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Ant Gardens

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Ant gardens are original associations involving a few species of arboricolous ants (i.e., nesting and dwelling on trees) with epiphytic plants (i.e., growing onto other plants), in which an ant society nests into the root system of a cluster of epiphytes. The presence of ants nesting in the roots of epiphytic plants is very common throughout the tropics. However, in most cases, this complex does not constitute an ant garden. Ant gardens, which are only known from the Neotropics and South-East Asia [4], arise when a colony settles first on the supporting tree and builds a nest, followed by the growth of seeds incorporated into the nest [2, 3, 5].

AQ1

AQ2

AQ3

In 1901 the German naturalist Ernst Ule was the first to describe and name this kind of ant-plant association, which he observed in Brazil. Ule hypothesized that the ants initiated the installation of the epiphytes, hence his characterization of the complex as a “garden.” William Morton Wheeler, the leading specialist on ants of the first half of the twentieth century, thought this scenario was far-fetched, considering that the ants arrived secondarily in an already established structure. Ule’s hypothesis was validated by field observations much later in the 1980s and 1990s.

Initiation of an Ant Garden

The process leading to an ant garden was first described in detail for the ponerine ant *Neoponera goeldii*. In this case, a group of several founding queens select a pioneer tree well exposed to sunlight and build a small carton nest rich in humus. They then incorporate seeds belonging to several species of epiphytes in the walls of the nest. The ants specifically harvest seeds that are particularly attractive to them, mainly *Aechmea mertensii* (Bromeliaceae), *Codonanthe calcarata* (Gesneriaceae), and *Anthurium gracile* (Araceae) (Fig. 1). The epiphytes germinate and develop on the rich substrate, quickly producing roots that penetrate and wrap the walls of the nest, so that they hold it firmly to the supporting branch. As the colony grows, workers continue to add organic matter – as well as other seeds when available – to the garden, in which the plants thrive (Fig. 2a).

Fig. 1

Neoponera goeldii collecting a seed of the epiphyte *Anthurium gracile*, French Guiana. (Photo by Jérôme Orivel)

Fig. 2

In French Guiana, in the ant gardens housing the Bromeliaceae *Achmea mertensii*, the morphology and physiology of the plant will be modified according to the ant species initiating the association. **(a)** Ant garden initiated and inhabited by *Neoponera goeldii*. **(b)** Ant garden initiated and inhabited by *Camponotus femoratus* and *Crematogaster levior* living in parabiosis

In the same area, ant gardens involving the same main epiphytes species are commonly initiated by two other ant species, *Camponotus femoratus* (Formicinae) and *Crematogaster levior* (Myrmicinae). These ants live in a very close association with each other, called parabiosis (Figs. 2b, 3, and 4). Considering their large geographic range around the Amazonian forest and beyond, ant gardens initiated by *N. goeldii* and by the two parabiocic ants can be regarded as a markedly successful association.

Fig. 3

A young ant garden initiated by *Camponotus femoratus* and *Crematogaster levior* living in parabiosis

Fig. 4

An old ant garden initiated by *Camponotus femoratus* and *Crematogaster levior* living in parabiosis, French Guiana. (Photo by Jean-François Carrias)

Identity of the Ant and Plant Partners

The true garden ants represent very few species, as do the garden plants with which they obligatorily associate. Both in the New World and Old World known garden ants are drawn from four subfamilies: Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae.

To initiate a garden, an ant must show two essential characteristics: it must (a) build an arboreal nest with materials rich in humus, and (b) collect and incorporate into the nest seeds of suitable epiphytes. Few species among those that are commonly found in ant gardens have been studied in detail in either the field or the laboratory, and therefore it is not possible to know with certainty if they initiated the ant garden or not. Especially when they get old, ant gardens can secondarily be occupied by opportunistic arboreal ants which are not true garden ants, either because the ant colony that initiated the ant garden died or because other ants have partially invaded the ant garden. Good

candidates as true garden ants, then, are those that are never encountered nesting outside of ant gardens, although even then we cannot be entirely certain without direct observation of the initiation process.

The essential characteristic of ant garden plants is that their seeds are attractive to ants. Some seeds have elaiosomes, while some other have volatile surface substances that are also found in glandular exudates of ants, such as methyl 6-methyl-salicylate (6-MMS), a compound used as a foraging-trail pheromone by some ants [7, 8].

