

Part IV

Effect of Invasive Ants on Plants and Their Mutualists

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12 Playing the System: The Impacts of Invasive Ants and Plants on Facultative Ant-Plant Interactions

Suzanne Koptur, Ian M. Jones, Hong Liu, and Cecilia Díaz-Castelazo*

Introduction

Extrafloral nectaries (EFNs) are sugar-secreting glands located outside of flowers; they are structurally diverse, and may be found on almost any vegetative or reproductive plant structure (Bentley, 1977a; Koptur, 1992). Although a wide range of ecological functions have been suggested for EFNs (Baker et al., 1978; Becerra & Venable, 1989; Wagner & Kay, 2002; Gonzalez-Teuber & Heil, 2009; Heil, 2011), they are most noted for providing indirect defense against herbivory by attracting natural enemies (Janzen, 1966; Inouye & Taylor, 1979; Koptur 1984; Heil et al., 2001; Heil, 2015). Ants represent the most common visitors to EFNs, and have regularly been observed to benefit host plant fitness (Bentley, 1977b; Koptur, 1992; Rosumek et al., 2009; Heil, 2015).

Myrmecophytes are plants that provide domatia, and food bodies and/or EFN, and engage in obligate interactions with ants (Chapters 10 and 11). A far greater number of plants, however, known as myrmecophiles, provide only EFN and engage in facultative interactions with ants. Because of the non-specialized nature of their interactions, the EFN that these plants provide is open to exploitation by any number of ant species, some of which may provide no benefits, or even negatively affect plant fitness (Koptur & Lawton, 1988; Torres-Hernandez et al., 2000; Ness et al., 2006). This variation in partner quality represents an important ecological cost of EFN production for plants. In this chapter, however, we focus not on the costs for individual plants, but on the costs for native species and ecosystems. We address the question: Does EFN in disturbed environments support and facilitate species invasions?

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The Role of Plant-Based Resources in Supporting Invasive Ants

In the southern United States, no invasive ant species is more ubiquitous than the red imported fire ant, *Solenopsis invicta*. The uncontrolled spread of this highly invasive species is, in part, a result of its ability to infiltrate mutualistic networks. Wilder et al. (2011) showed that a lack of interspecific competition in its invasive range has allowed *S. invicta* to dominate plant-based carbohydrate resources, both EFN and hemipteran honeydew. Indeed, stable isotope analyses have shown that *S. invicta* occupies a lower trophic position in the United States than in its native Argentina, where other arboreal foraging ants can exclude it from mutualist-derived resources (ibid.).

This kind of behavioral plasticity is a common feature of highly invasive species. Savage and Withney (2011) manipulated EFN availability on a native shrub, *Morinda citrifolia* (Rubiaceae), on the Samoan islands. The invasive ant, *Anoplolepis gracilipes*, responded more strongly to increased EFN availability, in terms of recruitment activity and aggressive behavior, than did native ant species. The invasion of *A. gracilipes* on the Samoan islands has progressed over recent decades, and its distribution is highly correlated with the presence of EFN-producing plants. Not surprisingly, in areas where *A. gracilipes* is present, the abundance and diversity of native ants has been reduced (Savage et al., 2009).

Other studies have also made the link between ant invasions and plant-derived resources. Eubanks (2001) described the patchy distribution of *S. invicta* in agricultural habitats in the southern United States and determined that much of the pattern could be attributed to the presence of ant-tended aphids. The Argentine ant, *Linepithema humile*, became dominant in South African vineyards only after the introduction of honeydew-excreting insects (Addison & Samways, 2000). The presence of EFN-producing plants may influence ant invasions in a similar manner (e.g., Lach, 2003; Ness & Bronstein, 2004).

Many highly invasive ant species share a suite of traits that allow them to dominate plant carbohydrate resources. Several of the most successful species, including both *S. invicta* and *L. humile*, produce multi-queened, multi-nested supercolonies that lack intraspecific aggression (Holway et al., 2002). Individual nests can also be highly movable in response to available resources. Colonies of *S. invicta*, for example, will often produce satellite nests at the base of plants when harvesting EFN or tending aphids (Kaakeh & Dutcher, 1992; Koptur et al., 2015). A high level of aggression is a character shared by almost all invasive ants (Lach, 2003) and some, including *L. humile*, even have modified crops that allow them to take in more liquid food (Davidson, 1998).

