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Ant-Plant Interactions between Native Ants and Non-Native Plants with Extrafloral Nectaries: New Insights from the Brissago Islands (Canton Ticino, Switzerland)

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Abstract: Many plants bear extrafloral nectaries (EFNs) that produce a sweet secretion attracting ants (and other arthropods), which in return often protect plants from herbivory. These interactions are common in the tropics and subtropics but rarer or absent in temperate regions. Yet, several plants with EFNs are cultivated in temperate regions, but it is unknown if their EFNs are functional, and if ants visit them. Therefore, we surveyed EFNs and visitors in 16 non-native plant species cultivated at the botanical garden of the Brissago Islands in the Southern Alps. EFNs appeared non-functional in *Bauhinia yunnanensis* and *Bignonia capreolata*, whereas nectar was visible in nine species (*Erythrina crista-galli, Gossypium hirsutum, Kennedia rubicunda, Passiflora caerulea, P. racemosa, Senna hebecarpa, S. mexicana, Tecoma stans, Thunbergia grandiflora*) and cryptic in the remainder (*Ba. corniculata, Clerodendrum bungei, Cylindropuntia imbricata, Opuntia engelmannii, Vanda coerulea*). Five ants (*Formica fusca, Lasius emarginatus* – the most common, *Myrmica rubra, Tetramorium* sp., *Temnothorax unifasciatus*) and two wasps (*Sceliphron destillatorium, Vespula vulgaris*) visited EFNs. *Tetramorium* appeared as the most abundant and resource dominant of the three ant species found on *S. mexicana.* EFNs of non-native plants cultivated outdoors in temperate regions could represent an important additional food resource for ants and other arthropods, thus, shaping their community nutritional ecology.

Key words: Ant-plant mutualism, exotics, invasive plants, plant defense, San Pancrazio

Riassunto: Interazioni tra formiche indigene e piante esotiche attraverso nettari extraflorali: novità dalle Isole di Brissago (Cantone Ticino, Svizzera)
Molte piante posseggono i nettari extraflorali (NEFs) che producono una secrezione dolce che attrae le formiche (e altri artropodi) i quali spesso ricambiano la pianta proteggendola da insetti erbivori. Queste interazioni sono frequenti nei tropici e nei subtropici ma più rare o assenti nelle regioni temperate. Nonostante ciò, diverse piante con NEFs sono coltivate in zone temperate, ma non si sa se i loro NEFs sono funzionali e visitati dalle formiche. In questo lavoro, abbiamo quindi studiato i NEFs e gli invertebrati che le visitano in 16 specie esotiche coltivate nel Parco Botanico delle Isole di Brissago al Sud delle Alpi della Svizzera. Il nettare extraflorale è stato osservato in nove specie (*Erythrina crista-galli, Gossypium hirsutum, Kennedia rubicunda, Passiflora caerulea, P. racemosa, Senna hebecarpa, S. mexicana, Tecoma stans, Thunbergia grandiflora*), era criptico in cinque (*Bauhinia corniculata, Clerodendrum bungei, Cylindropuntia imbricata, Opuntia engelmannii, Vanda coerulea*), mentre in due specie (*Ba. yunnanensis* and *Bignonia capreolata*) i NEFs sono risultati non funzionali. Cinque specie di formiche (*Formica fusca, Lasius emarginatus* – la più comune, *Myrmica rubra, Tetramorium* sp., *Temnothorax unifasciatus*) e due vespe (*Sceliphron destillatorium, Vespula vulgaris*) hanno visitato i NEFs. Delle tre specie di formiche trovate su *S. mexicana, Tetramorium* sp. sembra essere la più abbondante e quella che domina maggiormente le risorse alimentari. I NEFs di piante esotiche coltivate all'aperto in regioni temperate potrebbero rappresentare una risorsa alimentare importante per formiche e per altri artropodi, ciò che potrebbe influenzare l'ecologia nutrizionale delle loro comunità.

Parole chiave: Mutualistmo formiche-piante, piante invasive, difesa delle piante, San Pancrazio

INTRODUCTION

Ants on plants do not always mean harm for the plant. In fact, some ferns and members in at least 115 families of flowering plants bear extrafloral nectaries (EFNs) that secrete sugary water attracting ants and other aggressive arthropods that send off, remove, and/or kill insect herbivores (Bronstein et al., 2006; Weber & Keeler, 2013). These ecologically important EFN-mediated interactions, also called ant-plant protection mutualisms because both the plant and ants benefit from the interaction, are widespread in many kinds of vegetation worldwide, especially in the tropics and subtropics (Rico-Gray & Oliveira 2007). EF nectar can be an important food resource for ants, shaping the ecology of ant communities (e.g., Schroeder et al., 2010) and of entire canopy arthropod communities (Blüthgen et al., 2000).

