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Host-tree selection by the ant garden-initiating arboreal ponerine *Neoponera goeldii*

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From the Equator to subpolar areas, ants are very abundant, diverse, and ecologically dominant, occupying terrestrial environments from the soil to the crowns of large trees. They appeared 158–139 million years ago (Mya) (i.e., end of Jurassic, 201.3–145 Mya; early Cretaceous, 145–66 Mya) and later diversified from ground-dwelling predatory taxa, alongside the rise of angiosperms (Brady et al., 2006; Moreau et al., 2006). About 130–125 Mya, while foraging for prey on vegetation, some ant species incorporated plant-based food (e.g., sap, resin, gums, mucilage, and oils) into their diet, all while protecting the plants they patrolled through their aggressiveness and predatory behavior toward other animals ("dynastic-succession hypothesis"). This was the prelude to the establishment of diffuse defensive mutualisms, such as the evolution of extrafloral nectar (i.e., a sugary-rich ant reward offered by plants for biotic protection) that took place between the mid-Cretaceous (≈106 Mya) and the Neogene (23.03–2.58 Mya) (Lucky et al., 2013).

Arboreal nesting evolved first via arboreal nests made of carton or silk that appeared at the end of the Cretaceous (≈66 Mya). Later, plant cavities, called domatia, developed specifically for ants, characterize myrmecophytes, which appeared in Australasia and the Neotropics ≈19 Mya (Miocene), and later, ≈5 Mya, in Africa. In exchange for providing ants a nesting place, myrmecophytes are protected from phytophagous animals, competitors, and pathogens or obtain nutrients via the ant wastes that accumulate in certain domatia (Chomicki & Renner, 2015).

Ant gardens, known from the Neotropics and South East Asia, are mutualist associations between a few arboreal ant and epiphyte plant species. Their emergence was first described for the Neotropical ponerine ant *Neoponera goeldii*: a group of founding queens builds in a

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sun-exposed area of a host tree a small carton nest and then incorporates the seeds of certain epiphytes into the nest walls. After germination, the seedlings develop into mature epiphytes whose roots stabilize the nest carton, some of them also providing a food reward for the ants (e.g., extrafloral nectar, food bodies, and fruits). In turn, ant garden ants protect their epiphytes from herbivores and enrich the nest carton with nutrients. The most frequently selected epiphyte plants are *Aechmea mertensii* (Bromeliaceae), *Codonanthe calcarata* (Gesneriaceae), and *Anthurium gracile* (Araceae) (Corbara & Dejean, 1996). Furthermore, the selective attractiveness of volatiles released by the seed coat of the ant garden epiphytes is determinant, even though the seeds of some of these epiphytes have elaiosomes (i.e., food rewards mediating dispersal by ants) (Youngstead et al., 2008).

Because ant gardens represent one of the most unique forms of an ant–plant association, they need to be preserved because the epiphytes benefit from the three main advantages of ant–plant mutualisms (i.e., dispersion, protection from enemies, and food) while the ant nest is structurally secured. Ant gardens also contribute to canopy diversity through their ants and the epiphytes that are incorporated into ant nests, their commensals and parasites, and the aquatic organisms living in the tanks of bromeliads (Corbara, 2020; Orivel & Leroy, 2011; Youngstead et al., 2008). Thus, we sought to determine whether *N. goeldii* founding queens selected their host trees randomly or, alternatively, whether these trees were selected in a nonrandom way.

This study was conducted in French Guiana in 1996 for Petit Saut and 2013 for Régina (see Dejean, Petitclerc, et al., 2022, for the large number of trees with ant gardens in those years). In the lead-up to the Petit Saut dam (2750–3000 mm of yearly rainfall), between kilometer points 14 and 27 (5°6′10″ N; 52°57′52″ W–5°3′43″ N; 53°3′00″ W), we searched for the presence of ant gardens on trees or vines more than 1.5 m in height located within 250 (10 × 5 m) plots. The same approach was carried out near Régina (≈4000 mm of yearly rainfall) along Route 2 around kilometer point 118 (4°13′8″ N; 52°7′17″ W) corresponding to 90 plots (details in "Host tree survey counts" available in Dejean, Rossi, et al., 2022). Note that these ant gardens are too light to break branches during storms and so were not overlooked.

To verify if these ants selected their host plants, for each plant species sheltering an *N. goeldii*-initiated ant garden, we compared its proportion of plants to the same proportion for other species sheltering ant gardens using Pearson's chi-squared test. To ensure that the test results were not due to a particular distribution of forest communities in certain parts of the study area, we used a bootstrap procedure from the function prop.test in R. Except for species with more than 10 individuals (nonsignificant differences), we repeated the same proportion comparison tests 5000 times on subsamples of plots randomly selected from all the survey plots. We varied the sizes of these subsamples between 50% and 100% of the total number of plots inventoried in increments of 5% (for details see Appendix S1: Figures S1 and S2; Figure 1).