Although invasive ants are often well equipped to dominate plant-derived resources, it is less clear whether they make effective mutualistic partners for plants. On an EFN-producing tree, *Acacia lamprocarpa* (Fabaceae), invasive *A. gracilipes* ants display greater recruitment behavior and aggression toward herbivores than the native Weaver ants, *Oecophylla smaragdina*. Herbivore damage to the leaves of *A. lamprocarpa*, however, is greater in the presence of invasive ants, than when

native ants are resident (Lach & Hoffman, 2011). In South Africa, *L. humile* ants displace native ants on *Protea nitida* (Proteaceae), where they tend membracid planthoppers. Unlike the native ants, however, *L. humile* are often found in the inflorescences, and have been shown to deter pollinators (Lach, 2007). These examples highlight that invasive ants can negatively impact their plant partners; however, the majority of studies have shown that invasive ants do benefit plants, whether it be through a reduction in herbivory (Koptur, 1979; de la Fuente & Marquis, 1999; Oliveira et al., 1999; Fleet & Young, 2000; Ness, 2003), an increase in fruit or seed production (Koptur, 1979; Horvitz & Schemske, 1984; Oliveira et al., 1999; McLain, 1983; Fleet & Young, 2000) or an increase in plant growth rate (de la Fuente & Marquis, 1999).

Mutualisms play a key role in the functioning of ecosystems. In disturbed habitats, however, generalist interactions between ants and plants often involve introduced species. In these cases, such interactions can enhance invasion success, and further disrupt ecosystem integrity. The most commonly documented impact of ant invasions is, not surprisingly, the displacement of native ant species. Since its arrival in the southern United States, *S. invicta* has substantially reduced the range of its congener, *Solenopsis geminata*, along with numerous other ant species (Gotelli & Arnett, 2000). In the Galapagos Islands, the little fire ant, *Wasmannia auropunctata*, has had a similar impact on several native ant species (Lubin, 1984). The effects of invasive ants are, however, not limited to other ant species. In Hawaii, the loss of numerous and diverse native insects has been attributed to the invasion of *Pheidole megacephala* (Zimmerman, 1970). On Christmas Island, the arrival of *A. gracilipes* ants has impacted the populations of the red land crab, a keystone species on the island, with cascading effects on the entire ecosystem (Green et al., 1999).

The Role of Ants in Supporting Invasive Plants

While it appears that plant-based resources have facilitated invasions by several ant species, the exploitation of facultative ant-plant interactions is a two-way street. Of the approximately 4,000 plant species that bear EFNs, the majority are pioneer plants capable of adapting and thriving in changeable abiotic and biotic conditions (Weber & Keeler, 2013). Here we explore how this characteristic has contributed to the spread of EFN plants into new environments, particularly those that have been heavily impacted by humans. We address the question: Do generalist ants, either native or invasive, facilitate plant invasions?

The evolution of increased competitive ability hypothesis (EICA) predicts that, in the absence of their coevolved natural enemies, plants should decrease their investment in indirect defenses and, instead, focus their resources toward growth and reproduction (Blossey & Notzold, 1995). Indeed, populations of the Chinese tallow tree, *Triadica sebifera* (Euphorbiaceae), in their native range have been shown to produce more EFN than their invasive conspecifics in the United States (Carrillo et al., 2012). As an extension to this theory, one would predict that investment in

EFN would be reduced in urban or highly disturbed environments. Indeed, Rios et al. (2008) collected seeds of *Chamaecrista fasciculata* (Fabaceae) from populations in natural and urban environments, and reared them in controlled greenhouse conditions. Plants derived from urban populations had smaller EFNs and produced less EFN. Conversely, EFN-producing plants in their native range are better equipped to exploit local ant populations than their invasive competitors. In Chinese tallow, induced EFN production is significantly greater in response to damage by specialist herbivores found only in their native range, than to damage by generalist herbivores (Carrillo et al., 2012b). Also, in China, a native passion vine, *Passiflora siamica* (Passifloraceae), produces significantly more EFN per leaf than its invasive congener, *P. coccinea* (Xu & Chen, 2009).

One factor that appears to contribute to the success of non-native EFN plants, however, is the arrival or presence of invasive ants. The invasive Argentine ant, *Linepithema humile* (*Iridomyrmex humilis*, previously), for example, may have facilitated the naturalization of two non-native vetch species, *Vicia sativa* and *V. augustifolia* (Fabaceae), across northern California (Koptur, 1979) by reducing damage to leaves from surface-feeding herbivores. In Mauritius an invasive ant, *Technomyrmex albipes*, has been shown to benefit an invasive tree, *Leucaena leucocephala* (Fabaceae), by removing herbivores. In contrast, the same invasive ant negatively impacts a native tree, *Scaevola taccada* (Goodeniaceae), by tending sap-sucking hemipterans (Lach et al., 2010). In Puerto Rico, the population of a non-native orchid, *Spathoglottis plicata* (Orchidaceae), had been kept in check by a native weevil seed predator. The arrival of fire ants, *S. invicta*, on the island, however, has led to the deterrence of these weevils, and the elevation of *S. plicata* to invasive status (Ackerman et al., 2014). Invasive ants may also outcompete native ants, especially in altered habitats: fire ants and invasive *Pheidole* ants colonized clear-cut forest areas, and numbers of native ants were significantly reduced (Zettler et al., 2004).

