, there are thousands of insect species, feeding on innumerable other insects (see Stork 1988). Thus, this group of organisms acts both as bottom-up and top-down forces of the food webs, being essential for the maintenance of the most diverse ecosystems (Price *et al.* 2011). On the other hand, there are 350,000 vascular plant species (<http://www.theplantlist.org>), of which about 305,000 are angiosperms. Insects and plants

together correspond to most of living macroscopic organisms on Earth.

The origin of these two groups has been studied extensively and evidence indicates that their success is related to their mutual interactions (Toresan-Silingardi 2012). Although the first plants appeared in a period prior to the first insects (Misof *et al.* 2014), the largest group of extant plants, the angiosperms, arose in the Cretaceous period, when the insects were abundantly present (Labandeira & Sepkoski 1993, Grimaldi & Engel 2005, Schoonhoven *et al.* 2005). The period of greater diversification of the insects is superimposed with that of angiosperms', showing how this interaction is ancient and interrelated (Kukalová-Peck 1991, Labandeira 1998, Del-Claro 2012).

The earliest interactions between plants and insects recorded so far occurred at the beginning

of the Devonian, about 400 million years ago (Labandeira 1998, Schoonhoven *et al.* 2005, Misof *et al.* 2014). Some fossils indicate that the first interaction between these two groups was antagonistic (herbivory) (Figures 1a and 1b), in which the insects fed on plant spores or had a perforation and suction habit of other plant tissues (Labandeira & Sepkoski 1993, Labandeira 1998, Schoonhoven *et al.* 2005). Records of potentially mutually beneficial relationships between insects and plants emerged in the Permian, 290 million years ago (Labandeira 1998, Grimaldi & Engel 2005), and apparently, spores, "pre-pollen", and pollen were important components of the diets of insects (Labandeira 1998). This feeding strategy is an important precursor to the Paleozoic pollinating mutualisms (Labandeira 1997).

