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Biotic Defenses Against Herbivory

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Learning Objectives

After completing this chapter, you should have an understanding of the following:

1. The terms biotic defense and indirect defense.
2. Several examples of biotic defense relationships between different organisms.
3. The potential benefits and costs to each organism involved in a biotic defense relationship.
4. The variation in generality and specificity of biotic defense partnerships.

5.1 Introduction

Herbivory is a strong negative pressure known to shape the diversity and distribution of numerous plant species (Marquis and Braker 1994). As an evolutionary response to the negative effects of herbivory, plants have developed a myriad of defensive strategies that can be further categorized as direct or indirect defenses (Price et al. 1980; Dicke and Sabelis 1988). Direct defenses are traits that reduce herbivory by acting directly upon herbivores without any additional mediators; this includes the production and presence of chemical compounds that function as repellents and toxins, and physical structures that harm or deter herbivores, such as thorns and spines. These defenses are mostly constitutive and are continuously expressed in plants across ontogeny (Boege and Marquis 2005). The other category, indirect defenses, are traits that do not directly affect herbivores, but rather enhance plant fitness by altering the behavior or presence of natural enemies of herbivores (Pearse et al. 2020), and are considered inducible defenses (Zangerl and Rutledge 1996). Although indirect defenses can still involve plant chemistry (in the form of volatile attractants or nutrient-rich extrafloral nectar and food bodies), their proximal mechanism is the predators they attract, which act as biotic agents of defense, or “biotic defenses”. While many studies address the impacts of direct defenses in plants, biotic defenses are still overlooked, especially if the definition of biotic defense is expanded to include interactions beyond classic plant-herbivore-predator relationships (e.g., Heil 2014).

5.1.1 A Classic Example of Biotic Defense: Myrmecophily and Extrafloral Nectar

Perhaps the most classic example of biotic defense involves the interaction between plants bearing extrafloral nectaries (EFNs) and ants, spiders, and other predators (▣ Figs. 5.1 and 5.2). EFNs are nectar-secreting structures not associated with the pollination of mature flowers, but rather are found on other above-ground plant parts, such as leaves, stems, stipules, and flower buds (e.g., Machado et al. 2008; Schoereder et al. 2010; Marazzi et al. 2013). EFNs produce liquid comprising carbohydrate-rich compounds but also small amounts of other organic compounds such as amino acids and lipids (González-Teuber and Heil 2009). Plants with EFNs are characterized as myrmecophilous (“ant-loving”) organisms due to their ability

Fig. 5.1 Myrmecophilous ants feeding on extrafloral nectaries. **a** *Camponotus crassus* ant using nectar from an extrafloral nectary (EFN) of a bract on *Ouratea spectabilis* (Ochnaceae); **b** *Ectatomma tuberculatum* with an extrafloral nectar droplet in its mandibles from a *Qualea multiflora* (Vochysiaceae) petiolar EFN (D. Lange picture)

to attract and interact with ants. Numerous studies have demonstrated that EFNs may specifically attract aggressive omnivorous ants (Koptur 1994; Blüthgen et al. 2004; Bixenmann et al. 2011), which can then increase plant performance by preying upon and decreasing the damage caused by herbivores (Cuautle et al. 2005; Baker-Méio and Marquis 2012). A meta-analysis conducted by Rosumek et al. (2009) concluded that plant fitness decreased by almost 60% when ants were excluded from plants. Furthermore, Trager et al. (2010) demonstrated that the presence of ants enhanced plant reproductive output by 49% and decreased herbivory by 62%. From this perspective, recent studies strongly suggest that extrafloral nectaries may act as inducible defenses decreasing costs and maximizing benefits against herbivores (Calixto et al. 2020).

Relationships between plants and ants are widespread and diverse (Rico-Gray and Oliveira 2007; Del-Claro et al. 2016; Calixto et al. 2018), with EFNs occurring in at least 100 plant families around the world (Weber and Keeler 2013). Consequently, these relationships are usually generalized and highly facultative (Rosumek et al. 2009; Chamberlain and Holland 2009; Del-Claro et al. 2018; Calixto et al. 2018). Nectaries of different shapes and locations, secreting nectar at different times, composed of different micronutrients, evolved in parallel in several plant species, including Pteridophytes, Gymnosperms, and Angiosperms (Marazzi et al. 2013; Weber and Keeler 2013). This wide diversity of EFNs is matched with an equally diverse amount of interactions with various ant species (Buckley 1982; Rico-Gray and Oliveira 2007; Dáttilo et al. 2014; Del-Claro et al. 2018; Nelsen et al. 2018). As more studies are published, more species are included in the list of plant-protecting ants (Rico-Gray and Oliveira 2007; Trager et al. 2010; Calixto et al. 2018). Additionally, in tropical environments such as the Brazilian Cerrado, a single plant species can provide nectar for dozens of ants

Fig. 5.2 Spiders on plants. **a** *Zuniga magna* (Salticidae) is a spider that mimics ants to easily access extrafloral nectaries and feed on them unnoticed; **b** *Peucetia flava* (Oxyopidae) preying upon a bug nymph (Hemiptera) that was trapped on the glandular trichomes of a *Chamaecrista* shrub; **c** a crab spider (Thomisidae) preying upon a bee (*Trigona* sp.) pollinator in an EFN-bearing Leguminosae; **d** *Tmarus* sp. (Thomisidae) spider preying upon a *Pseudomyrmex* ant on an EFN-bearing plant

(Lange and Del-Claro 2014; Costa et al. 2016; Sendoya et al. 2016; Fagundes et al. 2018) and spider species (Nahas et al. 2017).

