PROFILE

A Pest is a Pest is a Pest? The Dilemma of Neotropical Leaf-Cutting Ants: Keystone Taxa of Natural Ecosystems

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ABSTRACT / Leaf-cutting ants of the genera *Acromyrmex* and *Atta* are considered the principal polyphagous pests of the Neotropics Although some members of these genera are of economic importance, have a broad geographic distribution, and are extremely good colonizers, others are endemic and closely interact with native ecosystems. Control is generally practiced against any colony, irrespective of its taxonomic status. Indiscriminate control coupled with habitat destruction threatens endemic species with extinction, and, through habitat simplification, favors other pest species. As nests of *Atta* are large, having several square meters of nest surface, the endemic taxa can be easily used as environmental indicators for natural ecosystems Likewise, the pest species can be used to detect environmental disturbance As these ants are keystone species and easily identified by nonspecialists, efforts should be made to integrate these into viable conservation programs

Leaf-cutting ants have attained notoriety in the Neotropics because some species are major economic pests (Cherrett 1986). Over the years, notable naturalists, such as Bates, Humbolt, Lund, and Saint Hilaire, described the large amounts of vegetation harvested by these ants. Moreover, from 1900 onward, most Latin American countries passed legislation obligating landowners to kill all ant nests on their property. Until recently, these laws were easier to decree than to enforce. Legislation is now no longer necssary, since most growers, irrespective of their property size, practice ant control with highly effective insecticides applied either in the form of baits or fumigants. Current methods of controlling and estimating the pest status of these ants are given in Fowler and Robinson (1979), Fowler and others (1986), and Cherrett (1986).

Collectively, these ants have been considered the major polyphagous insect pests of Latin America (Cramer 1967). However, the principal pest species are the widespread *Atta sexdens* (L.), *Atta laevigata* (Fr. Smith), and *Acromyrmex octospinosus* (Reich), all of which attack broad-leaf plants, and *Atta capiguara* Gonçalves and *Acromyrmex landolti* (Forel), which cut grasses. Naturally, we should question whether the other members of these genera are also pests; and if not, are the nonpest species affected by indiscriminate ant control? Finally, the role that these ants play in their coevolved ecosystems needs to be considered. We attempt to address these questions using published research data and our own field experience. We also emphasize the need for more rational management strategies for these ants in Latin America.

KEY WORDS: Environmental indicators; Keystone species; Neotropics; Leaf-cutting ants

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Background

The myrmicine tribe Attini is unique among ants in that its members cultivate fungi as a food source. The lower genera cultivate fungi on diverse substrates, although the most important is generally insect grass, which foraging workers collect in the field (Weber 1972). Colonies of such ants are generally small and inconspicuous, like the ants themselves. However, in the higher attine genera *Atta* and *Acromyrmex*, fungi are always cultivated upon freshly cut vegetation, and these genera are known as leaf-cutting ants. The fungus gardens are the focus of the social organization of these ants, yet the taxonomic status of the fungus is

Table 1. Taxa of leaf-cutting ants of the Neotropics and the type of plants cut, pest status and geographic dispersion.[a]

Species	Vegetation type cut	Pest status[b]	No. countries present[c]
Genus *Atta*			
A. bisphaerica Forel	monocots	+ +	1 (Brazil)
A. capiguara Gonçalves	monocots	+ + + +	2
A. cephalotes (L.)	dicots	+ + + +	17
A. colombica Guérin	dicots	+ +	5
A. goiana Gonçalves	monocots	?	1 (Brazil) E
A. insularis Guérin	dicots	+ +	1 (Cuba) E
A. laevigata (F. Smith)	both	+ + + +	6
A. mexicana (F. Smith)	dicots	+ +	6
A. opaciceps Borgmeier	dicots	+ +	1 (Brazil)
A. robusta Borgmeier	dicots	+ +	1 (Brazil) E
A. sexdens (L.)	dicots	+ + + +	14
A. silvai Gonçalves	dicots?	?	1 (Brazil) E
A. texana (Buckley)	dicots	+ +	2
A. vollenweideri Forel	monocots	+ +	5
Genus *Acromyrmex*			
A. ambiguus (Emery)	dicots		4
A. asperus (F. Smith)	dicots		4
A. coronatus (Fabr.)	dicots		10
A. crassispinus (Forel)	dicots		3
A. disciger (mayr)	dicots		2
A. diasi Gonçalves	monocots		1 (Brazil) E
A. gallardoi Santschi	monocots?		1 (Argentina) E
A. heyeri (Forel)	monocots		4
A. hispidus Santschi	dicots		6
A. hystrix (Latreille)	dicots		5
A. landolti (Forel)	monocots	+ +	9
A. laticeps (Emery)	dicots		5
A. lobicornis (Emery)	both		5
A. lundi (Guérin)	dicots		3
A. mesopotamicus Gallardo	monocots?		1 (Argentina) E
A. niger (F. Smith)	dicots		1 (Brazil)
A. nobilis Santschi	dicots		1 (Brazil) E?
A. octospinosus (Reich)	dicots	+ + + +	20
A. pulverus Santschi	monocots?		1 (Argentina) E
A. rugosus (F. Smith)	dicots		7
A. striatus (Roger)	monocots		5
A. subterraneus (Forel)	dicots		6
A. sylvestrii Emery	monocots?		3
A. versicolor Pergande	dicots		1 (US) E

[a]Only species-level taxa are included.