In both the Petit Saut and the Régina areas, nine tree or vine species sheltered *N. goeldii*-initiated ant gardens out of 17 and 15 species, respectively (Table 1). We saw a range of tree attractiveness, even for common species. First, *Davilla alata*, *D. rugosa* (Petit Saut), *Vismia guianensis*, and *V. sessilifolia* were well represented in both areas ($p < 0.05$ in Appendix S1: Figures S1 and S2; see also Table 1). Second, the results in Table 1 are nonsignificant when the p-value was higher than 0.05 (e.g., *Bellucia grossularioides* and *Isertia coccinea* in Petit Saut). Third, although likely to shelter ant gardens, certain tree species are significantly less selected than all others with ant gardens (e.g., *V. latifolia*: $p < 0.05$ in Petit Saut; Appendix S1: Figure S1 and Table 1). Finally, there are trees that are not attractive to *N. goeldii* founding queens: *Astrocaryum sciophilum* (attractive to *Anochetus emarginatus*), *Clusia* spp. (attractive to social wasps), *Jacaranda copaia*, *Byrsonima aerugo*, *Passiflora coccinea* (which very rarely shelter ant

FIGURE 1 A *Neoponera goeldii* ant garden with the tank bromeliad *Aechmea mertensii* in bloom; several seedlings are visible on the spherical nest, which was installed on a top branch of a *Vismia guianensis* (photo by Jean-François Carrias).

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TABLE 1 Plant species recorded in Petit Saut and Régina areas. For each species sheltering an ant garden we compared the proportion of individuals with a *Neoponera goeldii* ant garden to the same proportion for other species sheltering them.

Region and tree family	Tree species	No. individuals	Percentage individuals	No. with ant gardens	Percentage with ant gardens	Statistic
Petit Saut						
Arecaceae	*Astrocaryum sciophilum*	38	1.74	0	0	...
Calophyllaceae	*Mahurea palustris*	42	1.93	0	0	...
Clusiaceae	*Clusia grandiflora*	45	2.06	0	0	...
	Clusia cuneata	51	2.34	0	0	...
Dilleniaceae	*Davilla alata* (vine)	56	2.57	24	42.86	$p < 0.05$
	Davilla rugosa (vine)	24	1.10	11	45.83	$p < 0.05$
Euphorbiaceae	*Croton matourensis*	5	0.23	1	20.00	NS
	Croton nuntiens	3	0.14	0	0	...
Fabaceae	*Inga edulis*[a]	3	0.14	0	0	...
	Inga thibaudiana[a]	10	0.46	3	30.00	NS
Hypericaceae	*Vismia guianensis*	493	22.62	142	28.80	$p < 0.01$
	Vismia latifolia[c]	627	28.77	8	1.27	$p < 0.01$[c]
	Vismia sessilifolia	338	15.51	88	26.35	$p < 0.01$
Melastomataceae	*Bellucia grossularioides*	210	9.64	25	11.90	NS
Rubiaceae	*Isertia coccinea*	79	3.62	8	10.12	NS
Selastraceae	*Goupia glabra*	44	2.02	0	0	...
Urticaceae	*Cecropia obtusa*[b]	61	2.80	0	0	...
	Total	2179	...	310	14.2	...
Régina						
Bignoniaceae	*Jacaranda copaia*	5	1.05	0	0	...
Clusiaceae	*Clusia grandiflora*	25	5.25	0	0	...
Dilleniaceae	*Davilla alata* (vine)	23	4.83	15	65.22	NS
	Davilla rugosa (vine)	1	0.21	1	100.00	NS
Fabaceae	*Senna latifolia* (vine)[a]	8	1.68	3	37.50	NS
Hypericaceae	*Vismia guianensis*	209	43.91	126	60.29	$p < 0.01$
	Vismia latifolia	66	13.87	23	34.89	NS
	Vismia sessilifolia	31	6.51	25	80.65	$p < 0.05$
Malpighiaceae	*Byrsonima aerugo*	9	1.89	0	0	...
Melastomataceae	*Bellucia grossularioides*[c]	35	7.35	4	11.43	$p < 1e\text{-}3$[c]
	Clidemia sp.	1	0.21	0	0	...
	Miconia sp.[c]	13	2.73	1	7.69	$p < 0.02$[c]
Passifloraceae	*Passiflora coccinea* (vine)[a]	2	0.42	0	0	...
Selastraceae	*Goupia glabra*	26	5.46	7	26.92	NS
Urticaceae	*Cecropia obtusa*[b]	22	4.62	0	0	...
	Total	476	...	205	43.07	...