Although EFN-mediated defensive interactions are widespread in land environments, the mechanisms and effects of biotic defense can easily become complicated and conditional on different biotic and abiotic factors (Del-Claro et al. 2016, 2018). For one, EFNs may not be the only resource incentivizing ants to spend time on plants. Shelter in the form of domatia (Letourneau 1983; Fiala and Maschwitz 1991) and other food sources such as food bodies and fruit (Fiala and Maschwitz 1992; Dutra et al. 2006) can also serve as rewards to ants that then patrol and protect the plant from herbivores. For example, although some *Macaranga* plants possess many EFNs that incentivize ant protectors, myrmecophytic (ant-inhabited)

Macaranga plants with hollow stems and food bodies have reduced or even absent EFNs (Fiala and Maschwitz 1991). In other shelter-based ant-plant systems, hollow stems or petioles provide shelter and nesting space for ant defenders, and the plants might provide food bodies instead of EFNs as an additional resource for the ants (Yu and Davidson 1997).

As Pearse et al. (2020) have argued, indirect defense can apply to relationships beyond the plant-herbivore-predator canon. Indeed, ant-plant relationships do not always involve trophic defense. Ants can also protect their host plants from competitors, removing vines (Schupp 1986; Fiala et al. 1989) and other nearby or encroaching vegetation (Frederickson et al. 2005) that might otherwise pose a competitive threat. However, biotic defenses do not always yield complete or even net benefits to the partner being defended. In many cases, the defender species can determine the effectiveness of defense (Young et al. 1996; Fagundes et al. 2017). In other cases, defenders might also deter other plant mutualists, such as pollinators (Assunção et al. 2014), and species-specific combinations of defense efficacy and pollinator deterrence can lead to variability in the net costs and benefits of biotic defense (Ohm and Miller 2014).

In the rest of this chapter, we will call attention to the diversity of biotic defenses beyond the classic ant-plant mutualism mediated by extrafloral nectaries, a diversity in large part due to the lack of specificity in the mechanisms that induce biotic defense. Ants are not the only predators attracted to EFNs and other plant rewards, but rather other insects and even spiders can also use these resources and then act as biotic defenders (▣ Fig. 5.2). Investigating these non-ant defenders can lead to a broader understanding of the partner generality of biotic defense; we will use spiders as an example of this. Additionally, plants are not the only organisms that secrete sugary solutions in return for ant defense—we will use myrmecophilous hemipterans and lepidopterans as examples of how an animal's biotic defense can compete for, directly counteract, or otherwise interact with a plant's biotic defense. Throughout these examples, we will point out commonalities in how these defense interactions are selected for and maintained. Considering these diverse types of biotic defense relationships can lead to a deeper understanding of the various costs and benefits of biotic defense, and ultimately help us predict and understand the evolutionary trajectories of these relationships and their contributions to overall biodiversity.

5.2 Spiders as Plant Bodyguards and the Role of Extrafloral Nectaries

Although the interactions between EFN-bearing plants and ants are relatively well-studied, interactions involving other species of nectar-consuming animals (Heil 2015) such as wasps (Cuautle and Rico-Gray 2003), beetles (Agarwal and Rastogi 2010), flies (Agarwal and Rastogi 2010), bees (Thorp and Sugden 1990), neuropterans (Limburg and Rosenheim 2001), and spiders (Taylor and Foster 1996; Nahas et al. 2017) are underexplored. The latter is particularly surprising, considering that spiders are among the most common arthropods inhabiting vegetation (Wise 1993; Foelix 2011) and have been observed feeding upon EFNs (Ruhren and Handel 1999; Cross and Jackson 2009; Nahas et al. 2017, ◘ Fig. 5.2a). Spiders inhabiting vegetation have adaptations that facilitate their relationship with host plants. These are generally sensory adaptations, which allow spiders to find and discern specific plant species through visual, olfactory, and tactile stimuli (Vasconcellos-Neto et al. 2017). Further evidence that spiders regularly consume EFN can be demonstrated by using cold-anthrone tests for the presence and concentration of fructose in the bodies of spiders found on EFN-bearing plants (Nyffeler et al. 2016). In the Brazilian Cerrado, such methods have provided evidence that 39 species across seven spider families consume EFN from at least eight different host plant species (Nahas et al. 2017). Thus, EFN-feeding behavior is common in spiders, and sugar-rich solutions like extrafloral nectar can be a beneficial energy source for spiders (e.g., Taylor and Bradley 2009; Nahas et al. 2012; Patt et al. 2012), supplementing the animal-based aspects of their diet.