[b]Data compiled principally from Cherrett (1986) and Fowler and Robinson (1980): + + + +, a generally serious pest; + +, occasionally serious pests; ?, pest status unknown.

[c]For species represented by only one country, the country is specified, and its endemic status (E) indicated if it has a documented limited geographical distribution.

still debated. Furthermore, the symbiosis between the ants and fungi is still largely unstudied, although certain aspects of the relationship are known (Weber 1972). The leaf-cutters can be split into two broad categories based upon the vegetation that they harvest for fungal substrate, namely, those that cut grasses and those that cut broad-leaf vegetation (Table 1). For a given ant species, the fungal garden's form and general appearance, and possibly even the type of fungi involved, are closely linked with the type of vegetation used as a substrate (Fowler 1985).

The origin of the attine ants remains a mystery, and this is basically a result of the paucity of fossil remains. All currently recognized taxa of leaf-cutters are Neotropical (Table 1), being absent from the Pacific Coast of South America and poorly represented in Central and North America. Although it has long been assumed that the Attini evolved in the Amazon Basin (Weber 1972), all genera of Attini are more richly represented in the southern subtropical regions of South America (Fowler 1983a), leading to a higher species richness and packing per unit area (Fowler 1983b). This conflicts with the hypothesis that these ants are of tropical rain forest origin. Moreover, the Amazon is poorly represented in species of leaf-cutting ants, and this pattern holds also for Central America. In these areas, the pests *A. sexdens, A. laevigata,* and *A. octospinosus* are generally the only higher attines (Cherrett 1968), where they generally occur in disturbed areas (Fowler 1983b).

Leaf-Cutting Ants as Keystone Species

In spite of the spectacular nature of some of the leaf-cutting ant species, relatively little is known about the role of these ants in their native ecosystems. Because of the large quantities of vegetation harvested (Fowler and Forti 1989a), these ants undoubtedly affect the demography of individual plants. If defoliation is not intense, which is the case for natural ecosystems but not for crops, these ants may stimulate plant growth and facilitate an increased plant species richness within native ecosystems. Preliminary evidence suggests that some assemblies of leaf-cutters may do precisely this (Fowler and Hanes 1983).

At another level, leaf-cuters are really part of the decomposer food web. Through their fungus gardens, these ants accelerate the process of decomposition and consequently have the potential to shorten nutrient cycling times. This aspect has been investigated briefly by Lugo and others (1973), Hanes (1975), and Coutinho (1984). Through these investigations, it was established that colonies of *Atta* have a tremendous impact on the rates of energy and nutrient transfer, and they may even be a key regulatory sink in the nitrogen and phosphorus cycles.

Finally, the nest structures of colonies of *Atta* may be important for natural ecosystems. Given the tremendous amounts of soil moved and consequent pedoturbation of tropical and subtropical soils, nests serve as nutrient-rich sites for plant growth and colonization. Alvarado and others (1981) and Coutinho (1982) have documented these effects. Furthermore, the successional patterns originating on the nests of these ants (Fowler 1977, Jonkman 1978, Coutinho 1982) suggest that nest structure may be focal point of ecosystem renovation and promote an increased plant species diversity. Thus, leaf-cutting ants may be keystone species not only through their impact as herbivores and decomposers, but also through their large input on soil structure.

Many other faunal elements, ranging from armadillos and anteaters, through millipedes, spiders, other ants, beetles, flies, etc., are dependent upon these ants (Weber 1972, Fowler and Forti 1989b). Many of these animals use the ants or their brood or fungus as a food source, use the fungus garden as incubation chambers, decompose the spent fungus garden, or use the nest for a living or hiding place. Many of these organisms are specialized in their associations with leaf-cutters (Fowler and Forti 1989b), which further magnifies their role as keystone species.