The Hawaiian Islands represent an ideal system in which to study the impacts of invasive ants, as it is generally accepted that ants were absent from the island prior to their human introduction (Keeler, 1985; Krushelnycky et al., 2005). As one would expect, very few plant species that are endemic to these islands possess EFNs; however, many invasive species bearing EFNs have proliferated on the islands since the arrival of ants (Junker et al., 2011). In addition to defending invasive plants, ants have been shown to act as nectar robbers on many native plants that lack the floral defenses exhibited by many of their invasive counterparts (Bleil et al., 2011; Junker et al., 2011).

Ant-Plant Interactions in South Florida

In south Florida the native flora contains a high proportion of plants that bear EFNs, many of which have been shown to facilitate mutualistic interactions with ants and other beneficial insects (Koptur, 1992; Koptur et al., 2015). The human

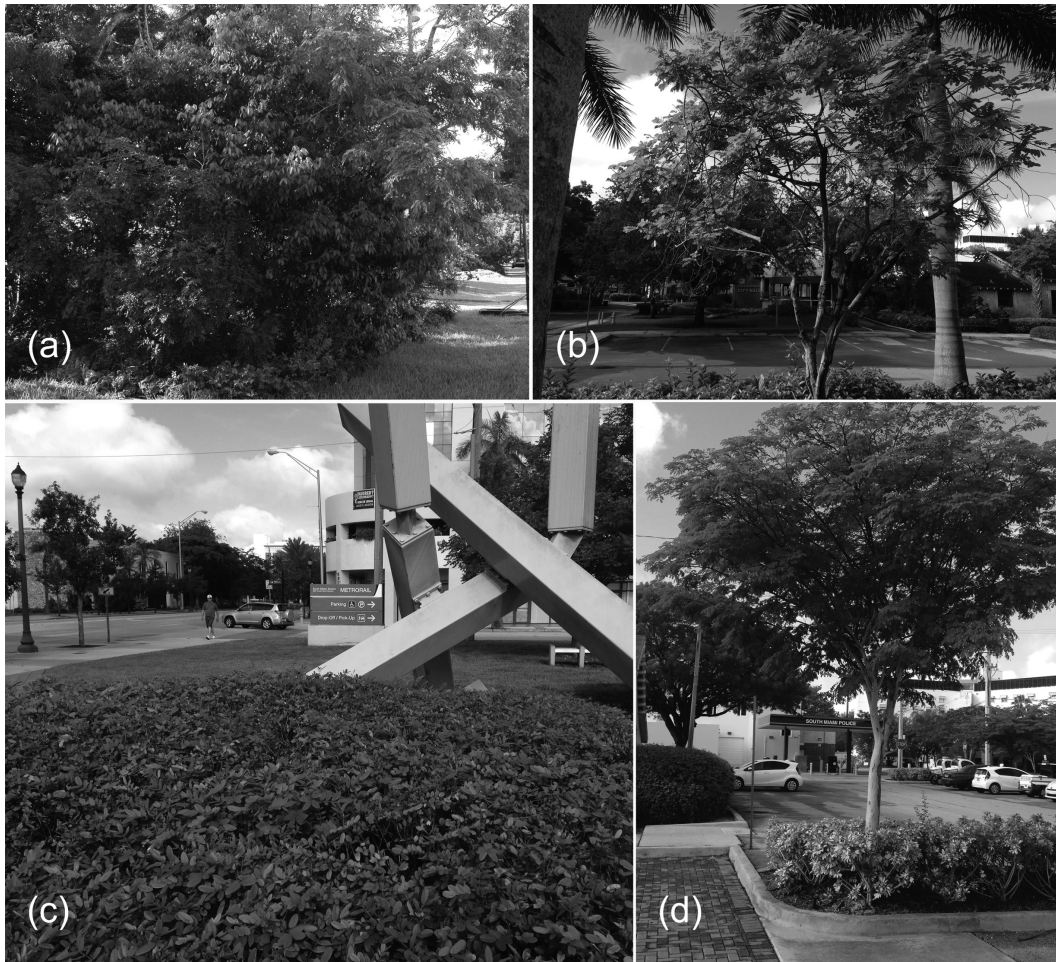


Figure 12.1. Legume plants with extrafloral nectaries in the urban environment – clockwise from upper left: (a) Native plant landscape with *Senna ligustrina* and *S. chapmannii* (foreground), *Lysiloma latisiliquum* canopy; (b) *Senna surattensis* in landscape in front of South Miami city hall; (c) *L. latisiliquum* as parking lot tree; (d) *Senna chapmannii* hedge in front of sculpture by Metrorail station.