Similar to ants, spiders are generalist predators that can reduce the number of herbivores on a plant while also feeding upon nectar from EFNs (Stefani et al. 2015; Del-Claro et al. 2017). This can work in the plant's favor when such predation is enough to reduce foliar herbivory and increase productivity (Nahas et al. 2012; Nelson and Jackson 2013; Stefani et al. 2015). In some cases, plants receive even more defense from herbivores, so the fitness increases when spiders co-occur with ants (Nahas et al. 2012), although spiders and ants can also compete for the same resources (Halaj et al. 1997, ◘ Fig. 5.2d). For instance, Stefani et al. (2015) showed that visitation by both spiders and ants had strong synergistic effects on seed production of *Eriotheca gracilipes*, an EFN-bearing plant. Plants visited by both spiders and ants produced an average of 13 viable seeds, which was higher than the average seed production of plants visited by either spiders (3) or ants (5) alone. However, just as with ants, spiders can also have negative effects on plants. Spiders can reduce plant fitness by preying on or deterring pollinators (◘ Fig. 5.2c), thereby reducing pollination rates and consequently the average flower fertility rate (Romero and Koricheva 2011).

However, EFNs are not the only plant resource available to spiders. Spiders can also eat other plant-derived food, including floral nectar, food bodies, and pollen (Nyffeler et al. 2016). Additionally, plants can provide spiders with resources such as refuge, favorable microclimatic conditions, anchorage points for webs, and places for nuptial encounters, oviposition, and hunting (Greenstone 1984; Uetz 1991; Dennis et al. 1998; Silva et al. 2020).

Spiders can also serve as biotic defenders in plants that have glandular trichomes on the surfaces of their leaves and stems (◘ Fig. 5.2b). These structures produce sticky substances that trap and kill small insects, a direct defense against herbivores and pathogens (Duffey 1986; Vasconcellos-Neto et al. 2017). However, these trichomes can also act as indirect defenses, as some families of spiders (e.g., Thomisidae and Oxyopidae) are often found foraging on insects trapped by glandular trichomes, and can positively contribute to plant defenses in the process (Romero et al. 2008; Krimmel and Pearse 2013). This protection was verified by

Silva et al. (2020), who demonstrated that spiders reduce the abundance of herbivores on plants with glandular trichomes (*Chamaecrista neesiana*, Fabaceae), resulting in lower herbivory and increased seed production.

5.2.1 Future Directions in the Study of Spiders as Biotic Defenders

Although studies on the interactions between spiders and plants have increased in the last 15 years, research is still incipient, and anecdotal studies show both positive and negative effects of spiders on plants. A major step is to identify all nectar-consuming spiders and how they interact with herbivores and ants (Del-Claro et al. 2017). If spiders, specifically nectar-feeding species, play a positive role in defending the plant against herbivory in conjunction with ants (Nahas et al. 2012), then the occasional negative interactions between ants and spiders should not be enough to reduce the benefits of spiders, ants, and the host plant. However, spiders are more aggressive and attack more herbivores when they are consuming nectar (Stefani et al. 2015; Del-Claro et al. 2017), therefore the influence of the host plant rewards on spider behavior and predation needs to be more thoroughly studied. Additionally, spiders have strong chemical senses, which may help them detect herbivore attacks on plants through plant release of volatile organic compounds, but the extent to which chemicals mediate spider behavior as a biotic defense remains to be explored.

5.3 Ant-Hemipteran Associations: Animal-Animal Biotic Defense and Plant Impacts

Aphids and membracids (Hemiptera) are important trophobiont (organisms that provide food rewards) herbivores that employ ants as biotic defenses. Even though the terms biotic and indirect defenses are usually applied to plants, trophobiont hemipterans can also recruit ants as bodyguards by releasing a sugar-rich solution (honeydew) (Way 1963; Stadler and Dixon 1999; Shingleton et al. 2005; Styrsky and Eubanks 2007). The consequences of this interaction can extend up beyond the local trophic chain, not only influencing the fitness of the insects involved, but also that of the aphid host plants and their associated herbivores (Styrsky and Eubanks 2007; Yao 2014).

Honeydew is a by-product of phloem ingestion by hemipterans, composed of a series of sugars (and also organic acids, amino acids, lipids, and proteins), and is a key mediator of the reciprocal interaction between ants and aphids (Völkl et al. 1999; Leroy et al. 2011a; Sabri et al. 2013). Ants will tend honeydew-producing hemipterans, reducing the abundance of hemipterans predators on the plant and increasing hemipterans fitness (Flatt and Weisser 2000; Renault et al. 2005, Vilela and Del-Claro 2018, ◘ Fig. 5.3a). Ants may also benefit aphids by protecting their eggs from fungal infections without receiving any apparent benefit (Matsuura and

Fig. 5.3 Ants tending lycaenid caterpillars and a membracid. **a** *Camponotus* ant visiting extrafloral nectaries of a Malpighiaceae and simultaneously tending a trophobiont hemipteran (*Enchenopa* sp., Membracidae); **b** *Camponotus* ant tending a larval Lycaenidae (*Rekoa marius*; A. Bächtold picture); **c** *Ectatomma tuberculatum* approaching a lycaenid caterpillar on a flower bud (E. Alves-Silva picture); **d** *Camponotus* sp. tending a caterpillar (E. Calixto picture)

Yashiro 2006). Without ant bodyguards, aphids are vulnerable to predation: during feeding, aphids insert their stylets (long mouthparts) into the leaves, preventing them from any rapid escape from natural enemies. In addition, these insects are gregarious (and thus conspicuous to predators) and have few direct defenses against natural enemies (Stadler and Dixon 2005; Suzuki and Ide 2008).