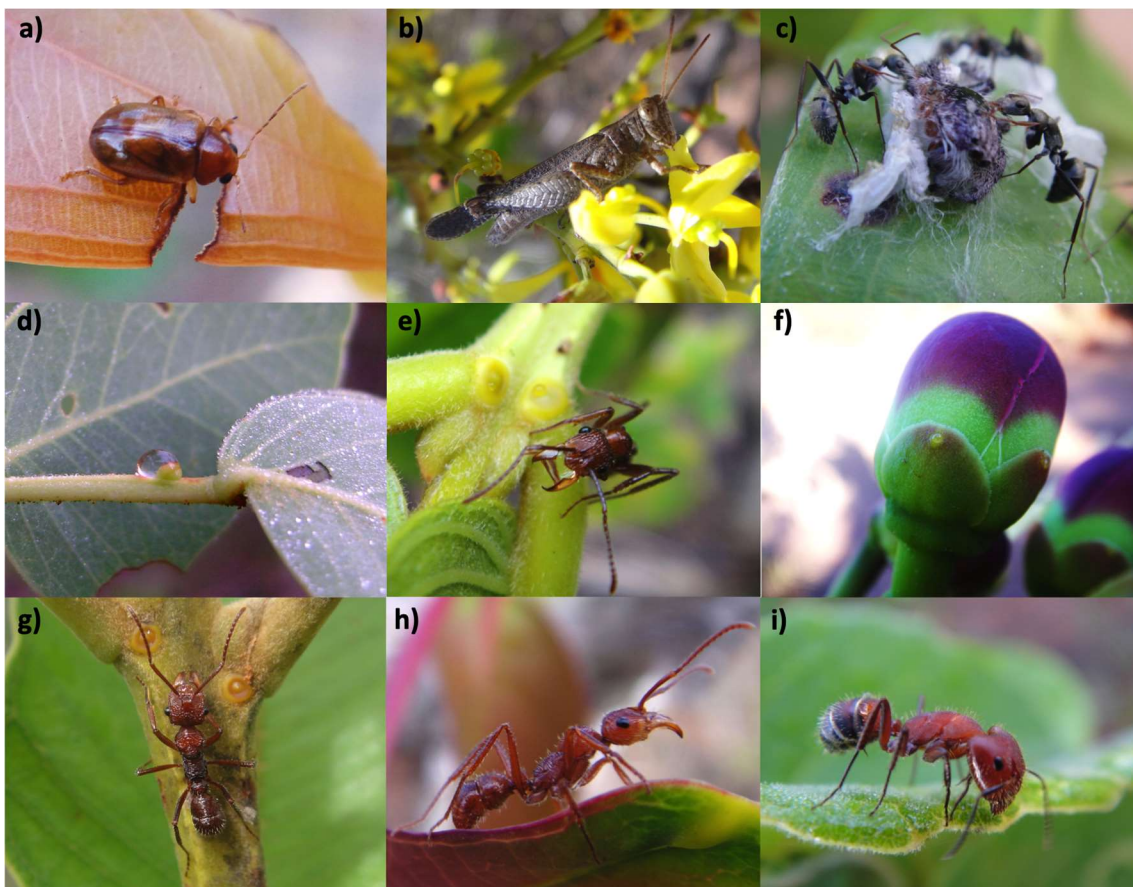


Figure 1. Insect-plant interactions: (a-b) herbivores feeding on vegetative and reproductive tissues of plants; (c) *Camponotus* sp. Mayr, 1861 (Hymenoptera, Formicidae) ants capturing and preying spider; (d) extrafloral nectar drop in *Stryphnodendron adstringens* (Fabaceae); (e) *Ectatomma tuberculatum* (Olivier, 1792) (Hymenoptera, Formicidae) with mandibles full of nectar; (f) extrafloral nectary on the sepals of *Caryocar brasiliense* (Caryocaraceae); (g-h) *E. tuberculatum* on extrafloral nectary of *Qualea multiflora* (Vochysiaceae) and *Lafoensia pacari* (Lythraceae); and (i) *Camponotus leydigii* Forel, 1886 foraging in *C. brasiliense*. Photos by Denise Lange.

Associations involving insects and plants (whether antagonistic or mutual) correspond to most of the existing ecological interactions, considered as the structural basis of natural ecosystems (Torezan-Silingardi 2012). However, it was only at the end of the 19th century that studies addressing interactions between insects and plants emerged (*e.g.*, Packard 1890, Riley 1892), becoming numerous in the last 30 years. From the 1960s until the early 1980s, several studies were carried out, proposing new mechanisms to explain the pattern of interaction observed between vascular plants and insects, strengthening the multidisciplinary character of the theme (*e.g.*, Ehrlich & Raven 1964, Berenbaum 1983). In the last two decades (Figure 2), a greater interest in the mechanisms that generate the biodiversity has appeared, focusing on complex associations between plants and insects (Thompson 1994, 2014, Del-Claro 2004), as well as studies including ecological communities (Hunter *et al.* 1988), cladistic classifications (Vane-Wright *et al.* 1991), hierarchical composition of different organization levels (Noss 1990), and complex network analysis (*e.g.*, Bascompte & Jordano 2007, Dáttilo *et al.* 2016).

Therefore, the purpose of this review is to present how the scientific and academic areas are working to provide and improve the knowledge about insect-plant relationships, particularly mutualism between ants and plants, and how these interactions can shape the ecosystem. In other words, our review aims to work specifically with ant-plant mutualism mediated by extrafloral nectaries (EFNs) and try to show the plants/ants-eye view, how this theme has been approached in recent years and to provide future perspectives, going beyond the general ant-plant interaction themes presented in other recent revisions. We hope that our review can provide new perspectives to research in this area and to inspire new studies that will help in the understanding of these fascinating ecological interactions.