Invasive ant species visiting EFN-bearing plants can affect the ecology of native ant communities (e.g., Savage *et al.*, 2009), with still poorly known consequences for natural and agricultural environments (Oliver et al., 2008; Lach & Thomas, 2008). Such consequences have been found to be rather detrimental for the native species (e.g., Savage et al., 2009; Eichhorn et al., 2011), although in few cases, both invasive and native ants may benefit from the EFNs (e.g., Lach et al., 2009). From the plant's perspective, EFN-bearing plants in regions that naturally lack ants, such as Hawaii, may actually benefit from invasive ant species (Keeler, 1985), whereas the reverse case of non-native EFN-bearing plants visited by native ants is to our knowledge undocumented.

An opportunity to study this reverse case is represented by mild temperate regions in which several subtropical plants are cultivated, some of which may bear EFNs. Compared to subtropical and tropical communities, temperate plant communities have a lower proportion of EFN-bearing plants or none (e.g., Keeler, 1980; see Rico-Gray & Oliveira, 2007, for a review). Therefore, EF nectar is probably not a mayor dietary component of ants in temperate regions. However, it remains unclear, whether this pattern can change in places with cultivated EFN-bearing plants accessible to native ants. Also, it is unknown whether EFNs of such plants are actually functional.

To fill this gap in our knowledge, here we report about non-native, EFN-bearing subtropical plants cultivated in the botanical garden of the Brissago Islands on the Lake Maggiore (southern Switzerland). Owing to the mild microclimate formed by the lake and the surrounding mountains, most of these subtropical plants are cultivated outdoors in the garden, and their EFNs are thus accessible to native ants of the islands. We asked: (1) Are EFNs of these non-native cultivated plants functional? (2) What ants and other arthropods visit them? (3) Are there any patterns in ant distributions on the plants? To address these questions we gathered observational data during the main flowering period of the selected EFN-bearing plants in the garden, coinciding also with the main period of ant activity. We finally discuss implications of our findings for our understanding of these interactions in mainland regions of the Southern Alps where such non-native EFN-bearing plants can be cultivated in private yards and public spaces.

MATERIAL AND METHODS

The study was carried out at the botanic garden of the Brissago Islands (San Pancrazio Island, Canton Ticino, Switzerland; latitude 46° 08' and longitude 08° 44'), which is located on Lake Maggiore at about ca. 1km from the coastal village of Porto Ronco. For our survey we selected 16 non-native EFN-bearing species from eight families (Acanthaceae, Bignoniaceae, Cactaceae,

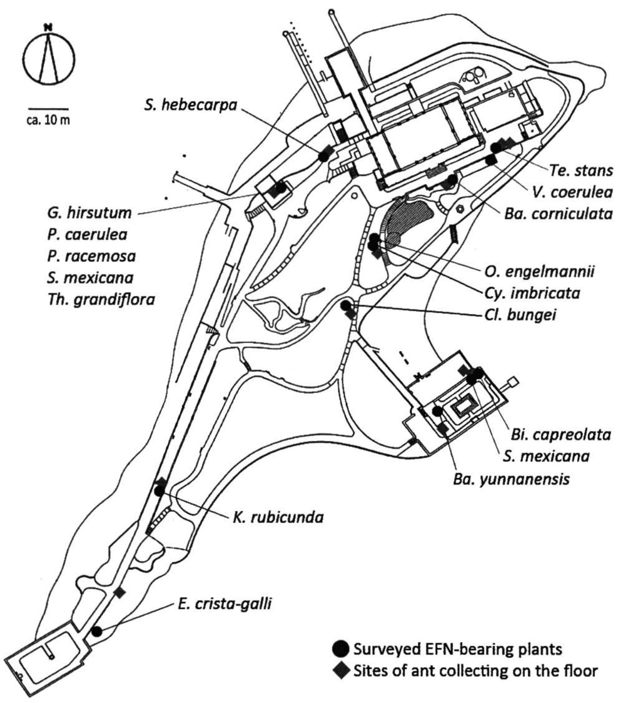

Figure 1: Location of surveyed EFN-bearing plants in the botanical garden of the Brissago Island and sites of ant traps. The botanical garden occurs on the larger of the two Brissago Islands, called San Pancrazio. See tab. 1 for full scientific names of plants. Map courtesy of Parco Botanico del Cantone Ticino, Isole di Brissago.

Lamiaceae, Leguminosae, Malvaceae, Orchidaceae, Passifloraceae), from different parts of the world, and with EFNs on different locations on the plant (see table 1 for the full information for each species). The location of these plants in the garden is illustrated in figure 1. For species selection we compared the data base of plant species cultivated at the garden of the Brissago Islands (Parco Botanico del Cantone Ticino, Isole di Brissago, Index Plantarum, unpublished list) with lists of known genera bearing EFNs (Keeler, 2012, accessed July 2012; Marazzi et al., 2012), and verified EFN presence in situ. We excluded myrmecophytic species.