Despite the benefits provided by ants, most hemipterans are not tended by ants, and for those species that are actually tended, they can also be attacked and even preyed upon by ants (Billick et al. 2007). Aside from harassing and preying upon aphids, ants can also prevent hyperparasitoids from attacking parasitized aphids (Völkl 1992). Additionally, ants can fail to detect and defend aphids from specialist predators that mimic their chemical profile and then remain unnoticed by ants (Lohman et al. 2006). Furthermore, ant-tending behavior may be related to the presence of certain sugars, so aphids that do not release or metabolize specific sugars may go unattended by ants (Fischer and Shingleton 2001). Competition for ant attention exists when more than one species of aphid inhabits the same plant, and this too directly affects aphid fitness and persistence (Addicott 1978; Cushman and Addicott 1989).

In addition to the ways in which ants can reduce aphid fitness, honeydew may also cue parasitoids to the presence of aphid colonies on host plants (Budenberg 1990). Aphid feeding also prompts the release of volatile allelochemicals (herbivore-induced plant volatiles, or HIPVs), which natural enemies use to locate aphids (Hatano et al. 2008). In other instances, parasitoids of aphids feed on honeydew, although this is not their preferred food source (Lee et al. 2004). More recently, studies have shown that bacteria from aphid guts produce volatiles that effectively attract natural enemies as well (Leroy et al. 2011b). This shows that honeydew, although a necessary component of the ant-mediated biotic defense of aphids, can also have important and sometimes detrimental side effects for the aphids.

5.3.1 Aphid-Ant Effects on Plants

If ants can serve as biotic defenders of plants, but also as biotic defenders of aphids, what is the overall impact of ants on aphid host plants? After all, when ants protect aphids, they are protecting an herbivore of that plant—many of the 4000 described aphid species are most known for their direct negative effects on plants. By constantly feeding on phloem, aphids often cause severe damage to plants, particularly crops (Ragsdale et al. 2011). In addition, their high reproductive rates due to parthenogenesis, efficient settlement, and resistance to insecticides make aphids one of the most abundant pests (Stadler and Dixon 2005; Giordanengo et al. 2010; Jaouannet et al. 2014). Aphid damage to plants can range from microscopic (pathogen transmission, changes in nutrient flow, especially nitrogen and sugar allocation) to macroscopic (wilting of leaves and aesthetic damage on fruit surface), with devastating results (Jaouannet et al. 2014).

Hundreds of plant species consumed by aphids, coccids and also membracids possess EFNs (Del-Claro and Marquis 2015) which scientists have hypothesized can distract ants from trophobiont hemipterans (and other myrmecophilous insects), leaving the honeydew-producing insects vulnerable to natural enemies (distraction hypothesis – reviewed in Del-Claro et al. 2016). In fact, aphid species that are not attended by ants may suppress the production of EFN, thus weakening the plant's defense and deterring plant-bodyguards (ants, wasps) from visiting the plants (Yoshida et al. 2018). Historically, the distraction hypothesis has had good support because other forms of plant defense are less effective against aphids, as excreted honeydew incurs fungal infection on plants and also suppresses the JA pathway, which is used by plants as a form of chemical defense (Stadler and Müller 1996; Schwartzberg and Tumlinson 2014). For example, Engel et al. (2001) showed that the EFNs of *Vicia faba* (Leguminosae) can displace ants from aphids by producing nectar with more sugar than honeydew.

However, despite being herbivores, the effect of some aphids on EFN-bearing plants is negligible in terms of plant fitness loss (Suzuki et al. 2004), causing no severe damage (Rico-Gray and Castro 1996). In some cases, aphids might even indirectly benefit the plants—evidence shows that ants might shift their patrolling behavior from EFNs towards aphids and their honeydew, and that the presence of aphids can increase the number of ants on the plant (Sakata and Hashimoto 2000; Katayama and Suzuki 2003, reviewed in Styrsky and Eubanks 2007). A review by Zhang et al. (2012) also demonstrated that the mutualism between ants and honeydew-releasing hemipterans has a wide range of ecological effects on the host plant, such as reduced herbivory, low abundance of herbivores, and low fruit removal. In fact, the abundance of ants on some EFN plants is only enhanced in the presence of aphids. In *Vicia angustifolia* L. (Leguminosae) the number of *Lasius japonicus* ants visiting EFNs was 10% of the total of ants foraging on the plant; however, when aphids were present, the number of foraging ants on plants increased two-fold and 50% of ants foraged on honeydew (Suzuki et al. 2004). This shows the extent to which aphids influence the natural history of the host plants, and can be an important facilitator of biotic defense for the plant. Nonetheless, the herbivory of trophobiont insects might outweigh the suppression of other herbivores. Plants will only benefit if the cost of feeding the trophobiont is lower than the cost of suppressing other herbivores, thus a trade-off is expected (Styrsky and Eubanks 2007).