MATERIAL AND METHODS

For acquisition and choice of articles in this review, we initially used Google Scholar ([https://scholar.](https://scholar.google.com)

[google.com](https://scholar.google.com)) and complemented with Web of Science ISI database set (<https://apps.webofknowledge.com/>) and JStor (<http://www.jstor.org>). To make the Figure 2, we used the total number of articles per year from Google Scholar and we refined the search with the following terms: “ant-plant mutualism” OR “ant-plant mutualisms” (Figure 2a), “ant-plant interaction” OR “ant-plant interactions” (Figure 2b), “extrafloral nectaries” OR “extrafloral nectar” OR “extrafloral nectary” (Figure 2c), and “biotic defense” OR “biotic defence” (Figure 2d). We used this methodology to reach the largest quantity of articles available with these terms. All available and relevant papers until 2017 were used. In addition, some references within articles chosen by database systems have been acquired. Our search for these topics showed a large number of works with the term “extrafloral nectaries” OR “extrafloral nectar” OR “extrafloral nectary” (Figure 2c) and a small number of published works with “ant-plant mutualism” OR “ant-plant mutualisms” (Figure 2a), “ant-plant interaction” OR “ant-plant interactions” (Figure 2b) and “biotic defense” OR “biotic defence” (Figure 2d). These data showed us a great amount of papers dealing with protection mutualism and helped us to better understand how this topic has been approached over the years considering certain characteristics.

ANT-PLANT INTERACTION

Ants are dominant insects in most terrestrial environments, with key roles in energy and nutrients flow within ecosystems. Currently, 15,933 valid ant species are known (Ant Web 2018), although it is estimated that there are about 21,800 species in the world (Agosti & Johnson 2003). In many habitats, especially in tropical regions, ants comprise most of the arthropod fauna found on vegetation (Oliveira & Freitas 2004). Several ant species have established interactions with plants using plants' surfaces as a foraging substrate to search for live (Figure 1c) or dead prey, nectar (Figures 1d and 1e), exudates from herbivorous insects or from the plants themselves, as well as sites to build their nests. As a result, ants form facultative or obligate associations with plants and