Photo credits: Suzanne Koptur.

population in southern Florida has grown dramatically over the past century (Barrios et al., 2011), and development in Miami-Dade and Monroe Counties has progressed rapidly from very little to almost complete urbanization.

Many native EFN-producing plants are utilized in the urban landscape as garden plants and shade trees (Figure 12.1a, d). Non-native congeneric species, also bearing EFNs, have been introduced as ornamentals in the same area (Figure 12.1b, c), and some have become invasive. The proliferation of human activity in south Florida has also seen the introduction of several non-native ant species, most

notably the red imported fire ant *S. invicta* and the now naturalized *Pseudomyrmex gracilis*. In this section we describe ant-plant interactions in several native legume plants, in natural areas where they have been studied. We describe patterns of interactions among native plants and their exotic relatives with ants, both native and introduced species. We consider the effects of invasive ants on extrafloral nectary-mediated mutualisms in south Florida, the impact of these interactions on populations of native herbivores, and the resulting fitness benefits to plants (both native and non-native) bearing EFNs.

Wild tamarind, *Lysiloma latisiliquum* (Fabaceae), is an EFN-producing tree native to south Florida. Ant exclusion experiments, conducted in Everglades National Park, showed that ants provide *L. latisiliquum* with protection against leaf-feeding herbivores, particularly during leaf expansion and development (Koptur, unpublished data). Extrafloral nectaries on the leaves attracted four species of ants (*Pheidole dentata*, *Pseudomyrmex elongata*, *P. gracilis* and *Solenopsis geminata*), two of which are non-native. The most abundant ant on the plants was *P. gracilis*, the elongate twig ant. This species was introduced to the Miami area in around 1960 (Whitcomb et al., 1972) and now is present worldwide (Wetterer, 2010). This solitary forager nests in twigs and is an important predator on caterpillars and other arthropods, including the cloudless sulfur, *Phoebis sennae*, a native pierid butterfly that utilizes *L. latisiliquum* as a hostplant, preferentially ovipositing on the new foliage. Future work should consider how the introduction of *P. gracilis* (and other aggressive ants) has affected populations of these native butterflies.

Most *Pseudomyrmex* ants that form mutualisms with plants prefer hexose-rich nectar, as they lack invertase, the enzyme that cleaves sucrose. As a result, many myrmecophytic plants produce hexose-rich nectar as a way to discourage nectar robbing by non-mutualistic ants (Kautz et al., 2009). *Pseudomyrmex gracilis*, however, provides an exception to this rule, as it does produce invertase. This species is, therefore, well placed to exploit generalist ant-plants, such as *Lysiloma bahamensis*, that produce largely sucrose-based nectar. A congener of wild tamarind, *Lysiloma sabicu*, has been widely used in landscaping in south Florida, and non-native generalist ant-plants like this may well have facilitated the spread of invasive ants. As a close relative of a native plant, however, *L. sabicu* may also provide a service for native herbivores, creating connections between remaining natural landscape fragments. Indeed, *L. sabicu* has recently been shown to host the rare pink spot sulfur butterfly, *Aphrissa neleis* (Warren, 2011).

Senna is a species-rich genus of caesalpinoid legumes, the diversification of which has been attributed to the evolution of EFNs (Marazzi et al., 2013). Many species of the genus, both native (Figure 12.2) and non-native (Figure 12.1 b, c), are abundant in south Florida, and represent important host plants for sulfur caterpillars. *Senna mexicana* var. *chapmanii* (henceforth, *S. chapmanii*) is native to pine rockland habitats, and the presence of ants has been shown to reduce herbivory and increase plant reproductive fitness in this species (Koptur et al., 2015; Jones et al., 2016). Nine ant species were observed foraging on *S. chapmanii*, including both *P. gracilis* and *S. invicta* (Koptur et al., 2015); similar studies, conducted a decade



Figure 12.2. *Senna* extrafloral nectaries with ant visitors – left to right: (a) *Senna chapmannii* with *Wasmannia auropunctata*; (b) *Senna ligustrina* with same ant species; (c) *Solenopsis invicta* on *Senna chapmannii*. Photos by Maria Cleopatra Pimienta (a & b) and Ian Jones (c). (A black-and-white version of this figure will appear in some formats. For the color version, please refer to the plate section.)

later, also observed foraging by the little fire ant, *Wasmannia auropunctata*, a more recent arrival in south Florida (Figure 12.2; see also Wetterer & Porter, 2003; Jones et al., 2016). *Senna occidentalis* is a close relative of *S. chapmanii*, and is invasive in south Florida where it serves as a host plant for the sulfur butterflies. In Texas, another part of its invasive range, *S. occidentalis*, has been shown to benefit specifically from the presence of the red imported fire ant, *S. invicta*; these aggressive ants dominate the EFNs, and remove sulfur caterpillars (*Phoebis sennae* and *Eurema nicippe*) from the plants (Fleet & Young, 2000).