The herbivory-reducing effects of ant-hemipteran associations are higher compared to plants that rely solely on EFNs; however, plants that provide direct benefit to ants (e.g., EFNs, domatia, and food bodies) generally exhibit increased growth and reproduction whereas ant-hemipteran presence does not significantly affect plant performance (Chamberlain and Holland 2009, but see Fiala and Maschwitz 1991). This shows that the presence of direct rewards to ants is more beneficial to one aspect of plant life history, while the presence of trophobiont insects benefits other aspects.

It is evident that tritrophic interactions involving ants, aphids, and plants are extremely complex and conditional, thus it is hard to make generalizations (Stadler and Dixon 1999, 2005; Stadler et al. 2002). The role of honeydew goes far beyond simply mediating the aphid-ant mutualism. It is both a blessing and a curse for the aphids themselves as well as their host plants, and many questions remain unanswered about honeydew-mediated interactions. For instance, how do physiological changes incurred by aphid herbivory in host plants influence other insects, such as herbivores and pollinators? How do aphid-plant interactions affect the biodiversity of the entomofauna associated with plants? Aphid feeding behavior elicits plant antiherbivore defenses, some of which are constitutive and general, while others are local or systemic (Jaouannet et al. 2014), but further consideration of the fitness effects of such defenses is needed. In addition, some other insects may avoid aphid-infested plants. By investigating the oviposition patterns of Alcon Blue butterflies (*Maculinea alcon*), researchers found that aphid presence on the host plant strongly inhibited the oviposition of butterflies (Arnyas et al. 2009). If we are to understand biodiversity and multitrophic interactions in their full magnitude, such topics deserve further evaluation and detailed investigations.

5.4 Myrmecophilous Lepidoptera

Plants and trophobiont hemipterans are not unique in their myrmecophily. Some butterfly larvae also secrete sugary liquids that attract ant bodyguards (Pierce et al. 2002, ◘ Fig. 5.3b–d). This lepidopteran myrmecophily is broadly known and documented for two butterfly families: Lycaenidae and Riodinidae (DeVries 1991;

Pierce et al. 2002), which combined compose 30% of all butterfly species (Shields 1989). In these families, 75% of species interact with ants during their larval stages, exhibiting a variety of associations varying from obligatory to facultative and parasitic to mutualistic (Fiedler and Hölldobler 1992; Stadler et al. 2001).

Just as with EFN-bearing plants, the ants involved in these interactions protect their food source against natural enemies, and therefore these associations are known as defense or protective mutualisms (Agrawal and Fordyce 2000). Butterfly larvae possess specialized glands that produce nutritive secretions, which serve as ant food (Stadler et al. 2003; Daniels et al. 2005). In counterpart, the butterflies receive ant protection against predators and parasitoids during their most vulnerable life stage (pupal and larval instars), representing another case of animal-animal biotic defense (Pierce et al. 2002).

In addition to providing liquid rewards, myrmecophilous butterflies have also developed a series of morphological, behavioral, acoustic, and chemical characteristics to attract, pacify, alarm, or even trick ants into exhibiting defensive behavior (see review by Casacci et al. 2019). The resulting interaction is complex, with varied costs and benefits for the organisms involved (butterflies, ants, and plants), depending on the mechanisms (► Box 5.1) and the interaction degree, as discussed in the following sections.

Box 5.1 Mechanisms of Butterfly Myrmecophily

Ant-associated organs: Among the different chemical mechanisms responsible for attracting and maintaining ant's attendance of butterfly larvae, the nectary organs in Lycaenidae and Riodinidae deserve special attention. In Lycaenidae, the exudate is produced by the dorsal nectar organ (DNO) (Newcomer 1912) and in Riodinidae by the tentacle nectar organs (TNOs) (DeVries 1988). These secretions are composed mostly of amino acids and carbohydrates and are even richer in amino acids than extrafloral nectar and hemipteran honeydew (Yao and Akimoto 2002; Blüthgen et al. 2004; Daniels et al. 2005). It is important to consider exudates when evaluating this system's trade-off since the secretion quality and quantity influences ant persistence in attending the larvae (Wada et al. 2001; Hojo et al. 2015) and consequently ant permanence on the plant.

The eversible tentacle organs (TOs) in some lycaenid larvae and the anterior tentacle organs (ATOs) in riodinids, as well as the perforated cupola organs (PCOs) present in almost all species of both families, facilitate chemical communication between butterflies and ants (Malicky 1970). Authors have reported that eversion of the TOs is related to the liberation of volatile composites that incite alert and aggressive behavior in patrolling ants (Axén et al. 1996).

Cuticular hydrocarbons (CHCs): To avoid ant attacks, some myrmecophilous butterfly species mimic ant CHCs in order to be recognized as a colony member (Hojo et al. 2009). Beyond these, other CHC strategies used by butterflies include chemical insignificance, in which the larvae become "invisible" to the ants by reducing their cuticular chemical components, and chemical camouflage, in which the larvae take on the cuticular profile of the host plant via diet or contact (see review by Barbero 2016). The important role of CHCs is evident in insect-plant interactions, but the benefits to the emitter or the receiver are little understood.