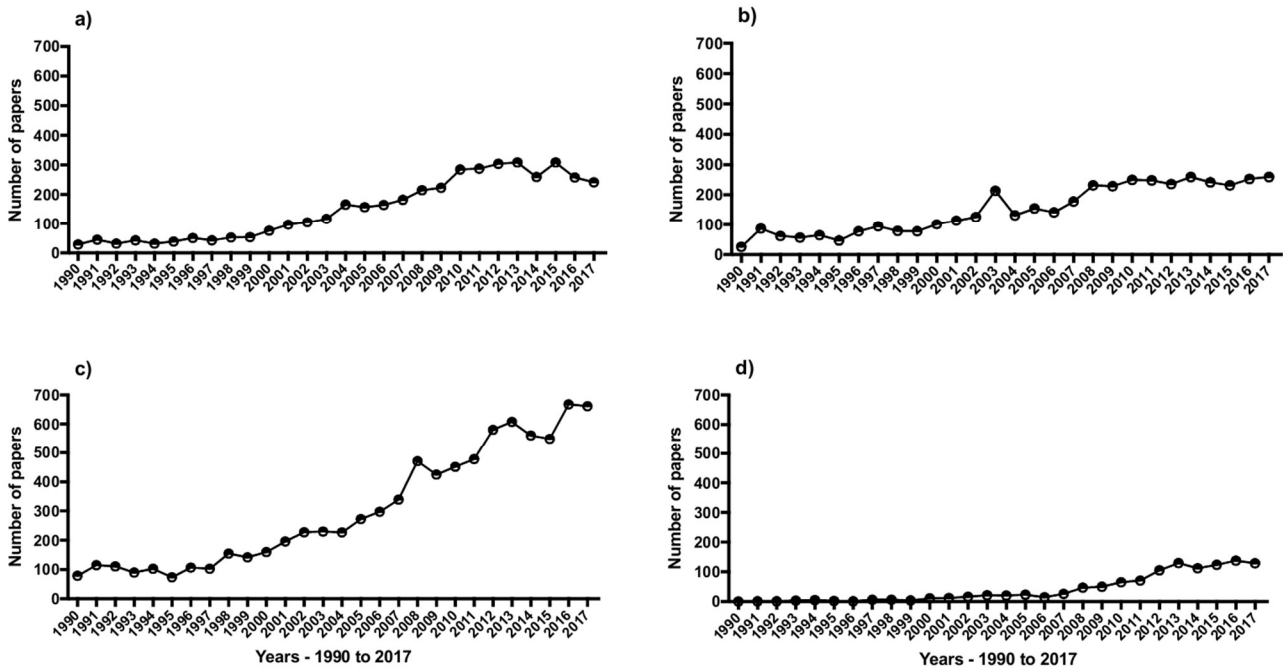


Figure 2. Number of published papers per year from 1990 to 2017 found in the Google Scholar database. The search was refined with the following words (a) “ant-plant mutualism” OR “ant-plant mutualisms”, (b) “ant-plant interaction” OR “ant-plant interactions”, (c) “extrafloral nectaries” OR “extrafloral nectar” OR “extrafloral nectary”, and (d) “biotic defense” OR “biotic defence”.

contribute to the decrease of herbivore population, mediating interactions between herbivores and plants (Del-Claro *et al.* 2016).

Some species of plants, known as myrmecophytes, have adequate and specific structures for the colonization and nesting of ant colonies (Rico-Gray & Oliveira 2007). These structures can originate from modifications of several plants parts, such as leaves, trunk, bulbs or even roots, called domatia (the plural of *domatium*, meaning ‘home’). The diversity of myrmecophyte plants and ants associated with them is quite high in several regions, with approximately 250 species of myrmecophytes in the Neotropics, distributed in 14 families (Benson 1985). The association between swollen-thorn *Acacia cornigera* (Fabaceae) and *Pseudomyrmex ferrugineus* (Pseudomyrmecinae) is the best-known example of ant-plant mutualism; in this association plants offer several different resources to ants, including domatia, extrafloral nectar, and Beltian food bodies (Janzen 1966). The case of *Tococa guianensis* Aublet (Melastomataceae) in the Brazilian Cerrado is also a typical example of this type of interaction, in which individuals of this

shrubby plant have colonies of ants in their hollow thorns (Michelangeli 2005).

There are also myrmecophilous plants (plant species associated with ants, but not specialized) (Rico-Gray & Oliveira 2007). These species can provide food through food bodies and extrafloral nectaries (EFNs) (Figures 1d-1h). Food bodies are structures rich in lipids, carbohydrates, proteins and amino acids and may be present at the base of leaf petiole, as occurs in species of the genus *Cecropia* (Urticaceae). The EFNs are secretory glands that are not involved with pollination (Koptur 1992, Del-Claro *et al.* 2016), but produce an aqueous liquid rich in sugars and several other diluted compounds, such as amino acids, lipids, phenols, alkaloids and volatile organic compounds (Baker & Baker 1983, Koptur 1994, Wäckers 2001, González-Teuber & Heil 2009). These structures are extremely variable in structure and morphology (Díaz-Castelazo *et al.* 2005, Machado *et al.* 2008, Aguirre *et al.* 2013), and can occur in practically all plant organs.

Among the resources provided by plants for insects, extrafloral nectar is the main classical example (Bentley 1977, Beattie 1985, Rico-Gray &

Oliveira 2007, Heil 2015), attracting a great diversity of predatory arthropods, such as wasps (Cautle & Rico-Gray 2003, Eubanks & Styrsky 2005, Wäckers *et al.* 2005), spiders (Ruhren & Handel 1999, Whitney 2004, Nahas *et al.* 2012), and mainly, ants (Rosumek *et al.* 2009, Marazzi *et al.* 2013, Del-Claro *et al.* 2016) (Figure 1i). The EFNs can be found in 3,941 species belonging to 108 families of vascular plants (see the world list of extrafloral nectaries <http://www.extrafloralnectaries.org>; Weber & Keeler 2013). Many examples of EFNs are found in Brazilian savannas, occurring in 8 to 31% of the plant individuals and in 15 to 26% of the tree species in these regions (Oliveira & Leitão-Filho 1987, Oliveira & Pie 1998), including the most abundant trees (Lange & Del-Claro 2014).