The proliferation of *S. invicta* in south Florida has undoubtedly had a negative effect on native ant species, and may pose a threat to a host of other native organisms as diverse as butterflies and sea turtles (Allen et al., 2001). Although controlling the spread of these invasive ants has proven difficult, it may be possible to utilize them as part of biological control programs that protect other native organisms. Two native *Opuntia* species (Cactaceae) – *O. stricta* and *O. humifusa* – host the highly invasive moth, *Cactoblastis cactorum*, in south Florida. Aggressive ants, in particular *S. invicta*, have been shown to reduce *C. cactorum* numbers by attacking eggs and larvae. The numbers of defensive ants on *Opuntia* species can be enhanced by planting the native EFN-producing legume *Chamaecrista fasciculata* beneath the cacti (Jezorek et al., 2011).

In recent times, there has been a move to increase the numbers of native plant species in human-dominated environments, for many reasons: to enhance the surroundings for wildlife, including butterflies, bees, and birds (Minno & Minno, 1999; Mathew & Anto, 2007; Koi & Daniels, 2015); to educate the public about native plants in landscaping, making connections with the natural heritage of the region (Wild Ones®, 2004), promoting place-based learning so that connections can be made with the larger environment of the planet (Billick & Price, 2010); and to provide connections between remaining natural landscape fragments (Haddad et al., 2003; Maschinski & Wright, 2006). It is interesting to compare the ant-plant associations of native plant species in natural areas versus urban areas, and compare their interactions with those of non-native congeneric or closely related plants as well. In this study we defined natural areas as places that have been relatively undisturbed by humans, where plants occur naturally; urban areas are those where vegetation has been removed by human development, and then replanted with plants in landscaping and gardens.

We sought to document associations of ants and plants; so to augment our ongoing observations from various studies in our plant ecology lab, we used pit-fall traps. We attached vials of soapy water upright to smaller branches of plants, with their openings at the surface of the branch, so that wandering insects fall in and do not leave; these traps were placed on individual plants in urban and natural areas to collect ants and other arthropods on different plants in different situations. Each plant monitored received three vials, which were collected after one week; these were refrigerated until contents were examined in the lab and specimens pointed for determination and vouchers. We aimed to monitor ten individuals of each plant species in each situation, but for several species in the urban areas there were fewer

(a)

	NATURAL AREAS plants / ants																								
	1 - <i>Brachymyrmex obscurior</i> *	3 - <i>Camponotus emeryoidicatus</i> *	4 - <i>Camponotus floridanus</i>	5 - <i>Camponotus inaequalis</i> *	6 - <i>Camponotus planatus</i> *	7 - <i>Camponotus rasilis</i> *	9 - <i>Camponotus tortuganus</i>	8 - <i>Camponotus sexguttatus</i> *	10 - <i>Cardiocondyla emeryi</i> *	11 - <i>Odontomachus brunneus</i>	12 - <i>Odontomachus ruginodis</i>	13 - <i>Paratrechina longicornis</i> *	14 - <i>Pheidole dentata</i>	16 - <i>Pheidole moerens</i> *	17 - <i>Pseudomyrmex ejectus</i>	18 - <i>Pseudomyrmex elongatus</i>	19 - <i>Pseudomyrmex gracilis</i> *	20 - <i>Pseudomyrmex simplex</i>	21 - <i>Solenopsis geminata</i>	22 - <i>Solenopsis invicta</i> *	25 - <i>Wasmannia auropunctata</i> *				
B - <i>Acacia pinetorum</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
D - <i>Erythrina herbacea</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	
F - * <i>Leucaena leucocephala</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
G - <i>Lysiloma latisiliquum</i>	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	
J - <i>Pithecellobium guadalupense</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
K - <i>Pithecellobium unguis-cati</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
M - * <i>Senna bicapsularis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
N - <i>Senna ligustrina</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0	
O - <i>Senna chapmannii</i>	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	1	1	0	1	1	0	1	1	1	

(b)