We surveyed one to two specimens per species, every three to four days in the morning (07:30-09:30) and early afternoon (13:00-15:00) during eight consecutive weeks in July-September 2012 (for a total of 12 survey days). We also surveyed them once (to twice) a week in the morning for three consecutive weeks in July-August 2013 (for a total of four survey days). Whenever possible we selected sunny days to avoid biases towards absence of visitors caused by adverse climate conditions. Three taxa were surveyed only in 2012, because they were not available in 2013.

For each selected plant we recorded the presence or absence of nectar, ants, and other arthropods visiting the EFNs. Presence of EF nectar was considered "visible", if a droplet could be recognized by naked eye or using hand magnifier lenses, and "cryptic", if no droplet was visible, but ants would visit the supposed EFN location indicative of nectar secretion. We also documented the presence of aphids and whether ants were tending them.

In cases with more than one ant species occurring simultaneously on a plant, we additionally documented which ant species and approximately how many individuals of each species were present on a given branch during 10-30 seconds per branch (to avoid to count the same ant on different branches). Ant abundance was divided in three ranges of minimum-maximum number of individuals observed: i) 1-5, ii) 5-10, and iii) more than 10. To obtain the total abundance of each species on the plant we summed the minimum estimates for each branch and day. To test whether differences in abundance of these species on the plant and their presence alone or with another species on individual branches were significant we applied the non-parametric Kruskal-Wallis rank analysis for more than two independent samples implemented in the software InfoStat 2013 (Di Rienzo et al., 2013; significance level at p=0.05).

Throughout the study, we documented EFNs and ants in situ with color photographs without using filters or altering colors with image processing software (original photographs can be requested by email to Brigitte Marazzi). A number of workers per ant species was collected and fixed in alcohol for identification.
Finally, to know whether there were any ant species that were not visiting EFNs we assessed ant species diversity on the ground surrounding the EFN-bearing plants. We used sweet traps consisting of chocolate powder and breadcrumbs on the ground at about 0.5-1 m from the EFN-bearing plant (each trap was on a piece of colored paper for easy recognition; see fig. 1). We set up a total of 12 traps over two non-consecutive days (eight and four traps, respectively), left them for about 2.5 hours (11:30-14:00), and then collected and fixed the ants in alcohol for identification. We compared our results of ant diversity with published ant lists from other places in the Southern Alps where the myrmecofauna is well known, including the Sant'Apollinare Island next to the San Pancrazio Island with the botanic garden (Della Santa, 1988; Pronini, 1989; Giacalone & Moretti, 2001; Neumeyer, 2005; Isabella Giacalone-Forini & Anya Rossi-Pedruzzi, 2012-2013, unpublished data). Note that, throughout this paper, when names of genera are abbreviated, we indicate the minimum amount of letters necessary to easily distinguish genera beginning with the same letters (for example: *Ba.* for *Bauhinia* vs. *Bi.* for *Bignonia*).

RESULTS

Results of the surveys for each selected EFN-bearing species and visiting arthropods are summarized with scientific names and authorities in tables 2, 3, 4 and illustrated in figure 2. Weather conditions during the survey days were sunny, warm, except one partly rainy day in 2013. Next, we present results for each research question.
Are EFNs in non-native cultivated plants functional? --- Yes. We observed visible EFN secretion in nine species during the entire period of the survey (tab. 2; see also fig. 2). Nectar secretion was cryptic in five species where ants appeared to promptly remove the nectar. EFNs on axillary buds of *Bignonia capreolata* appeared non-functional, as ants were only observed on leaves (therefore, we are unable to use ant presence as an indication of cryptic EFNs in this case). In *Bauhinia yunnanensis*, stipules did not appear to be modified into secretory structures, and ants were never observed around stipules (yet, in few cases in 2013, they were visiting floral nectaries).
EFNs on inflorescences secreted nectar as long as floral buds were developing. EFNs on leaves and stipules secreted also during the vegetative phase, especially during early to late leaf developmental stages. Only in *Senna* species were EFNs of older leaves also secreting.
What ants and other arthropods visit EFNs? --- All EFN-visiting taxa observed belong to the order Hymenoptera and families Formicidae (5 species [spp.] from the genera *Formica*, *Myrmica*, *Lasius*, *Tetramorium*, and *Temnothorax*) and Vespidae (2 spp. from the genera *Sceliphron* and *Vespula*) (see tab. 3 and fig. 2). An additional four ant species were found only on the ground (*Formica cinerea*, *L. psammophilus*, *Solenopsis fugax*, and *Tem. nylanderi*; tab. 3). We observed no aphids on plants in 2012, while some occurred on inflorescences of *Tecoma stans* in 2013, and ants both tended the aphids and visited the EFNs. Ants occurred on almost all plants with actively secreting EFNs (except *Passiflora* spp.). *Lasius emarginatus* was by far the most common ant species, regularly visiting the EFNs from a total of 13 plant species, whereas *Tetramorium* sp. was found only on *S. mexicana* (Bagno Romano) and *Myrmica rubra* on *Clerodendron bungei*. Both wasp species regularly visited *Ba. corniculata* (fig. 3), and *Sceliphron* was observed on EFNs of *S. hebecarpa* in one occasion. These observations appeared obvious enough that no statistical analyses were necessary.
Are there any patterns in ant distribution on plants? --- Nine EFN-bearing plants were each visited by one ant species throughout the survey, and five plants were each visited by simultaneously two to three ant species (tab. 2). EFNs were never visited by more than one species at the time. In *Cl. bungei*, *Cy. imbricata*, and *Kennedia rubicunda* the respective two observed ant species usually appeared on separate parts of the plant, whereas in *Clerodendron* and *Opuntia engelmannii* they sometimes co-occurred on the same branch (data not shown; but see fig. 2N). In contrast, in *S. mexicana* of the Bagno Romano the three ant species occurred simultaneously on the same plant, but only two species at the time shared the same branch. This cultivated *Senna* shrub (up to 80 cm tall) consisted of 11 branches reaching out from the main plant axis near the ground. In the detailed survey (for a total of nine survey days; tab. 4), *Tetramorium* sp. was almost significantly more abundant than *F. fusca* and *L. emarginatus* (p=0.0525; tab. 5), with a peak of a minimum estimate of 37 individuals on the plant (fig. 3). The combinations of presence or absence of species on individual branches during the survey were significantly different among each other (p=0.0039; tab. 5). *Tetramorium* sp. tended to be more frequently the only species on a given branch than were the other species and, when together with another species, it was


