

## Latitudinal gradients and diversity of the leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera: Formicidae)

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**Abstract:** Current biogeographic patterns of the 12 genera of the gardening ant tribe Attini are examined. Six of the genera are more concentrated in the southern subtropics of South America, and the true leaf-cutting ants, *Atta* and *Acromyrmex*, markedly so. No pattern of taxonomic diversity following phylogeny emerges, and the hypothesis that leaf-cutting ants evolved in the tropical rain-forest cannot be assumed to be confirmed. The taxonomic diversity of attine ants on Caribbean islands was examined in terms of biogeographic theory. Island surface area and distance from the mainland were important in predicting species numbers present, yet these two factors only explained less than 50% of the observed taxonomic diversity.

Taxa of the Neotropical Myrmicine tribe Attini all cultivate a garden of symbiotic fungi, and collectively are known as gardening ants. Attines are generally abundant in Neotropical habitats, and are among the most characteristic faunal markers of the Neotropics. Two genera of attines, *Atta* and *Acromyrmex*, depend almost exclusively upon freshly harvested vegetation as a fungal garden substrate, and constitute the true leaf-cutting ants. The remaining genera, except for *Pseudoatta* which is an obligate social parasite, collect fallen vegetation and insect frass as a fungal substrate, although occasionally may, in the case of *Trachymyrmex*, harvest small amounts of vegetation. Thus, all attines may be viewed as components of the decomposer food web, although both taxa of *Atta* and *Acromyrmex* proximately affect the ecosystem as herbivores.

It is commonly assumed that the attines are of a tropical derivation. For example, Weber (1972) proposed that the Attini evolved in the moist tropical lowlands of northern South America. However, no attine fossils have ever been recovered, and their strictly Neotropical distribution suggests that the attines are a

relatively young group. Moreover, the absence of attines from the western coasts of Chile and Perú suggests their evolution after the formation of the Andes, and a drastically reduced taxonomic diversity in Central America northward also attests to their relatively late evolution. Here, I examine the biogeographic patterns of the attines on a large scale, and discuss these findings in terms of our current hypothesis concerning the evolution and behavior of this unique group of ants.

### METHODS

Although detailed measures of species diversity have been proposed, most indices rely upon a knowledge of the relative abundances of the component taxa (Pielou, 1977). Few quantitative studies are available on the composition of leaf-cutting ant communities (Fowler, 1983). Therefore, the measure of taxonomic diversity employed here is the number of described taxa per 10° latitude in width. Data were taken from Kempf's (1972) catalog, and were supplemented by recent records (Fowler, 1980). Only species level taxons were included in the following discussion.

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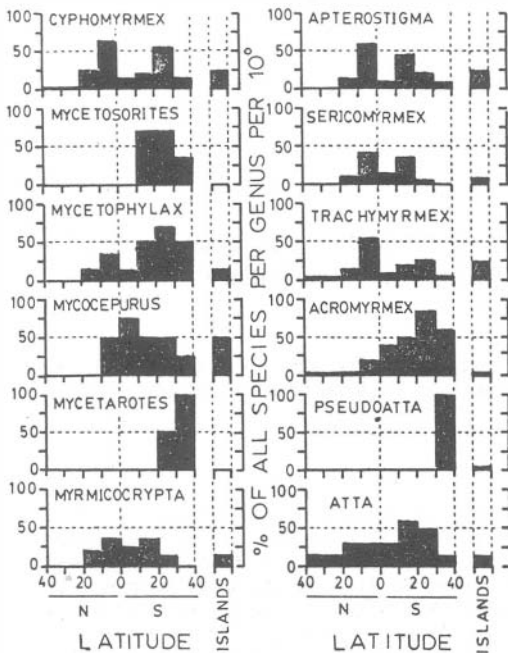


Fig. 1. The taxonomic richness for each genus of attine ants per  $10^{\circ}$  latitudinal band. Genera are arranged in assumed phylogenetic order, from *Cyphomyrmex* through *Atta*, and plots demonstrate the percentage of described species from that genus per latitudinal band. Islands refer to the percentage of the described taxa that occur in the Antillean island chain.

## RESULTS

Latitudinal ranges were represented graphically in terms of the percent of the number of described taxa occurring in successive latitudinal belts for all recognized genera of attines (Fig. 1). Taxa of the true leaf-cutting ants, *Atta* and *Acromymex*, and their associated parasitic genus *Pseudoatta*, are all concentrated in the southern subtropics. Other genera with decidedly southern subtropical distributions include *Mycetosorites*, *Mycetophylax*, and *Mycetarotes*. Tropically centered distributions are found in *Cyphomyrmex*, *Mycocepurus*, *Myrmicocrypta*, *Apterostigma*, *Sericomyrmex* and *Trachymymex*. As these taxa are arranged in the assumed phylogeny of evolution, based upon morphological and behavioral traits (Weber, 1972), it is difficult to interpret the contemporary distributions along phylogenetic paths. Based on contemporary distributions, it is also difficult to ascribe a tropical origin to

leaf-cutting ants. It is possible that the concentration of taxa of *Atta* and *Acromymex* in the southern subtropics of South America is a reflection of posterior diversification of a parent stock from the tropics, a subtropical origin of this group is just as possible based upon the available data.

Because the attines are markedly Neotropical in distribution, we may assume that they evolved after the fragmentation of Gondwanaland, and are consequently not present in Africa. Similar patterns are present in many exomalopsine and nomadine genera of bees (Michener, 1979). The taxa present in the Antillean islands (Fig. 1) may give some clue to the dispersal ability of the various genera of attines, and, perhaps, give us additional clues on their antiquity.