	URBAN plants / ants																								
	1 - <i>Brachymyrmex obscurior</i> *	2 - <i>Camponotus castaneus</i>	4 - <i>Camponotus floridanus</i>	5 - <i>Camponotus inaequalis</i> *	8 - <i>Camponotus sexguttatus</i> *	9 - <i>Camponotus tortuganus</i>	10 - <i>Cardiocondyla emeryi</i> *	13 - <i>Paratrechina longicornis</i> *	15 - <i>Pheidole megacephala</i> *	16 - <i>Pheidole moerens</i> *	17 - <i>Pseudomyrmex ejectus</i>	18 - <i>Pseudomyrmex elongatus</i>	19 - <i>Pseudomyrmex gracilis</i> *	20 - <i>Pseudomyrmex simplex</i>	22 - <i>Solenopsis invicta</i> *	23 - <i>Tapinoma melanocephalum</i> *	24 - <i>Technomyrmex difficilis</i> *	25 - <i>Wasmannia auropunctata</i> *							
A - * <i>Acacia chundra</i>	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	
B - <i>Acacia pinetorum</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
C - * <i>Cassia bakeriana</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
D - <i>Erythrina herbacea</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
E - * <i>Erythrina variegata</i>	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
F - * <i>Leucaena leucocephala</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
G - <i>Lysiloma latisiliquum</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
H - * <i>Lysiloma sabicu</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
I - * <i>Pithecellobium arboreum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
J - <i>Pithecellobium guadalupense</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
L - * <i>Senna alata</i>	1	1	0	0	0	1	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	
M - * <i>Senna bicapsularis</i>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
N - <i>Senna ligustrina</i>	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	
O - <i>Senna chapmannii</i>	1	0	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	0	1	1	0	
P - * <i>Senna polyphylla</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Q - * <i>Senna surattensis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	

Figure 12.3. Legume plants with extrafloral nectaries and ants in (a) natural and (b) urban habitats in south Florida – species not native are highlighted.

individuals available (*C. fistula* – 4; *S. bicapsularis* – 5; *L. sabicu* – 4). Combining our past observations with the results of the deliberate samples, and including only the plant species and ant species for which we had documented an association, we can create a matrix of interactions for plants in natural and urban environments (Figure 12.3).

We can see that there is a greater variety of legume plants with EFNs in urban areas (16 species vs. 9 in the natural areas for the genera monitored in our study), as many of the urban plants are non-native (10 of the 16 species monitored) and only 2 non-native plants were encountered in the natural areas. There are more species of ants observed to be associated with the nectary-bearing legume plants in natural areas (21 species vs. 18 observed in urban areas). In both urban and natural areas, more than half of the ant species associated with EFN-producing legumes are not native to south Florida (13/21 in natural areas; 12/18 in urban areas).

The more common a plant species is in natural areas, the larger number of associated ant species it had: *Senna chapmannii* was observed in association with 17 of the 21 ant species in natural areas. This species is also one of the most popular and heavily promoted plants for butterfly gardening (Minno & Minno, 1999) and is widely planted in both home landscapes and city beautification projects (Figure 12.1 a, d); in urban sampling we found that it was associated with 12 of the 18 ants encountered in urban samples.

It appears that the more common a plant species is, the greater the proportion of its ant associates are non-native: of the ants associated with *S. chapmannii*, in natural areas all of the non-native ant species were its associates, and only five out of eight native ant species were its associates. In urban sampling, all but one of the non-native ant species were its associates, and only one of the six native ant species encountered associated with *S. chapmannii*. Less common in natural areas, *Senna ligustrina* is associated with a total of six species of ants in natural areas, and four of those are native ants; in urban areas, where it is also widely planted for butterfly gardens, three of the four associated ant species are non-native. Also infrequent in natural areas, but very characteristic of the pine rockland habitat, *Acacia pincetorum* was found associated with only two ant species in natural areas, one native, the other non-native; in urban areas, where it is utilized as a hostplant in butterfly gardening, both of its ant associates were non-native.

Lysiloma latisiliquum, a native pioneer tree species in pine rocklands that grows larger as succession proceeds to hardwood hammocks, is associated with seven ant species in natural areas, five of which are native ants; it is widely planted in native plant landscaping (Figure 12.1 a), and in urban area sampling we found only two ant associates, one native, one non-native. This apparent sparsity of urban ant associations contrasts with some very attractive non-native woody species which, in urban areas, had many more associated ant species than some of the native hostplants (e.g., *Acacia chundra* with four species, three of which were non-native; *Senna alata* with nine species, four of which were non-native). The invasive *Leucaena leucocephala* and *Senna bicapsularis* were each associated with only two ant species, and all of those ant associates are non-native.