Vibroacoustic signals: Both Lycaenidae and Riodinidae can produce sound via stridulation, a mechanism that may play an important role in the maintenance of their interactions with ants (DeVries 1990; Mathew et al. 2008). Stridulation organs are also present in non-myrmecophilous lycaenids (Álvarez et al. 2014), but can nonetheless influence the ant protective behavior in myrmecophiles. Travassos and Pierce (2000) show how the larvae and pupae of *Jalmenus evagoras* use a complex repertoire of sounds to improve the attendance of associated *Iridomyrmex* ants. Furthermore, pupae of the lycaenid *Spindasis lohita* do not possess secretory organs but still communicate with *Crematogaster rogenhoferi* ant attendants via vibration (Lin et al. 2019).

5.4.1 Benefits of the Ant-Butterfly Biotic Defense Relationship

The benefits of attracting ants as biotic defenses are widely studied from the butterfly perspective (Pierce et al. 1987; Baylis and Pierce 1991; Stadler et al. 2001; Kaminski et al. 2013; Bächtold et al. 2014; Mizuno et al. 2019). Experimental manipulations have demonstrated that butterfly eggs and larvae are less parasitized, larvae show better development, and survive at significantly higher rates when attending ants are present (Pierce et al. 1987; Nakabayashi et al. 2020). From the ant's point of view, however, the costs and benefits are less studied. Ants presumably benefit from feeding on the nutritive secretions, and lab experiments have shown higher colony survivorship in the presence of butterfly larvae (Cushman et al. 1994; ▣ Fig. 5.1). Nonetheless, the energetic and opportunity costs of tending butterfly larvae should also be included when evaluating the costs and benefits for ants. For example, the costs for ants could outweigh the benefits when butterfly larvae manipulate the ant behavior by means other than liquid rewards, such as CHC volatile emissions and stridulation.

5.4.2 How Does Lepidopteran Myrmecophily Affect Plants?

At first glance, the butterfly-ant interaction is detrimental to host plants, since Lycaenidae and Riodinidae larvae may directly reduce leaf area through herbivory (DeVries 1989) and directly reduce plant reproductive success by consuming floral buds and flowers (Bächtold et al. 2013). In this sense, the protection provided by ants to caterpillars might reduce plant fitness by allowing the larvae to damage host plants. On the other hand, the ants involved in this interaction are generally not specialists on butterfly secretions, but also attack and consume other arthropods on the plant (Davidson 1997). The aggressive predatory behavior of ants may reduce the abundance and feeding activity of other herbivores, which may have a positive effect on the plant. The net result for the host plant thus depends on whether the reduction of non-butterfly herbivory is greater than the extent of the myrmecophilous butterfly larvae's herbivory (Oliveira 1997; Rico-Gray and Oliveira 2007). Therefore, butterfly-ant associations may confer biotic defense value to their host plants, since the constant ant presence induced by the myrmecophilous larvae may negatively impact other herbivores and limit the areas free of natural enemies for herbivores (◘ Fig. 5.1).

Although the results of these interactions depend on factors that vary in space and time such as plant phenology and density (Rodrigues et al. 2010), Rico-Gray and Oliveira (2007) proposed three criteria that the butterfly-ant association must follow in order to benefit the plant: (1) the butterfly must not be the main plant herbivore; (2) ant attendance cannot increase the population density of the myrmecophile; and (3) associated ants must deter other plant herbivores (Rico-Gray and Oliveira 2007).

Unfortunately, the effects of the butterfly-ant interaction on plant reproductive success remain largely unknown. DeVries (1991) suggested butterfly myrmecophily evolved as a consequence of lasting interactions between ants and angiosperms, in a complex system that also involves EFN-bearing plants and those with trophobiont hemipterans. Despite the notable importance of vegetation in the evolutionary and ecological context of these interactions (Moreau et al. 2006), their impacts on and interactions with plants have received little attention. For instance, several studies have shown that ant presence mediates host plant selection by adult butterflies (Atsatt 1981; Fraser et al. 2002; Bächtold et al. 2016). The role of plant chemistry (CHCs or volatile emissions) in host plant choice by myrmecophilous butterflies is unknown. Also, the possibility that myrmecophilous organisms may manipulate the ant's behavior via multiple strategies and how that affects plant fitness is still little understood (Mannino et al. 2018; Casacci et al. 2019). By being a multitrophic interaction, the interaction between ants and butterflies have multiple ecological effects, since the presence of myrmecophilous larvae alters the abundance and behavior of ants on plants. Exploring the effects of this butterfly-ant association on other trophic levels (Elgar et al. 2016), such as host plants, constitutes the key to the ecological and evolutionary comprehension of the mutualism between myrmecophilous Lepidoptera and ants.

5.5 Methodological Approaches and Biotic Defense Networks

As we have observed throughout this chapter, biotic defense interactions are complex, context-dependent, and involve many distinct species. Faced with this complexity, an equally complex methodology is necessary to synthesize this plethora of interactions into patterns that can be analyzed and generalized (Huxley and Cutler 1991; Beattie and Hughes 2002; Del-Claro et al. 2018). Graph Theory, which studies three-dimensional geometrical shapes transforming vertices and edges into three-dimensional networks of points connected by lines (Barnes and Harary 1983; Biggs et al. 1986; Bascompte 2010), provided one such approach to describe and model complex biological relationships in interaction networks (Pascual and

Dunne 2006; Dale 2017; Dáttilo and Rico-Gray 2018). The Theory of Ecological Networks (see references in Ings and Hawes 2018) emerged from this integrative approach, providing a way to study the multitrophic and multispecific nature of complex plant-ant-herbivore interactions (Bascompte 2010; Dehling 2018; Dáttilo and Rico-Gray 2018).