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Figure 2: Surveyed EFN-bearing plants and EFN visitors in the botanical garden of the Brissago Islands. Detailed species information is listed in tables 1-3; locations of plants are illustrated in figure 1. Arrowheads indicate the respective EFNs. **A-D**, stipular EFNs in *Bauhinia corniculata*, visited by: **A**, *Formica fusca*; **B**, *Lasius emarginatus*; **C**, *Sceliphron destillatorium*; **D**, *Vespula vulgaris*. **E-H**, EFNs in inflorescences of *Clerodendrum bungei*: **E**, EFNs on dorsal side of bracts; **F**, EFNs on the calyx of floral buds; **G**, *L. emarginatus*; **H**, *Myrmica rubra*. **I-J**, EFNs on areoles of *Cylindropuntia imbricata*, visited by: **I**, *L. emarginatus*; **J**, *Temnothorax unifasciatus*. **K**, leaf EFNs in *Erythrina crista-galli*, visited by *L. emarginatus*. **L**, EFNs on the dorsal leaf side with a small nectar droplet in *Gossypium hirsutum*. **M**, EFNs at the base of pedicels in *Kennedia rubicunda*, visited by *L. emarginatus*. **N-O**, cryptic EFNs in areoles of *Opuntia engelmannii* visited by: **N**, *L. emarginatus* (the larger ant) and *Tem. unifasciatus* (the two smaller ants); **O**, *Tem. unifasciatus*. **P**, petiolar EFNs with nectar droplets in *Passiflora racemosa*. **Q**, EFNs at the base of petioles in *Senna hebecarpa*, visited by *L. emarginatus*. **R-T**, EFNs at the base of petioles in *S. mexicana*, visited by: **R**, *F. fusca*; **S**, *L. emarginatus*; **T**, *Tetramorium* sp. **U-V**, EFNs on the calyx of floral buds in *Tecoma stans*: **U**, close-up of EFNs (some with nectar droplets); **V**, EFNs visited by *L. emarginatus*. **W**, inconspicuous EFNs on the calyx of floral buds in *Thunbergia grandiflora*, visited by *L. emarginatus*. **X**, cryptic EFNs at the base of floral buds in *Vanda coerulea*, visited by *L. emarginatus*.

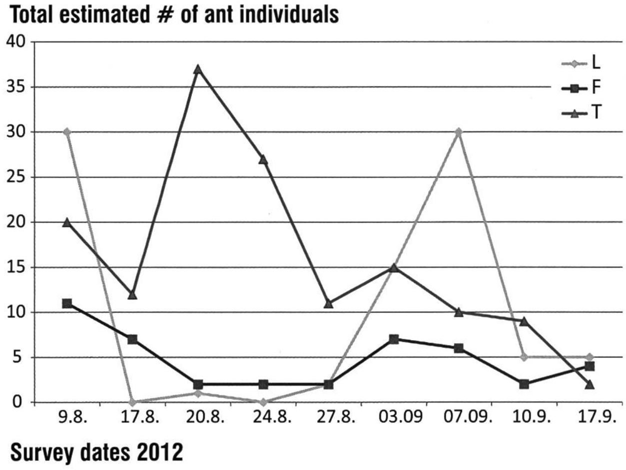

Figure 3: Total abundance of ant species visiting EFNs in *Senna mexicana*. The total number (#) of individuals for *Formica fusca* (F), *Lasius emarginatus* (L), and *Tetramorium* sp. (T) corresponds to the sum of the minimum estimate of individuals on each of the 11 surveyed branches (see tab. 4 and Material and Methods for details).