Network nestedness analysis using ANINHADO software (Aninhado 3.0.2) (Guimarães & Guimarães, 2006), and network-level analysis using BIPARTITE package (Bipartite 2.05) for R software (R software v. 3.1.2, R Development Core Team, 2014) (Dormann et al., 2009), allows us to compare the structure of these different communities in a preliminary analysis. Such analyses can elucidate

Table 12.1 Network Metrics for Interactions between Selected Legume Plants and Ants in Natural versus Urban Habitats of Southern Florida

Network metrics	Natural habitat	Urban habitat
Number of plant species	9	16
Number of ant species	21	18
Number of associations	42	52
Mean number for plant species	1.00	1.49
Mean number for ant species	1.94	1.28
Network connectance	0.245	0.180
Nestedness value (NODF)	46.78 ($P < 0.01$)	40.13 ($P < 0.01$)
Robustness/resilience to random extinction of partners for plants	0.750	0.676
Robustness/resilience to random extinction of partners for ants	0.674	0.695

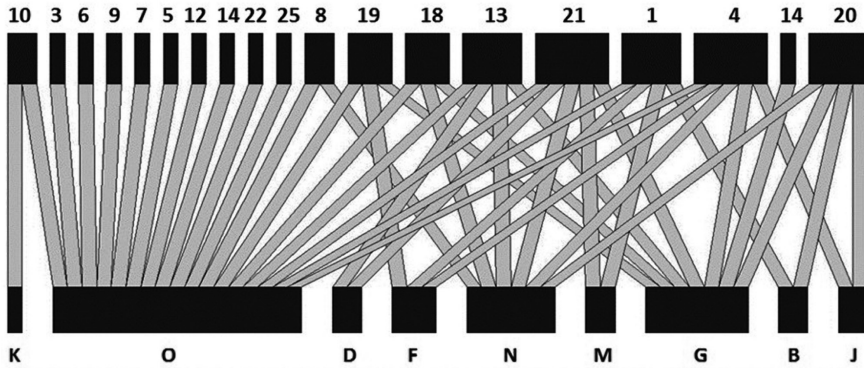
Values of specialization or dependence asymmetry cannot be calculated for qualitative data (binary matrices).

the general patterns of ant-plant interactions, as well as the extent of nestedness (Lewinsohn & Inacio Prado, 2006) and specialization of interactions in these different communities across the south Florida landscape, as others have done for ant-plant associations in other parts of the world (Diaz-Castelazo et al., 2010; Dattilo et al., 2013). Our sampling was not as extensive or as quantitative as some recent studies have been (Ivens et al., 2016; Sendoya et al., 2016), but we present our findings as they allow another basis for comparison.

Using the qualitative data from the simple matrices of associations shown in Figure 12.3, we estimated the nestedness value (NODF estimator) compared to the nestedness value for each one of the 1,000 network replicates for each interaction matrix, using ANINHADO software. We found that both networks (natural and urban areas) were significantly nested (Table 12.1): both the network for natural areas, with its NODF value of 46.78, and the network for urban areas with its NODF value of 40.13, were higher ($P < 0.01$) than the NODF values of 1,000 random networks. For the same qualitative interaction matrices, we estimated with BIPARTITE package of R software (Dormann et al., 2009) using the “Networklevel” function, the Shannon diversity of interactions, the Niche overlap of each trophic level and the Robustness for each trophic level (against secondary extinctions); network-level specialization and dependence asymmetry were not estimated given that our interaction data were binary matrices.

For natural areas (Figure 12.4a; Table 12.1), the network has low connectance (0.245, 1 being the highest connectance possible). With more species at the higher trophic level (ants), 5 was the highest degree of association for ant species (the most connected ant species in the network had interactions with five plant species). It is a non-modular network since it has only one compartment or module. This network