Protective mutualism involving ants and plants mediated by EFNs is characterized by foraging of predatory ants on plants (myrmecophilous or myrmecophytes), resulting in benefits to plants (herbivory decrease and/or fitness enhancement). In exchange, ants receive direct or indirect food from plants that increase colony growth and survivorship (Byk & Del-Claro 2011). The first study evaluating the interaction between ants and tropical plants was proposed by Belt in 1874. Subsequently, the classic work developed by Von Wettstein in 1889 with Asteraceae species, *Jurinea mollis* and *Serratula lycopifolia*, demonstrated for the first time that plants benefit with the interaction, a decrease in leaf area loss. Oliveira *et al.* (1987) were the first to present experimental evidence in EFNs-bearing plants in the Brazilian savanna (*Cerrado*). Since then, interactions involving ants and plants, especially in tropical regions, have increasingly drawn the attention of biologists to the importance of the various processes involved and the factors that govern their establishment (Del-Claro 2004, Rico-Gray & Oliveira 2007, Oliveira *et al.* 2012, Del-Claro *et al.* 2016). Recently, studies have been directed to specific questions about these interactions, looking at conditional features of systems (biotic and abiotic) that influence the outcomes.

“PLANTS-EYE” VIEW

Herbivores exert high evolutionary pressure on

plants (Marquis 2012, Thompson 2013) that responded and developed different anti-herbivore mechanisms, such as direct chemical and physical defenses (Crawley 1983, Coley & Barone 1996, Fürstenberg-Hägg *et al.* 2013, Calixto *et al.* 2015). Besides chemical and physical defenses, plants have other defensive strategies, such as biotic defense, a kind of indirect defense mainly promoted by EFNs (Beattie 1985, Rico-Gray & Oliveira 2007).

This defensive plant system is dynamic, where plants can synchronize their defenses over time to have a better performance in protection or can produce different amounts and qualities of extrafloral nectar influencing the foraging of mutualistic ants (Lange *et al.* 2017). Plants can replace defensive strategies over their phenological development, as in *Qualea multiflora* (Vochysiaceae) that presents different defenses during foliar development (trichomes, toughness and EFNs), where each defense is expressed and presents peaks of effectiveness according to leaf stage (Calixto *et al.* 2015). This study corroborates the Optimal Defense Theory (McKey 1974, 1979, Rhoades 1979), where plants seek to minimize costs of producing defenses and maximize herbivore resistance. According to this theory, plants allocate their defenses to structures according to their value (plant-related tissues) and the probability of attack. In this way, it is predicted that constitutive defenses (see next paragraph) should be used in plants parts of high value and/or probability of attack, whereas induced defenses, *e.g.*, EFNs, should be used in parts of lower value and/or probability of attack.

From another perspective, plants may exhibit defenses that are either constitutive, defenses that are always expressed, or induced, defenses that are expressed after damage or a risk of damage, or both (Zangerl & Rutledge 1996, Karban & Baldwin 1997). Some studies have shown that after herbivorous attack, plants increase the levels of biotic defenses (*e.g.*, Ness 2003, Heil & Silva-Bueno 2007, Heil 2008, Pulice & Packer 2008, Bixenmann *et al.* 2011), which may negatively affect herbivorous insects (Karbon 1993, Stout & Duffey 1996, Marquis 2012). Genetic and molecular manipulations have provided evidence of various biochemical mechanisms and signaling pathways in the induction process (*e.g.*, Baldwin & Preston

1999, Paschold *et al.* 2007, Heil & Land 2014, Duran-Flores & Heil 2016). Induced responses of plants to herbivory are analogous to immune responses of animals and aim to reduce the performance and/or preference of herbivores by changes in their chemical composition and/or the quality of their tissues (Baldwin & Schultz 1983, Karban & Myers 1989, Karban & Baldwin 1997, Agrawal 1998, Korndörfer & Del-Claro 2006). Other factors should be considered within the induction system of extrafloral nectar by herbivorous (Heil *et al.* 2000), as the induction trigger (natural or artificial damage) (*e.g.*, Heil *et al.* 2000), the stage of plant development or the region that suffered the damage (Jones & Koptur 2015, Holland *et al.* 2009) and the nature of the attacker (Carrillo *et al.* 2012).