The Value of Leaf-Cutting Ants

As we have emphasized, leaf-cutting ants can be serious economic pests. However, the vast majority of leaf-cutting ant species are not pests (Fowler and others 1989a). Furthermore, many species of leafcutters are endemic to restricted geographic regions (Table 1, Figure 1). These endemic species show a high correlation with other endemic groups (Figure 1) and thus are probably more highly integrated into these ecosystems than the more widespread pest species. Because these endemic taxa reflect the presence of certain plant communities, they are ideal bioindicators, just as Erlich and Erlich (1981) noted for butterflies. The advantage of using endemic species of leaf-cutting ants is that their nests are large and easily recognized even by nonspecialists. Like butterflies, these ants are useful to monitor vegetation, because they can be considered as herbivores. Given that these ants are keystone species in their native ecosystems, their presence serves as a reliable indicator of ecosystem homeostasis.

Even widepsread species have the potential to provide information on those ecosystems in which they occur. For example, *Atta colombica* and *Atta cephalotes* are characteristic species of tropical rain forests and can be used to monitor the status of certain areas. Indeed, wood ants (*Formica rufa* group) have been shown to be good indicators of forest vigor in Europe (Gosswald 1985). Conversely, the occurrence of notorious pest species, such as *A. sexdens, A. laevigata,* and *A. octospinosus* could be used as indicators of forest degradation in areas in which endemic species of leaf-cutters exist (Fowler and others 1989b).

Unplanned urbanization, logging and mining practices, agriculture, and indiscriminate pest control strategies threaten endemic species while favoring pest species (Fowler 1983b). Because endemic leaf-cutters reflect the presence of other endemic plant and an-

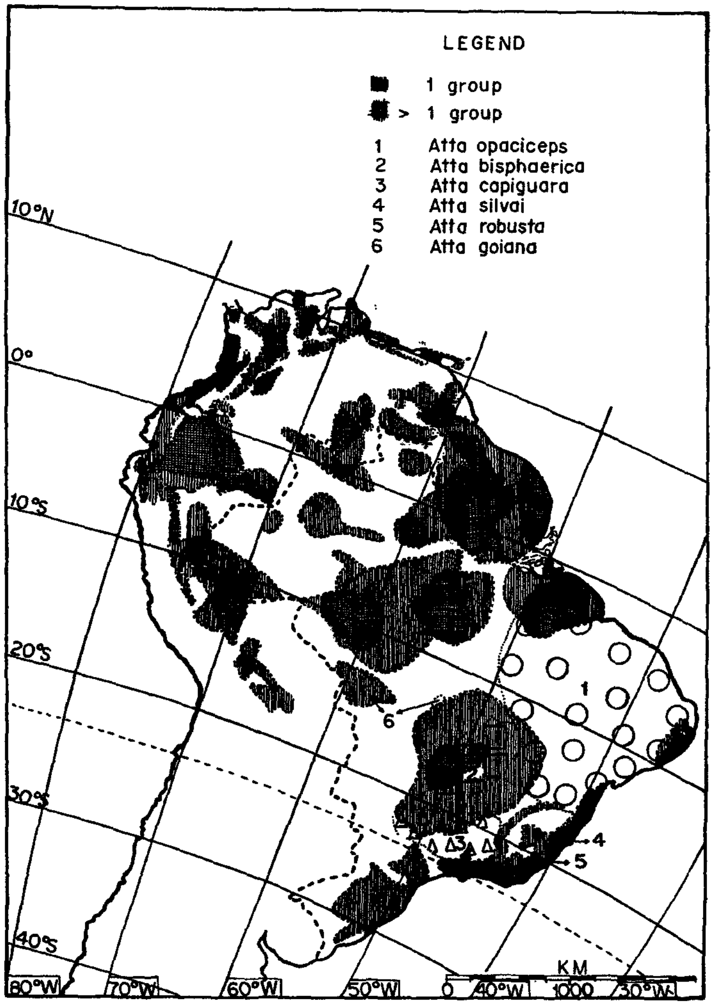

Figure 1. Congruence of endemic species of *Atta* with other endemic groups: *Anolis* lizards (Vanzolini and Williams 1970), orchids (Brieger 1969), vascular plants (Prance 1973), birds (Haffer 1974), butterflies (Brown and others 1974), and mammals (Muller 1972). Congruence of one or more of these groups is given by shading.

imal species (Figure 1), their value as bioindicators is tremendous. The ants themselves also may have a tremendous value. They developed and perfected agriculture long before man, which means that we may be able to learn much from them. The variety of chemicals produced by these ants to regulate their fungal gardens has been largely uninvestigated. Undoubtedly, endemic species of leaf-cutters have different chemicals and strategies adapted to a narrower and more specified range of conditions. They may, therefore, contain a potentially rich source of products and methods for man to more efficiently use the land that is now under cultivation.

For these reasons, as well as others that will be uncovered with increased research, the development of more rational management strategies is needed. As these ants are keystone species in their ecosystems, their importance as bioindicators is magnified. The extinction of the endemic leaf-cutters could undermine the biotic diversity of unique plant communities; thus educational programs must also emphasize that a pest is not necessarily a pest.

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