observed significantly more often with *F. fusca* than with *L. emarginatus* (tab. 5). Finally, *Tetramorium* sp. appeared to stay consistently on a same branch for longer periods of time (for up to eight consecutive observation days), while the other species appeared less consistent (no more than four consecutive observation days; tab. 4).

DISCUSSION

Focusing on cultivated non-native plants bearing EFNs in the botanical garden of the Brissago Islands, we documented presence and absence of EFN visitors during the main period of flowering and arthropod activity. This is the first survey documenting interactions between non-native plants bearing EFNs and native ants and other arthropods in a temperate region.

EFNs in cultivated non-native plants --- All but two species effectively bear functional extrafloral secretory structures, with nectar either visible in form of droplets or cryptic and revealed by ant presence (tab. 2, fig. 2). Plants differed in timing and location of nectar presentation on the plant: some species offered nectar during the flowering season only (e.g., *Clerodendron*, *Tecoma*, *Thunbergia*, *Vanda*) or also during the vegetative phase (e.g., *Bauhinia*, *Passiflora*, *Senna*). This is probably due to the fact that ants are attracted where most protection from herbivores is needed: on developing inflorescence and floral buds, in the former case, and on developing shoots and leaves, in the latter case (McKey, 1989; see also Marazzi et al., 2013). For the ants, different timing of nectar presentation means that some plant species represent a longer lasting and perhaps also a more reliable resource of food than other species.

Ants and other arthropods visiting the EFNs --- A total of five ant species and two wasp species were observed to visit EFNs (tab. 2, fig. 2). All nine ant species are native. EFN-visiting ants differed in their diversity across sites and on individual EFN-bearing plants, with *L. emarginatus* as the most common ant, found on almost all plants surveyed, and *Myrmica rubra* as the least common and found exclusively on *Cl. bungei*. Ants failed to find the conspicuous nectar droplets of the two *Passiflora* vines cultivated in the greenhouse (see fig. 2P). However, because the nearby specimens of other EFN plants (*S. mexicana* and *Thunbergia grandiflora*) were visited by *L. emarginatus*, it is possible that the vines were unattractive to the ants, were outside the ants' exploration range, or were visited outside our survey times.

Both wasps (Papp & Rezbanyai-Reser, 1997) and ants (Della Santa, 1988; Pronini, 1989; Giacalone-Forini & Rossi-Pedruzzi, 2013, unpublished ant survey) on the Brissago Islands have been studied before. In general, the five ant species foraging on EFN plants are very common and diffuse in the region (Giacalone-Forini & Rossi-Pedruzzi, 2013, unpublished ant survey). *Lasius emarginatus* is a ubiquitous ant and also the most commonly found ant species in the adjacent mainland regions (Giacalone & Moretti, 2001) and is widespread in Switzerland (Neumeyer & Seifert, 2005). *Tetramorium* species are generally common too, but their identification is impossible with morphology, which means that a genetic approach is necessary to correctly identify species (see Steiner et al., 2010; also, a survey of genetic material of sampled species is currently ongoing as part of the Swiss Barcode of Life project). *Myrmica rubra* and *Tem. unifasciatus* are usually found on trees in open land and forest habitats.

Not all ants found in the botanic garden appeared interested in or were able to detect the secreting EFNs

Table 1: Studied EFN-bearing species cultivated in the Botanical garden of the Brissago Island. The information of the specimen site in the park consists of the park section code, the description of the park area, and the accession number of the cultivated individual. Sites are illustrated on fig. 1.