The relationship between induced defense and biotic defense mediated by EFNs has been demonstrated in many systems. There is an increase in number or productivity of EFNs located on leaves and buds after being damaged by herbivores (Agrawal & Rutter 1998, Heil *et al.* 2000, Pulice & Packer 2008, Jones & Koptur 2015). In addition to these examples, studies have also shown the functioning of EFNs located in flowers, inflorescences and/or fruits (Rico-Gray 1989, Díaz-Castelazo *et al.* 2005, Falcão *et al.* 2014) to promote both the protection of vulnerable parts and seed dispersal. These EFNs on reproductive parts also respond to simulated herbivory, providing more examples of induced defense (Zangerl & Rutledge 1996, Wäckers & Bonifay 2004, Holland *et al.* 2009). Other works related to induced defense have shown that some plants can develop systems of damage recognition through certain substances or molecules present in insect saliva or eggs (Arimura *et al.* 2005, 2011, Carrillo *et al.* 2012), showing that this defensive strategy is complex and deserves more attention.

ANTS-EYE VIEW

For ants, plants may be a source of food and place for nesting. Several authors have shown that ants prefer to forage on plants with EFNs than in other plants (Rico-Gray & Oliveira 2007). In plants with EFNs, at times when there is more nectar production, there is also more ant species foraging

on plants, decreasing competition and increasing coexistence (Lange *et al.* 2013, Belchior *et al.* 2016). In addition, plants that produce nectar in higher quantities and richer in calories are more visited by ants (Fagundes *et al.* 2017, Lange *et al.* 2017) and this supply of nectar varies during the day (Lange *et al.* 2017). Therefore, the nectar produced in these structures is a key resource for the ant-plant interaction.

Byk & Del-Claro (2011) experimentally showed that extrafloral nectar consumption from *Chamaecrista desvauxii* (Caesalpiniaceae) has a positive effect on the colonies of *Cephalotes pusillus* (Myrmicinae), regarding the number of individuals per colony, body weight and number of eggs. On the other hand, in addition to extrafloral nectar, ants can feed on various other types of resource, for example, Hemiptera exudates (“honeydew”) and sources rich in nitrogen, such as captured or dead arthropods and carrion (Hölldobler & Wilson 1990, Blüthgen & Feldhaar 2010, Cerdá & Dejean 2011). According to Davidson (1997), the main sources of nitrogen for arboreal ants are animals, both prey and carrion. Thus, ants find in EFNs-bearing plants a perfect place to supplement their diets with nitrogen, sugars, amino acids, lipids, and water (Ness *et al.* 2009).

Several ant species forage on EFNs-bearing plants around the world, mainly in the tropics. Of the 17 Formicidae subfamilies, five have common representatives foraging on plants: Pseudomyrmecinae, Dolichoderinae, Ponerinae, Formicinae and Myrmicinae. In addition to the species diversity, there is behavioral diversity, ranging from opportunistic to extremely aggressive species, and from generalists, who nest on the ground and occasionally forage on plants, to specialists, who nest and feed exclusively on EFNs (Hölldobler & Wilson 1990, Silvestre *et al.* 2003). Many species can forage on the same plant, coexisting, depending on the aggressiveness of each species, while in some cases, the aggressiveness of ant species inhibits the presence of other species (Davidson *et al.* 1989, Heinze *et al.* 1994).

Niche partitioning is also present in ant communities associated with EFNs. Some forage exclusively at night, others only during the day, patrolling extrafloral nectar (Dáttilo *et al.* 2014, Lange *et al.* 2017). All these aspects demonstrate

that ants that forage on plants do not have this resource always available and free from competitors. They must deal with biotic and abiotic factors to obtain the resource.