According to the Theory of Ecological Networks, ecological interactions are multispecific, that is, a given species can simultaneously interact with many other species. This creates a three-dimensional network, in which the tangle of different interactions regulates each other and together contribute to the overall structure and properties of the network (Bascompte 2010). This network can be visualized through a network graph, a three-dimensional geometric figure in which the species are represented as points, and the interactions between the species are represented by lines that connect these points (Dehling 2018). Several parameters can be calculated from this network structure, including form, degree of connection, diversity and specificity of connections, and the position of species in the network, so changes in these parameters can be used to model changes in the patterns of interactions (Pascual and Dunne 2006; Bascompte 2010; Dehling 2018). These parameters quantify interactions between species, often measured by the number of encounters between a set of coexisting species (Bascompte and Jordano 2007). For instance, an interaction between ants and plants can be conceived when individual ants collecting nectar from different plants are used to establish a network of species interactions (Dáttilo et al. 2014; see also Luna and Dáttilo, ► Chap. 10).

Ecological networks can assume different arrangements, ranging from a more specialized, modular pattern (Grilli et al. 2016), to a more generalized, nested pattern (Bascompte et al. 2003; Fortuna et al. 2010). Interactions between ants and plants (Bascompte et al. 2003) are typically nested, as described for several ant-plant networks in Brazil (Guimarães et al. 2006; Dáttilo et al. 2013, 2014; Lange and Del-Claro 2014; Costa et al. 2016; Fagundes et al. 2016; Del-Claro et al. 2018) and worldwide (Nielsen and Bascompte 2007; Vázquez et al. 2009; Chamberlain et al. 2010; Díaz-Castelazo et al. 2010; Rico-Gray et al. 2012). In nested networks, there are unequal interactions between species, where a few (central) species interact with many others, but most species are less interactive (peripheral, Dáttilo et al. 2014). In these nested networks, the low specialization of interactions and high sharing of partners leads to a high redundancy of interactions, as peripheral species interact with the same species as central ones (Dehling 2018).

Ant-plant interactions are consistently nested within different communities (Dáttilo et al. 2013, 2014; Costa et al. 2016; Sendoya et al. 2016; Fagundes et al. 2018), under different environmental conditions (Rico-Gray et al. 2012; Dáttilo et al. 2013), at different periods of the day (Dáttilo et al. 2014) and seasons (Díaz-Castelazo et al. 2013; Lange et al. 2013; Santos et al. 2014), and even after severe disturbances (Falcão et al. 2014; Costa et al. 2018; Fagundes et al. 2018). Nested structures resist change due to a high overlap of interacting partners, which allows flexibility in the replacement of species without necessarily disrupting the network (Dáttilo 2012; Passmore et al. 2012). Therefore, there is evidence of evolutionary selection for interactions that strengthen the nested structure of the ant-plant networks (Del-Claro et al. 2018). However, few studies have tested whether community-level benefits to biotic defense remain after changes in species composition (Piovia-Scott 2011) or network structure (Plowman et al. 2017), because it is difficult to measure these benefits in the field.

Network approaches can also be used for biotic defense relationships beyond ant and EFN-bearing plants, and comparing the network structure of different biotic defense types can elucidate broader patterns or sources of variation. For example, when comparing different ant-mediated defense relationships, Cagnolo and Tavella (2015) found ant-lepidopteran and ant-myrmecophyte (domatia-bearing plants) networks to be highly modular (specialized), unlike more nested ant-EFN relationships. Furthermore, biotic defenses by definition involve at least three layers of interaction: the defender, the defended, and the offender. As network approaches become more widely used, they are being expanded to accommodate more complex interactions such as multiple trophic levels (Cagnolo 2018), which could allow more accurate descriptions of biotic defense relationships.

Ecological networks are not the only approach to studying biotic defenses, and indeed, other approaches are also warranted. Experimental tests of the immediate costs and benefits to both the defenders and defended organisms, the longer-term fitness ramifications, and the conditions that affect these costs and benefits will all provide insight to the intricacies of these relationships. For instance, there are trade-off effects between ant aggressiveness and plant protection. Although highly aggressive ants provide increased protection against herbivores, they may drive away potential pollinators, reducing the reproductive output of plants (Melati and Leal 2018). Resource quality also affects the outcomes of ant-defended plants. Nectar and honeydew rich in sugars and amino acids attract more ants and increase plant defense (Blüthgen et al. 2004; Alves-Silva and Del-Claro 2013; Fagundes et al. 2017; Pacelhe et al. 2019). However, as a facultative and non-specialized interaction, plants with EFNs are susceptible to robbers and visiting ants that provide little protection (Dáttilo et al. 2014). Further observation of natural history will also help expand the known diversity of biotic defense interactions and is an important key step in plant-animal interactions in general (Del-Claro et al. 2013).