Species name and authority (family)	**Specimen site in the garden (section code; description; accession number)**	**Geographic origin of species (source*)**	**EFN location on the plant**
1. Bauhinia corniculata Benth. (Leguminosae)	4D; ornamental area; XX0BRISS-0000572	Tropical South America (1)	stipules
2. Bauhinia yunnanensis Franch. (Leguminosae)	5D; ornamental area; XX0BRISS-20104366	China (2)	stipules
3. Bignonia capreolata L. (Bignoniaceae)	5D; Bagno Romano; XX0BRISS-19891506	s. North America (1)	axillary buds
4. Clerodendrum bungei Steud. (Lamiaceae)	13E; Asia; XX0BRISS-00001551	China (3)	calyx of buds, young bracts
5. Cylindropuntia imbricata (Haw.) F. M. Knuth (Cactaceae)	4E; Americas; XX0BRISS-20093756	s. North America (4)	areoles
6. Erythrina crista-galli L. (Leguminosae)	9C; coastal rocks; XX0BRISS-0000552	s. South America (5)	leaf stipels
7. Gossypium hirsutum L. (Malvaceae)	17F; northern greenhouse; XX-0-BONN-21438	Central America (1)	leaf venation
8. Kennedia rubicunda (Schneev.) Vent. (Leguminosae)	n/a ; "pergolato"; XX0BRISS-2005557	Australia (6)	pedicel, leaf stipels
9. Opuntia engelmannii Salm-Dyck ex Engelm. (Cactaceae)	4E; Americas; XX0BRISS-00003732	s. North America (4)	areoles
10. Passiflora caerulea L. (Passifloraceae)	17F; northern greenhouse; XX0BRISS-0000833	South America (5)	petiole
11. Passiflora racemosa Brot. (Passifloraceae)	17F; northern greenhouse; XX0BRISS-2009839	Brazil (1)	petiole, leaf lamina
12. Senna hebecarpa (Fernald) H.S. Irwin & Barneby (Leguminosae)	17C; near entrance stairs; XX0BRISS-00004761	s. North America (7)	petiole base
13a. Senna mexicana (L.) H.S. Irwin & Barneby (Leguminosae)	5D; Bagno Romano; XX0BRISS-20103817	southern N-America (7)	petiole base
13b. Senna mexicana (Leguminosae)	17F; northern greenhouse; XX0BRISS-20103817		
14. Tecoma stans (L.) Juss. ex Kunth (Bignoniaceae)	15B; terrace; XX0BRISS-20061517	Central and South America (5)	calyx
15. Thunbergia grandiflora Roxb. (Acanthaceae)	17F; northern greenhouse; XX0BRISS-20081533	India subcontinent to s. China (8).	bracts, calyx
16. Vanda coerulea Griff. ex Lindl. (Orchidaceae)	3E; southern greenhouse; XX0BRISS4579	India to s. China (9)	bract base

*Sources: (1) Tropicos.org. Missouri Botanical Garden. accessed 21.10.2013 URL: http://www.tropicos.org/ (2) Flora of China Editorial Committee (2010); (3) Flora of China Editorial Committee (1994); (4) Flora of North America Editorial Committee (2003). (5) Zuloaga et al. (2008); (6) APNI (Australian Plant Name Index; accessed 21.10.2013) URL: http://www.anbg.gov.au/cgi-bin/apni; (7) Irwin & Barneby (1982); (8) Parsons & Cuthbertson (2001); (9) Flora of China Editorial Committee (2009).

(tabs. 2, 3). For instance, *F. cinerea*, *L. psammophilus*, *S. fugax*, and *Tem. nylanderi* were never observed on EFN plants. This raises the question as whether they actually prefer other kinds of food. Interestingly, according to Seifert (2007) all but *Tem. nylanderi* are known to tend aphids and feed on sweet products in general, meaning that they could be censed using honey traps.

EFN-visiting ants differ in their abundance across EFN plants (tab. 2). When ants did visit EFN-bearing plants, some plants appeared more densely visited (e.g., *Senna*, *Tecoma*, *Thunbergia*) than others (e.g., *Cylindropuntia*, *Opuntia*) suggesting that EFNs in some plants are more attractive to ants for some reason. Ants are able to recruit other ants depending on the quality and quantity of the food resource found and differ in their

Table 2: Survey summary of EF secretion in non-native cultivated EFN-bearing plants and observed EFN-visiting native arthropods on the Brissago Islands (Switzerland). Summary for a total of 12 days in 2012 and 4 days in 2013. Observed presence and absence are indicated by plus (+) and minus signs (–), respectively. More than one plus sign indicates more abundant visitors (compared qualitatively with the other species on the plant). Arthropod visitors observed inconsistently throughout the survey are indicated in parenthesis. Abbreviations used: BR, Bagno Romano; GH, greenhouse.

EFN-bearing species name	EFN secretion	EFN visitor species name						
		Formica fusca	*Lasius emarginatus*	*Myrmica rubra*	*Temnothorax unifasciatus*	*Tetramorium sp.*	*Sceliphron destillatorium*	*Vespula vulgaris*
1. Bauhinia corniculata	cryptic	(+)	+	-	-	-	++	+
2. B. yunnanensis	none	-	-	-	-	-	-	-
3. Bignonia capreolata	none(?)	-	-	-	-	-	-	-
4. Clerodendrum bungei	cryptic	-	+	++	-	-	-	-
5. Cylindropuntia imbricata	cryptic	-	+	-	-	-	-	-
6. Erythrina crista-galli	visible	-	+	-	-	-	-	-
7. Gossypium hirsutum	visible	-	(+)	-	-	-	-	-
8. Kennedia rubicunda	visible	-	++	-	+	-	-	-
9. Opuntia engelmannii	cryptic	-	++	-	+	-	-	-
10. Passiflora caerulea	visible	-	-	-	-	-	-	-
11. P. racemosa	visible	-	-	-	-	-	-	-
12. Senna hebecarpa	visible	-	+	-	-	-	(+)	-
13a. S. mexicana (BR)	visible	+	++	-	-	+++	-	-
13b. S. mexicana (GH)	visible	-	+	-	-	-	-	-
14. Tecoma stans	visible	-	+	-	-	-	(+)	-
15. Thunbergia grandiflora	visible	-	+	-	-	-	-	-
16. Vanda coerulea	cryptic	-	+	-	-	-	-	-