CONTEXT-DEPENDENCE IN ANT-PLANT INTERACTION

Many studies have shown the effects that ants have on EFN-bearing plants acting as biotic defenses, mainly related to herbivory and the reproductive success of plants (Rico-Gray & Oliveira 2007, Rosumek *et al.* 2009, Zhang *et al.* 2015). However, this interaction does not always represent a benefit to the plant (*e.g.*, O'Dowd & Catchpole 1983, Rashbrook *et al.* 1992, Rosumek *et al.* 2009, Byk & Del-Claro 2010, Lange & Del-Claro 2014), revealing the existence of conditionalities (Bronstein 1994). The variation in protective mutualism involving ants and plants is dependent on associated ant species (Floren *et al.* 2002, Del-Claro & Marquis 2015, Anjos *et al.* 2017), ant density (O'Dowd & Catchpole 1983, Rashbrook *et al.* 1992), ant colony nutritional demand (Wilder & Eubanks 2010, Pohl *et al.* 2016), ant size (Rico-Gray & Thien 1989), herbivore defense strategy (Floren *et al.* 2002, Alves-Silva & Del-Claro 2014, Alves-Silva *et al.* 2015), associated plant species (Blüthgen *et al.* 2000, Lange & Del-Claro 2014, Koptur *et al.* 2015), and plant phenological stage (Lange *et al.* 2013, Vilela *et al.* 2014, Belchior *et al.* 2016). In addition, ants can scare away pollinators of EFN-bearing plants, or prey on them, decreasing the fruit set (Holland *et al.* 2011, Assunção *et al.* 2014). In this context, may plants produce more extrafloral nectar to distract ants from flowers (Chamberlain & Holland 2008; see next section "Evolutionary aspects")? Ants can also act as vectors of endophytic fungi, which diminish the photosynthetic plant leaf area, interfering with their fitness (Pires & Del-Claro 2014). These conditionalities point out to the complexity of ant-plant interactions. In addition, Baker-Meio & Marquis (2011) showed that the outcomes from interactions of co-occurring varieties of *Chamaecrista desvauxii* with ants are context dependent within and among taxa. They observed that the effectiveness of ants against herbivory depends on the variety of *C. desvauxii* considered

and on the presence of seed predators, as well as the EFNs size and the amount of nectar produced.

Bronstein (1998) argues that the presence of another trophic level, such as herbivores, alters the mutualistic interactions between plants and ants due to variations in behavior and feeding modes among different species of herbivores, in addition to variations in herbivore abundance and richness over time. Furthermore, morphological and behavioral characteristics of ants often have an impact on the density, spatial distribution and diversity of herbivorous assemblages (*e.g.*, Oliveira & Del-Claro 2005). On the other hand, the ant community structure has been studied in a variety of habitats and it is clear that ant assemblages are dynamic, with spatial and temporal variation that characterizes these communities (see review in Rico-Gray & Oliveira 2007). Thus, plants with EFNs usually associate with guilds of omnivorous ant species that change in composition and abundance over time and space, which may compromise the benefit magnitude received by the mutual partner (*e.g.*, Blüthgen *et al.* 2000).

Although biotic factors are often presented as the main reasons for spatiotemporal variations within ant-plant systems (Marquis & Braker 1994, Romero & Vasconcellos-Neto 2004), abiotic factors have relevant impact as determinants of the outcomes of mutualistic interactions (Bronstein 1994, 1998, Kersch & Fonseca 2005, Vilela *et al.* 2014). Some studies that recorded spatiotemporal variations in the ant-plant mutualistic interactions attributed the observed patterns to the hypothesis of climatic conditions variation (Rico-Gray *et al.* 2012, Dáttilo *et al.* 2013, Leal & Peixoto 2016) and environmental disturbances, *e.g.*, fire (Del-Claro & Marquis 2015, Fagundes *et al.* 2015). Leal & Peixoto (2016) demonstrated that the ant effect on performance of EFN plants increased as mean annual precipitation decreased, suggesting that ants provide greater benefits to plants in these environments to compensate the higher costs for production and maintenance of the EFNs. They also found that the frequency of dominant ants on EFNs-bearing plants increased in drier areas. Del-Claro & Marquis (2015) found that fire modified the impact of ants on the leaf area consumed by insect herbivores, but the ant-plant protective mutualism remained efficient after the fire. These results confirm that abiotic factors may increase

service costs and/or benefits of rewards offered by mutual partners.