In the neotropics, the main garden plants are from genera of Araceae (*Anthurium* and *Philodendron*), Bromeliaceae (*Aechmea*), Gesneriaceae (*Codonanthe*), and Piperaceae (*Peperomia*), and they are sometimes found among the Moraceae (*Ficus*) and Solanaceae (*Markea*). In Southeast Asia they include Asclepiadaceae (*Dischidia* and *Hoya*), Gesneriaceae (*Aeschynanthus*), Melastomataceae, Moraceae, Urticaceae, and Zingiberaceae. As in the case of ants, some plants may install themselves opportunistically on ant gardens, where they can thrive on the nutrient-rich substrate of suspended soil.

Shared Benefits

In ant gardens both partners benefit from the association. Plants clearly benefit from the dissemination of their seeds (myrmecochory) which are deposited on a support that is very favorable to germination. They also benefit from the regular supply of organic new material – plant fragments, vertebrate feces, etc. – that their ants continue to introduce into the structure as their society grows. Finally, the plants benefit from active protection by their ants against herbivores, in particular defoliating insects. As an example, in the mentioned ant gardens in French Guiana, the ant partners are aggressive and (especially *N. goeldii*) very effective predators of any insects that encroach on the gardens.

On their side, the ants mainly acquire a nesting site whose lifespan exceeds that of any structure they could have built alone or found preformed in pioneer trees. As they age and grow, ant gardens become increasingly attractive to other ants as nest sites. In French Guiana, they are also found to harbor colonies of stingless bees.

In ant gardens, although the main benefit for the ants is evidently a stable nesting site, the roots housing the nest do not show any particular structure related to housing ant colonies. This is in contrast to that found in myrmecophytes (specialized ant-plants), which have such features as hollow trunks and branches or specialized spaces (domatia) that serve as nest sites. At most, the roots of ant gardens are very densely packed, but there is nothing that could be interpreted as domatia. It should be noted that ~~in Asia~~ some epiphytes involved in ant gardens are myrmecophytes, as is seen [in Asia](#) with some Rubiaceae.

Moreover, ant-garden epiphytes do not produce specialized food-bodies, as do some highly specialized myrmecophytes (e.g., *Cecropia*, *Vachellia*). They often have extrafloral nectaries, as do many other tropical plants.

Other “Gardens” Associated with Ants

Ants are involved in the growth of vascular plants in other associations that are sometimes also termed “gardens” as the “devil’s gardens,” as well as “ant-farmed gardens” (see also the fungus-farming ants).

A devil's garden ("chacro del diablo" in Spanish) is quite distinct from an ant garden. In the Amazon rainforest it corresponds to a monospecific formation of myrmecophytic plants growing on the ground in the understory, whose associated ants of the genus *Myrmelachista* eliminate all other adjacent surface vegetation by sprinkling competing plants with formic acid [6].

Ant-farmed gardens in the Fiji islands of the South Pacific are much closer to ant gardens than devil's gardens, as in both cases the ants serve as seed dispersers of their associated plants [1]. In these the dolichoderine ant *Philidris nagasau* collects and plants the seeds of certain *Squamellaria* (Rubiaceae) which are myrmecophytes. They sow them under tree bark and fertilize their crop from the seedling stage. In contrast to garden ants, *P. nagasau* has lost the nest-building capability (many other *Philidris* are carton nest builders involved in paleotropical ant gardens) and they only inhabit the ready-made cavities provided by the epiphytes. Therefore the ants not only grow their food through floral food produced by mature plants but also their home. This association can be regarded as true agriculture, unlike in ant gardens. Firstly, because in ant gardens the ants do not rely on their plant partners for food. Secondly, because the fertilization of epiphytes in ant gardens is considered passive, while in the *P. nagasau/Squamellaria* associations it is active and targeted to specific structures resulting from a kind of domestication by the ants. However, in ant gardens, the passive/active dimension of the ants' behavior in fertilizing their associated plants probably needs further studies.

In an ant-garden, the ant society and the root complex of the plants are so intertwined that it is impossible to physically separate the nest as a construction from the suspended soil of the garden. Therefore, a term such as "ant nest-garden," to underline the primordial importance of the nesting function of the ant garden, would probably be more accurate. However, after a century of use, we are accustomed to call these unique associations ant gardens, if only to honor their discoverer, Ernst Ule, who correctly inferred the initiating role of ants.

Cross-Reference

Fungus-Farming Ants

Myrmecochory

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