behavior associated with discovering and controlling of the resources (Breed et al., 1987; Adler et al., 2007, Pearce-Duvet & Feener, 2010). To test whether this is the case, nectar content analyses and controlled experiments on nectar preference are necessary.

Compared to the ants, the EFN-visiting wasps almost exclusively visited *Ba. corniculata* where they were more abundant than the rather sporadic ants (tab. 2). Our observations add to the few studies on parasitoid and predatory wasps visiting EFNs in the tropics and subtropics (e.g., Wäckers, 2001; Cuautle & Rico-Gray, 2003). Interestingly, no wasp visited the visibly secreting EFNs on floral buds of the *Te. stans* cultivated nearby (see fig. 1), which were instead densely visited by *L. emarginatus*. We suspect that ant presence, or the ants themselves, on *Te. stans* could play a role in keeping the wasps away. Spiders have also been found to feed on EFN-bearing plants and protect them from herbivores (Ruhren & Handel, 1999; Whitney, 2004), but none was observed in this survey.

Patterns in the distribution of ants on plants --- The diversity of ant food search behaviors may explain at least some of the patterns that we observed in ant distributions on EFN plants. *Senna mexicana* at the Bagno Romano was visited by three species (fig. 2R-T), of which *Tetramorium* sp. was the most abundant and the only one on branches most of the time, or then preferably together with *F. fusca* than *L. emarginatus*, but the three species were never observed simultaneously on a given branch (fig. 3, tab. 4). This is reminiscent of the well-studied EFN-bearing fishhook barrel cactus (*Ferocactus wislizeni*) of the Sonoran Desert, in which the most aggressive ant species ensure control of the nectaries during the most favorable (i.e., coolest) hours of the day and allow less aggressive ants to access the EFNs only when they retreat as temperatures rise (Morris et al., 2005; Ness et al., 2006). Therefore, it is possible that the patterns in ant distributions observed in *S. mexicana* reflect differences in the ants' behavior towards ensuring access to food resources, and *Tetramorium* sp. would thus be the most resource dominant and controlling species. Controlled experiments involving also other ant spe-

Table 3: Taxonomic diversity of EFN-visiting ants and wasps and other ants surveyed on the Brissago Islands. EFN visitors are in bold.

Taxonomy	Species
Formicidae - Myrmecinae	
	Myrmica rubra (Linnaeus, 1758)
	Solenopsis fugax (Latreille 1798)
	Tetramorium sp. Mayr, 1855
Formicidae - Formicinae	
	Formica cinerea Mayr, 1853
	Formica fusca Linnaeus, 1758
	Lasius emarginatus (Olivier, 1791)
	Lasius psammophilus Seifert 1992
	Temnothorax nylanderi (Förster 1850)
	Temnothorax unifasciatus (Latreille 1798)
Vespidae	
	Sceliphron destillatorium Illiger 1807
	Vespula vulgaris (L., 1758)

cies and/or other food resources would allow us to determine whether other ants outcompete *Tetramorium* sp. or whether it is generally the most resource dominant and controlling ant.

Implications for ant-plant interactions in the Southern Alps --- Temperate regions are known in general for their lack or low proportion of EFN-bearing plants (e.g., Keeler, 1980). Although primarily descriptive, this study shows for the first time that, in such regions, EF nectar from non-native cultivated subtropical species can represent an additional food resource for many native ants (and wasps as well).

Some studies have shown that not only native but also invasive ants visit these EFN plants. For example, in Portugal, both the invasive Argentine ant (*Linepithema humile*) and a native species (*Plagiolepis pygmaea*) feed on experimentally induced extrafloral nectar in plants of *Acacia dealbata* (Eichhorn et al., 2011), an invasive Australian legume (Lorenzo et al., 2010). The Argentine ant and the invasive garden ant (*Lasius neglectus*) are well documented in several European countries, including regions of France and Italy near the Swiss border (Ugelvig et al., 2008; Rigato & Zizoli, 2008; Bertelsmeier & Courchamp, 2013). The garden ant has been reported in Switzerland (Neumeyer, 2008), and it is thus likely that both invasive species already occur and are widespread in the country and in the Southern Alps. Yet, the distribution of invasive ants in the Southern Alps is still poorly known, as only a few individuals of the invasive Pharaoh ant (*Monomorium pharonis*) have been reported so far, none of which on the Brissago Islands (Isa Giacalone-Fiorini and Anya Rossi-Pedruzzi, personal communications, in collaboration with the Swiss Biological Records Center CSCF/MCSN for the ant database currently in progress). Invasive ants would add another dimension to the study of EFN-ant interactions and the role of EFNs as a food resource for ants, as they might compete with native ants.