(a) Natural areas



(b) Urban areas

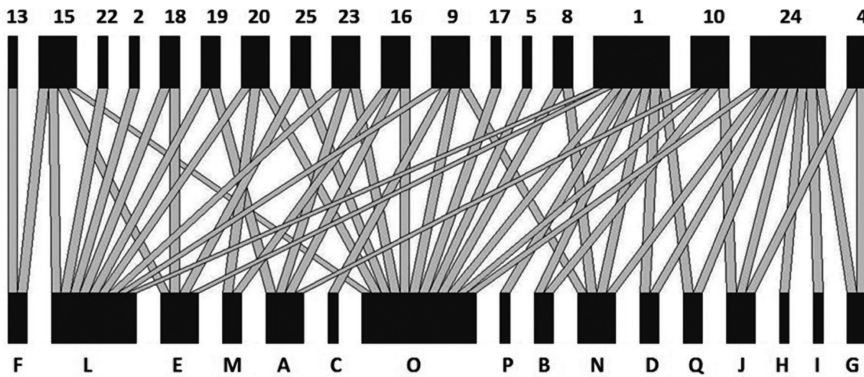


Figure 12.4. Graphs of interactions for ants and plants in (a) natural and (b) urban areas from network analyses. Plant species are: A, *Acacia chundra*; B, *Acacia pinetorum*; C, *Cassia bakeriana*; D, *Erythrina herbacea*; E, *Erythrina variegata*; F, *Leucaena leucocephala*; G, *Lysiloma latisiliquum*; H, *Lysiloma sabicu*; I, *Pithecellobium arboreum*; J, *Pithecellobium guadalupense*; K, *Pithecellobium unguis-cati*; L, *Senna alata*; M, *Senna bicapsularis*; N, *Senna ligustrina*; O, *Senna mexicana* var. *chapmannii*; P, *Senna polyphylla*; Q, *Senna surattensis*. Ant species are: 1, *Brachymyrmex obscurior*; 2, *Camponotus castaneus*; 3, *Camponotus emeryodicatus*; 4, *Camponotus floridanus*; 5, *Camponotus inaequalis*; 6, *Camponotus planatus*; 7, *Camponotus rasilis*; 8, *Camponotus sexguttatus*; 9, *Camponotus tortuganus*; 10, *Cardiocondyla emeryi*; 11, *Odontomachus brunneus*; 12, *Odontomachus ruginodis*; 13, *Paratrechina longicornis*; 14, *Pheidole dentata*; 15, *Pheidole megacephala*; 16, *Pheidole moerens*; 17, *Pseudomyrmex ejectus*; 18, *Pseudomyrmex elongatus*; 19, *Pseudomyrmex gracilis*; 20, *Pseudomyrmex simplex*; 21, *Solenopsis geminata*; 22, *Solenopsis invicta*; 23, *Tapinoma melanocephalum*; 24, *Technomyrmex difficilis*; 25, *Wasmannia auropunctata*.

has a Shannon diversity (of interactions) value of 3.73, in which plants have higher diversity of interacting partners (1.94), but ants have higher niche overlap than plants (0.53, vs. 0.25, of a possible maximum value of 1). In this natural areas network, plants are more robust or resilient to random extinctions of partners (i.e. ants) than the opposite.

For urban areas (Figure 12.4b; Table 12.1), the network has a very low connectance (0.180, lower than the natural areas network). This urban network also has more species at the higher trophic level (ants), as does the natural areas network, 8 being the highest degree of association for ant species (the most connected ant species in the network had interactions with eight plant species). It is also a non-modular network since it has only one compartment or module. Its Shannon diversity (of interactions) value is 3.95, in which plants have a slightly higher diversity of interacting partners (1.49), and ants have a slightly higher niche overlap than plants (0.282, vs. 0.218, out of a maximum value of 1), both less dramatic than the differences in the natural areas network. In the urban areas network, plants and ants are similarly robust or resilient to random extinctions of partners.

Like other mutualistic networks, ant-plant networks have been shown to be nested (Guimarães et al., 2006), with a core of reciprocal generalists plus specialist species that interact with generalists. Symbiotic interactions (such as those found with myrmecophytes) are species-poor and compartmentalized, compared with non-symbiotic interactions (such as those with myrmecophylic ant-plant interactions, like those in this study) which are species-rich and nested (Guimarães et al., 2007). In south Florida natural areas, the generalist ant species (with the highest number of plant associates) are *Camponotus floridanus* and *Solenopsis geminata*; the generalist plants are *S. chapmani* and *L. latisiliquum* (as discussed earlier), all native species. In urban areas, the ant species with highest number of plant associates are *Brachymyrmex obscurior* and *Tapinoma melanocephalum*; the most generalist plants are *S. chapmani* and *S. alata*, one native and one exotic species on each side of the interaction.

In a study comparing networks in the same location sampled ten years later, both networks had similar nested topology; even with the presence of new species a decade later, the contributions of each species to nestedness stayed the same (Diaz-Castelazo et al., 2010). Our comparison of disturbed urban environments and relatively undisturbed natural areas represents the most extreme case of how ant-plant networks have changed in south Florida over recent decades. The severity of these changes is such that species in the urban network show lower connectance and more resilience to random extinction of their partners. The pervasive use of pesticides to control arthropods in urban areas is common, and Miami gardens and city landscapes are no exception. This may be why there were fewer ant species and a lower number of associations found in urban areas. Future sampling should distinguish between “green” areas, where pesticide use is limited, and those maintained by conventional means.

Our first look at these comparisons provides suggestions of some interesting patterns in associations between legume plants with extrafloral nectaries and ants in natural and urban areas of south Florida. It seems that in many situations,

non-native ants are a perfect fit with legume plants with extrafloral nectaries in both natural and urban areas. These facultative mutualisms may facilitate the naturalization and colonization of horticultural species escaping from cultivation, especially if their ant partners provide them with some protection against generalist herbivores. Since introduced plants do not usually have to contend with coevolved, specialized herbivores, they may gain a competitive advantage. Future studies on the details of interactions of various plant species with the ants utilizing their nectar may allow us to see which ants are mutualists, and which are simply “*aprovechados*” (opportunists, sensu Soberon & Martinez del Rio, 1985), taking advantage of the reward but providing no services, or interfering with benefits from mutualist ant partners. Through this work we hope to better understand the ecology of ant-plant interactions in disturbed environments and assess their potential to facilitate invasive species.

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