Although attine ants are abundant on the mainland of South America (193 species), only 32-33 species ( $\sim 19\%$ ) are present on Caribbean islands, with Trinidad and Tobago, lying just off the coast, having the largest number of recorded species. Fitting the standard formula relating species to island area (MacArthur and Wilson, 1967), we obtain  $S = CA^{0.205}$ , for all islands. Excluding Trinidad and Tobago, the relationship is  $S = CA^{0.239}$ . Goodness of fit tests for all islands vs islands excluding Trinidad and Tobago ( $F = 2.74$ ,  $P = 0.1258$ ,  $R^2 = 0.200$ ; and  $F = 17.34$ ,  $P = 0.0024$ ,  $R^2 = 0.658$ , respectively) indicate that the influence of Trinidad and Tobago on the species-area relationship is great. In essence, Trinidad and Tobago may be best considered as continental. To further evaluate this relationship, a multiple linear regression was performed to account for surface area, distance from the mainland, and their interaction. These results are summarized in Table 1. When considered separately, area has the greatest effect, followed by distance from the mainland. However, considering all factors simultaneously, no one factor can be isolated as being the most important (Type IV SS; Table 1).

## DISCUSSION

Contemporary biogeographic patterns of the attine ants discussed here fail to provide a coherent picture of the evolution of this unique group. The relatively depauperate fauna of the Caribbean islands, although amenable to island biogeographic analysis, suggests that these ants

TABLE 1

*Analysis of variance of the relative contribution of distance from the mainland and island surface area on the occurrence of species of attine ants on the Caribbean islands. All variables entered are natural logs*

Source	D.F.	Type I. SS	Mean Square	F	Type IV SS
Ln (km from mainland)	1	2.9578**			0.2117
Ln (island surface area)	1	5.8072**			0.0616
Lnkm x LnHa	1	0.0008			0.0009
Total	3	8.7658	2.9219	12.27	
Error	9	2.1439	0.2382		
Corrected total	12	10.9098			

\*\* P 0.05

may have evolved late in the Tertiary Period, which may also explain their absence from the western coasts of South America, as the Andes are also of Tertiary origin.

More importantly, these patterns shed some doubt as to the tropical forest origin of the leaf-cutting ants, *Atta* and *Acromyrmex*. Biogeographic patterns of these ants run contrary to reported patterns for lizards (Pianka, 1966), mammals (Simpson, 1964; Wilson, 1974), swallowtail butterflies (Slansky, 1973), and ants as a whole (Kusnezov, 1957; Fischer, 1960). However, these patterns fit remarkably well with the patterns of specializations reported for xylomycetophagous beetles (Beaver, 1979), which likewise depend upon fungus for food. It is well documented that there exist latitudinal clines in the occurrences of plant allelochemicals which increase in concentration as one approaches the tropics, such as alkaloids (Levin, 1971). These compounds are generally highly fungicidal or fungistatic, and would thus greatly limit the fungal growth of these ants, which depend entirely upon freshly harvested vegetation as a fungal resource, unlike the minor genera which utilize fallen vegetation and insect frass. High concentrations of allelochemicals would greatly influence fungal survival, and thus ant survival.

Rates and constancy of predation are also assumed to be higher in the tropics (Paine, 1966), and especially by ants (Jeanne, 1979). High rates of predation may greatly influence leaf-cutting ant colony survivorship, but predation should affect all genera equally, and thus cannot be considered the key factor in explain-

ing the distinctly sub-tropical distribution of *Atta* and *Acromyrmex*. A combination of high rates of predation and high plant allelochemical diversity may work hand in hand to promote a pronounced pattern of higher colony incidences in structurally less complex habitats (Fowler, 1983). As tropical forests are also more structurally complex (Fowler and Stiles, 1980), polyphagism in harvesting vegetation may necessarily be too pronounced, and optimal time and space windows for harvesting suitable vegetation for fungal substrate too short and variable (Fowler and Stiles, 1980), to permit efficient resource tracking and harvest. Conversely, the trend toward resource specialization assumed for tropical animals (Dobzansky, 1950) may be too intense, and indeed work contrary to the possible low levels of allelochemical detoxification allowed by the fungus garden.

Finally, many taxa of *Atta* and *Acromyrmex* are restricted to grasslands and harvest only grasses (Fowler, 1983). Some taxa also demonstrate a strong congruence between present day distributions and Pleistocene vegetational patterns (Fowler and Haines, 1983). As the taxa of *Acromyrmex* (*Moellerius*) are assumed to provide the evolutionary link to the inferred more advanced taxa of *Atta* (Creighton, 1950), and as taxa of *A. (Moellerius)* are largely restricted to grasslands, the proportionally rarer expanses of grasslands in the tropics may well help to explain the decreasing taxonomic diversity as one approaches the tropics. A Pleistocene link may also explain the depauperate taxonomic diversity in Central and North America. These patterns may also shed some light on

the reversed cline of closer species packing and implicit higher resource utilization toward the subtropics than has been predicted.

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### RESUMEN

Los patrones biogeográficos actuales de los 12 géneros de las hormigas jardineras de la tribu Attini indican que 6 de los géneros tienen concentración taxonómica en los subtrópicos sureños de Sur América. Entre estos 6 géneros se encuentran las verdaderas hormigas cortadoras (zompopas en Centro América), *Atta* y *Acromyrmex*. No existe correlación entre la filogenia de la tribu y la diversidad latitudinal de sus miembros. La hipótesis de un origen tropical de estas hormigas no se puede confirmar. Se examina la diversidad taxonómica de Attini en las islas del Caribe con respecto a la teoría biogeográfica. El área de superficie y su distancia del continente fueron de mucha importancia para calcular el número de especies; aunque estos dos factores solamente explican menos del 50% de la diversidad taxonómica en las islas del Caribe.

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