Despite the existence of conditionalities in ant-plant mutualism mediated by ENFs, Chamberlain & Holland (2009) in their meta-analysis showed that ant effects on plants are not generally context dependent, but, instead, are routinely positive and rarely neutral. These data suggest that the costs and benefits of a mutualism may change, as well as its result. However, the benefit will occur most of the time proving that this interaction has a mutualistic character. On the other hand, when mutual species are inserted within a network of multitrophic interactions, it becomes hard to predict the ecological dynamics of the interaction (McCann 2000). Then, long-term studies can help us understand the maintenance and diversity of multitrophic systems.

EVOLUTIONARY ASPECTS

In spite of the amplitude and general occurrence of interactions, especially the factors related to plant resistance through ants attracted by ENFs, studies testing the proposed evolutionary theories are abundant in some aspects and rare in others. These evolutionary hypotheses become even more complex when we evaluate the evolutionary aspects of ant-plant interactions together with other trophic levels, such as herbivores (Ohgushi 2016), essential in the evolutionary direction of ant-plant with ENFs protection mutualism. According to Bittleston *et al.* (2016), morphology and/or structures help and can demonstrate a particular type of ant-plant interaction, and if a new plant species, with certain attractive structures such as domatia, food bodies and ENFs, was found, it is very likely that it would be an ancient and long-term association with ants, since all these structures are related to the attraction of predators, such as ants. However, despite the understanding that species evolution and interactions are intrinsically linked, it remains challenging to study ecological and evolutionary aspects at the same time over longer time scales (Weber *et al.* 2017).

The fact that ant-plant interactions may have conditionalities, and ENFs may not always be linked to plant protection, has led to questions

about possible other functions. Some alternative hypotheses related to the evolution and the functioning of ENFs have been raised (Marazzi *et al.* 2013, Heil 2015, Del-Claro *et al.* 2016): (i) ENFs may act as a distraction, preventing the foraging of ants on flowers (see Bécerra & Venable 1991), which may interfere with the plant's reproductive success, (ii) ENFs can be a food source, which induces the establishment of ant nests closer to plants and, consequently, can improve the plant nutrition (Wagner & Nicklen 2010), (iii) plants secrete extrafloral nectar to eliminate excess sugar (Bentley 1977, Baker *et al.* 1978, Koptur 2005), (iv) ENFs have a defensive/protective function (see review in Heil 2015, Del-Claro *et al.* 2016), and (v) ENFs can distract tending ants from myrmecophilous hemipterans (Bécerra & Venable 1989).

CONCLUSION

In our current perspective, biodiversity should be viewed and evaluated in a way that seeks to understand the ecological interactions, including aspects such as: (i) life history, biology, and behavior of related species (Oliveira & Del-Claro 2005, Del-Claro *et al.* 2013), (ii) observations of conditionalities within each interaction (*e.g.*, Byk & Del-Claro 2010, Holland *et al.* 2011, Assunção *et al.* 2014), (iii) sophisticated tools for analyzing certain parameters, such as those derived from graph theory, which can provide better conclusions of these interactions (Bascompte & Jordano 2013, Lange *et al.* 2013, Dáttilo *et al.* 2015), (iv) studies about several ecosystem levels (Lange *et al.* 2017), and (v) research related to the genetics and physiology of defense-related traits (Heil 2015). We suggest that it is also important to take into account the anthropic effects and climate change, evaluating how these factors are influencing ant-plant interactions (Leal & Peixoto 2016, Vilela *et al.* 2017). It is important to concentrate studies in places with strong influence of climatic seasonality, as in the Americas (Rico-Gray & Oliveira 2007), or even to evaluate direct impacts on interactions and ecosystem, such as fire events in very dry and/or propitious areas (Del-Claro & Marquis 2015, Fagundes *et al.* 2015). From these perspectives, biodiversity should be re-named "Interaction Biodiversity" (*sensu* Thompson 1996, 2005).

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