Plant selection by the leafcutter ant *Atta cephalotes* (Hymenoptera: Formicidae) in a lowland forest of Trinidad, West Indies

Most ants feed their colonies with animal prey, extrafloral nectar and/or honeydew from sap-feeding insects. The fungus-farming ants of the tribe Attini have made a radical shift to subsisting on fungi that they cultivate inside the nest in a manner analogous to crop-farming by humans. Among these is a monophyletic group of 52 known species (Schultz 2022) whose workers almost exclusively grow their mutualistic fungi on leaves and other fragments of living plants. These are the leafcutter ants, which also stand out for their extremely large colonies, conspicuous worker polymorphism and often impressive mound nests (Hölldobler and Wilson 2011, Mehdiabadi and Schultz 2010, Schultz 2021, 2022). Their foraging activities are on such a scale that they have often been characterized as the dominant herbivores of the New World tropics. This has especially been noted in agricultural areas, where they are recorded as pests of about 50 crops (Cherrett and Jutsum 1983, García-Cárdenas *et al.* 2022). As stated by Hölldobler and Wilson (2011 p. 3), "Through much of tropical America and wherever the ants invade gardens and cropland, they are the principal insect pests of agriculture."

Almost all leafcutter ants are in the genera *Acromyrmex* and *Atta.* The different species have an overall biological similarity. However, while recorded mature colony sizes in *Acromyrmex* are between 17 and 270 thousand, those of *Atta* are estimated at one to eight million. Accordingly, where members of both genera co-occur *Atta* tend to be much more apparent and presumably much more abundant. The two species present on the island of Trinidad, West Indies are *Acromyrmex octospinosus* and *Atta cephalotes* (Starr and Hook 2003).

A notable feature of leafcutter ants is that colonies harvest from a great variety of available plants. As an example, Wirth *et al.* (2003: Table 15) recorded 126 plant species from 40 families harvested by one *A. colombica* colony in Panama over one year. What is much less studied is those accessible plants that the ants do not attack. In this study, we recorded which plants in a lowland tropical forest showed evidence of attention from leafcutter ants and which did not.

Our study site was the Arena Forest Reserve (UTM 20P 691478E, 1168600N in central Trinidad, in December 2021 and June 2023. This is an area of rolling hills with numerous streams in an extensive closed-canopy evergreen forest over a relatively open understorey on sandy soil (Tudor *et al.* 2016). Our search areas showed evidence (trails, sometimes nest mounds) of the presence of active leafcutter colonies, although with little above-ground activity during the daylight hours of the study.

While previous studies of plant choice by leafcutter ants relied on direct observation of foraging, our approach was to look for after-the-fact evidence of their attention. We sought out common understorey plants in an effort to find at least 50 individuals of each species, recording which showed signs of leafcutter-ant damage. Where a cluster of stems arose together, we treated this as a single individual. Leafcutter damage is almost always readily distinguishable from cutting by other insects. As illustrated in Fig. 1, most insect herbivory (e.g. by caterpillars or grasshoppers) on leaves is irregular and often away from the leaf edge. That of leafcutter bees (Hymenoptera: Megachilidae) consists of individual neat crescents or spheroids at the leaf edges. In contrast, leafcutter ants cut a series of crescents or disks at the leaf edges, often so intensively as to reduce a leaf to little more than its main vein.

Of the two leafcutter ants known from our study site, it was our observation that *Atta cephalotes* predominated. Its foragers and often very large nest mounds are much more in evidence than those of *Acromyrmex octospinosus*. Accordingly, we assume that most or all instances of recorded leafcutter-ant damage were from *Atta*, rather than *Acromyrmex*.

We collected data from 15 species from eight families of flowering plants (Table 1). Of these, seven showed signs of leafcutter-ant cutting in at least one individual, although the fraction of plants affected was small in most species.

Our results are consistent with the general conclusion that *Atta* spp. harvest from a broad taxonomic range of available plants in the colony's habitat. Unlike earlier studies, we noted not only the plants that were harvested but those that were not. We found eight plant species that were accessible to the ants but not harvested. It is beyond the modest scope of our study to suggest what these plants have in common. At another site we observed no harvesting from two common palms (Palmae), presumably in large part due to the toughness of the leaves.

At the same time, two notes of caution are called for. First, it would be a mistake to make too much of the higher incidence of cutting of some species than others, and certainly our data cannot be taken as proportional. For example, in our study only one individual out of more than 100 of *Heliconia bihai* showed signs of harvesting, while a

Fig. 1. Manifestations of peripheral leaf damage by three kinds of insects. Clockwise from upper left: Irregular cutting, as by grasshoppers or caterpillars; disks cut by leafcutter bees (Megachilidae); ***Heliconia bihai*** cut by leafcutter ants, presumably ***Atta cephalotes***; and ***Costus*** sp. prob. ***scaber*** cut by leafcutter ants, presumably ***Atta cephalotes***.

Table 1. Incidence of various plants showing evidence of cutting by presumed ***Atta cephalotes***. The + column

Species (Family)	Number of plants surveyed	Number of plants (%) with Leafcutting damage
Costus prob. *scaber* (Costaceae)	66	6 (9%)
Heliconia bihai (Heliconiiaceae)	111	1 (1%)
Heliconia hirsuta (Heliconiiaceae)	67	0
Heliconia psittacorum (Heliconiiaceae)	36	4 (11%)
Ischnosiphon arouma (Marantaceae)	90	0
Monotagma spicatum (Marantaceae)	111	13 (12%)
Pentaclethra macroloba (Leguminosae)	50	0
Philodendron sp. (Araceae)	53	0
Piper sp. A (Piperaceae)	62	0
Piper sp. B (Piperaceae)	51	0
Protium cf. *guianense* (Burseraceae)	50	0
Psychotria uligonosa (Rubiaceae)	50	8 (16%)
Spathiphyllum cannifolium (Araceae)	50	2 (4%)
Warszewiczia coccinea (Rubiaceae)	66	0
Unidentified (Araceae)	50	12(24%)

substantially larger fraction of *H. psittacorum* individuals were cut. It has been our experience from outside this study that *H. bihai* in some habitats is a favoured target of *A. cephalotes*, while *H. psittacorum* is seldom cut. It would be best just to take our data as presence/absence indicators. Second, they provide only minimum indicators of which plants are harvested. Again, *H. bihai* provides a case in point. We knew in advance that it is cut by the ants, yet in our study we very nearly recorded no harvesting at all. While much is made of leafcutter ants as voracious harvesters of vegetation in many neotropical habitats, our observations do not suggest any major impact on overall forest structure at our study sites. The ants are very much in evidence, yet we found no significant swaths of defoliated plants. Their reputation may be mainly due to their role as crop pests.

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