Note: Ellipses (...) indicates no individual sheltering an ant garden.

[a]Plants bearing extrafloral nectaries.

[b]Myrmecophyte.

[c]Results significantly lower than for all other trees with ant gardens.

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nests, but foraging workers forage on them), and the myrmecophyte *Cecropia obtusa* (which shelters *Azteca* ants) (A. Dejean, personal communication). Food rewards do not play a role in *N. goeldii* host-plant selection because, of the 11 plant species hosting ant gardens, only *Inga thibaudiana* and *Senna latifolia* produce extrafloral nectar (Table 1). Thus, *N. goeldii* does not install its nests at random but rather selects certain tree taxa in the two pioneer vegetal formations studied.

How can this be possible? Before their nuptial flight and then their nest-site selection, *N. goeldii* queens, at both the larval and imaginal stages, are bred in contact with parts of host tree branches surrounded by the nest. Indeed, selective host tree attractiveness was demonstrated for ants building their nests in contact with host tree leaves as winged queens select them rather than those from other plant species. Here, both "preimaginal learning" (during larval life) and "early learning" (the first days of adult life) combine to determine which trees to select (Djiéto-Lordon & Dejean, 1999; this also shows that ants can be experimentally conditioned to a nonattractive plant by breeding them in contact with this plant during larval and early learning). Thus, a "local tradition" of nest-tree selection has been noted for many arboreal ants (Dejean et al., 2008; Gibernau et al., 2007; Rocha et al., 2020 and papers cited therein).

Hence, young *N. goeldii* queens are first attracted by certain host trees and then by ant garden epiphyte seeds thanks to a mixture of volatiles located on the seed surface; they then sow them into the nutrient-rich carton nest (later the workers take over). Common to other ant garden ants, this behavior seems genetically determined because these compounds are not attractive to other ant species (Corbara, 2020; Orivel & Leroy, 2011; Youngstead et al., 2008). This unusual double attractiveness with different origins, larval and early learning versus genetic attractiveness, likely occurs for other ant garden ants.

Because they also develop well in riparian areas, in terms of conservation, *N. goeldii*-initiated ant gardens are not at risk in Amazonia, where climate change translates into heavier rainy seasons, ensuring the presence of streams and rivers (Dejean et al., 2022). Furthermore, they abound in the scarce Guianese citrus tree orchards, showing that these trees, introduced into the Neotropics, contain adequate attractive compounds (Corbara et al., 1999). Attraction to introduced trees (e.g., citrus and mango trees) has been noted for the ant garden ant *Azteca gnava* (Dolichoderinae) (Morales-Linares et al., 2016). For *N. goeldii*, this is propitious, as long as farmers do not use insecticides. Indeed, this ant species provides biotic protection over its host plants by eliminating defoliators through its territoriality and predatory behavior, whereas it does not attend hemipterans, some being agricultural pests (Orivel & Leroy, 2011; A. Dejean and B. Corbara, personal observation).

Trees are characterized, among other traits, by their architecture, size, and chemical compounds (e.g., involved in plant defense from enemies). Architecture and size triggered a difference in habitat preferences among ant garden ants with some repercussions for epiphytes. For instance, since *N. goeldii* nests in sun-exposed areas, its associated tank bromeliads *A. mertensii* are small, with an amphora shape to limit light incidence, whereas those associated with *Camponotus femoratus*, which nests in shady areas, are larger and wider. For attraction based on chemical compounds, we show here a vast selection of trees and vines from attractive to nonselected trees and vines and all intermediate cases. Thus, *N. goeldii* falls between the case of *A. gnava*, with no specificity or *C. femoratus* (Formicinae) with a certain preference among canopy trees, and the case of two species of *Crematogaster* (Myrmicinae) that build their nests exclusively on giant bamboos in Malaysia (Dejean et al., 2022; Morales-Linares et al., 2016; Orivel & Leroy, 2011; this study).

In conclusion, we show that the different types of interactions with plants influence the environment of an insect through the selection of its host tree and a multispecific mutualistic association with epiphytes. This results in ecosystem engineering where nest construction involves complex associations with epiphytes that are selected, sown, grown, and preserved from enemies. Here, the selected host tree species, including pioneer, riparian, and introduced cultivars, should likely permit this association to survive global climate change.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Dejean, Rossi, et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.20154404.v4.

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