5.6 Reconsidering Biotic Defenses: Implications for Biodiversity and Future Directions

In the past centuries, researchers have investigated and proposed explanations for why communities and ecosystems differ in terms of biodiversity. Although climate and geography have been regularly used to explain species distribution since the time of Humboldt (Norder 2019), only after the 1960s did studies start recognizing the importance of ecological interactions for patterns of biodiversity (e.g., Janzen 1966; Paine 1966; Breedlove and Ehrlich 1968). Currently, we recognize that some species are so dependent on interactions that their extinction may cause cascading effects that ultimately lead to the extinction of their associated species (Forup et al. 2008). Although these effects are usually demonstrated with key predators and pollinators, there is also evidence that biotic defenses may contribute to the persistence of species in several systems (see Bronstein, ▶ Chap. 11).

Biotic defenses may contribute to biodiversity by increasing the performance and fitness of associated organisms. As we have seen in this chapter, plants with EFNs are not the only ones benefited by the presence of natural enemies such as ants, spiders, and parasitoids, since plants contribute to their defenders' survival by offering valuable resources. For example, Byk and Del-Claro (2011) showed that the offer of extrafloral nectar increased the survival and growth rate of myrmecophilous ants. Biotic defenses also affect the herbivore competition and host recognition with enough potential to shape entire populations and communities of arthropods (Agrawal and Sherriffs 2001; González-Megías and Gómez 2003; Ohgushi 2005; Kessler and Heil 2011). This was demonstrated in studies involving the experimental removal of herbivores of distinct guilds. As an example, Waltz and Whitham (1997) revealed that responses of cottonwoods attacked by a leaf-galling aphid (*Pemphigus betae*) maintain high levels of species richness and diversity through the attraction of natural enemies and other herbivores. When the aphids were removed, the species richness and relative abundance of arthropods decreased by 32% and 55%, respectively.

Given that biotic defense relationships play integral roles in the development and maintenance of biodiversity, understanding how anthropogenic and natural disturbances impact these relationships is an important part of predicting, managing, and when possible preventing the effects of future disturbances. Climatic changes are impacting all biotic interactions by disrupting some relationships and altering the outcomes of others. Many studies have shown that increasing temperatures and changing precipitation are shifting plant and animal phenology (Munson and Long 2017; reviewed by Cohen et al. 2018), with strong impacts on pollination and biotic defenses (Vilela et al. 2018). Furthermore, deforestation and habitat fragmentation may disrupt and weaken ecological interactions (Sabatino et al. 2010). However, modeling network techniques can be used to detect keystone species and predict the possible consequences of their extinction (Messeder et al. 2020). This knowledge can be used to set management and conservation strategies to mitigate ecological disturbances.

We have selected these example systems here to illustrate some of the main aspects of biotic defense, but we encourage readers to be open-minded in what they categorize as biotic defense. We and several authors before us have made the case that indirect defense encompasses more than simple plant-herbivore-natural enemy interactions—other organisms also manipulate natural enemies to reduce the effects of predation, and considering these alternate systems can lead to broader conclusions about defense as a whole (Pearse et al. 2020). Not all antagonistic threats are herbivores, and not all natural enemies are other animals—some fungal microbes might reduce more pathogenic fungi in fruit (Cipollini and Stiles 1993), although this hypothesis seems to have been left untested.

Conclusion

In this chapter, we discussed four examples of biotic defense systems and their mechanisms. We showed that plants protected by natural enemies such as ants and spiders exhibit less herbivore damage, produce more fruits and seeds, and may ultimately increase their fitness. The benefits provided by the biotic agents, however, are not pervasive and depend on the involved species and the ecological context. Additionally, plants are not the only organisms employing biotic defenses—honeydew-producing aphids and caterpillars also provide rewards to ants which can then provide protection from other natural enemies. These interactions can still benefit host plants by attracting natural enemies, but such benefits are tempered by the herbivory of the honeydew-producing insects. Such complex biotic interactions convey methodological challenges, but ecological networks provide a useful approach to studying biotic interactions and assessing how deforestation and climatic changes are extinguishing and disrupting biotic interactions across the globe. Despite the fact that biotic interactions contribute to the maintenance of biodiversity, most conservation efforts focus on species loss. However, biotic defense interactions are a major piece of biodiversity, and their conservation is necessary for maintaining healthy environments and essential ecosystem services.

Key Points

- The stability of biotic defense systems will depend on the costs and benefits to both partners, as well as the generality or specificity of the defense and rewards.
- Although the most widely-studied biotic defense interactions involve plants, extrafloral nectar, and natural enemies of herbivores, other organisms can also engage in biotic defense relationships.
- Honeydew-producing herbivores and extrafloral nectar-producing plants can attract the same biotic defenders, with synergistic or competitive effects depending on the fidelity of natural enemies to one or both rewards, the extent of herbivory, and the effectiveness of defense.

? Questions

- Which conditions determine the stability of biotic defense interactions?
- What other organisms participate in biotic defense systems, particularly understudied interactions?
- How will disturbance affect the outcomes of biotic defenses?

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