In conclusion, the numerous EFN-bearing plants cultivated at the botanic garden of the Brissago Islands provided a unique opportunity for a survey of EFN-facilitated interactions with ants at such northern latitude. Implications of our results could probably be extrapolated to nearby climatically similar regions. At least four of the studied species (*Cl. bungei*, *K. rubicunda*, *Opuntia* spp., and *Te. stans*) are cultivated outdoors in the Southern Alps, especially in private yards and public spaces in the surroundings of lakes, like the Lake Maggiore, but also elsewhere in milder places more to the South (Isabella Giacalone-Forini, Brigitte Marazzi, Guido Maspoli, personal observations). Furthermore, species of *Opuntia* are reported to be locally naturalized (Lauber et al., 2012). However, it is likely that

Table 4: Survey of the of ant species visiting EFNs along individual branches of *Senna mexicana* cultivated on the Brissago Island. Branches with only one ant species are shaded in light, medium, and dark gray according to the species, *Formica fusca* (F), *Lasius emarginatus* (L) and *Tetramorium* sp. (T), respectively. Numbers indicate estimates of individuals on a given branch: (1) 1-5, (2) 5-10, and (3) more than 10. Question mark indicates missing observation.

Branch	9.8.	17.8.	20.8.	24.8	27.8.	3.9.	7.9.	10.9.	17.9.
b1	F1, L2	F1,T1	T1	T1	F1, T	F1, T2	F1, T1	F1, T1	L1, T1
b2	0	T1	T2	T1	F1, T1	L2	L3	L1	F1, T1
b3	F1, L2	F1	F1, T1	F1, T1	L1	F1	F1, T1	T1	0
b4	L2	F1	T3	T1	L1	F1, T1	L2	L1	L1
b5	F1, L2	T1	T1	0	0	L2	L2	F1	F1, L1
b6	F1, L2	F1	L1, T1	0	0	F1, T1	F1	L1	F1
b7	F1, L2	T1	T1	T1	T1	F1, T1	T2	T2	F1
b8	F1, T3	F1, T1	T1	T3	T1	T1	F1, T1	0	0
b9	T3	T2	T3	T3	T1	T2	F1, T1	T1	0
b10	F2	F1, T1	F1, T1	T1	T1	F1	F, T1	L1, T1	L1
b11	?	F1, T1	T2	F1, T1	T1	F1, L2	L3	L1	L1

Table 5: Summary of Kruskal-Wallis test statistics on patterns of ant species distribution in *Senna mexicana* cultivated on the Brissago Island. Mean, standard deviation (SD), median, and H and p values from analyses (with N=9) of (a) the variable 'total abundance on the plant' and (b-c) the variable 'species distribution on branches' for the three species observed, *Formica fusca* (F), *Lasius emarginatus* (L) and *Tetramorium* sp. (T). (c) Rank list in which values sharing a common letter are not significantly different (p>0.05); letters in bold highlight the result that F+T is significantly different from L+T and F+L. Data for variables summarized in fig. 3 (for a) and table 4 (for b, c). Asterisk indicates statistical significance (p<0.05).

	Species	Mean	SD	Median	H	p-value
a)	F total	4.78	3.19	4	5.82	0.0525
	L total	9.78	12.35	5		
	T total	15.56	10.79	11		
b)	F alone	1.11	1.05	1	17.85	0.039*
	L alone	1.78	1.64	2		
	T alone	3.44	2.79	3		
	F+L	0.78	1.64	0		
	F+T	2.44	1.51	2		
	L+T	0.33	0.50	0		
	No ants	1.00	1.12	1		
c)	**Species**	**Ranks**				
	L+T	18.50	**A**			
	F+L	21.67	**A**	**B**		
	No ants	27.94	A	B	C	
	F alone	30.11	A	B	C	D
	L alone	35.56		B	C	D
	F+T	44.44			**C**	**D**
	T alone	45.78				D

more non-native, EFN-bearing species actually occur, cultivated and/or naturalized, in the Southern Alps and are visited by native ants (and wasps). Therefore, such EFN-bearing plants may contribute to shape, at least locally, the nutritional ecology of ant (and other arthropod) communities. More comprehensive studies are necessary to assess the role these plants play in the overall diet of ants (and wasps) inhabiting anthropogenic areas, as well as to understand the ants' behavior in finding and controlling the EFNs, and whether they actually provide any protection to the plants.

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