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RELATIVE REPRESENTATION OF *PHEIDOLE (HYMENOPTERA: FORMICIDAE) IN* LOCAL GROUND ANT ASSEMBLAGES OF THE AMERICAS

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RESUMEN

Participación relativa de *Pheidole* (*Hymenoptera: **Formicidae***) en **comunidades** locales de hormigas de suelo en las Américas

En 195 estudios publicados sobre comunidades de hormigas de suelo de las Américas, la representación faunística de ***Pheidole*** fue mayor que la de cualquier otro género. No se encontró una relación significativa entre el porcentaje de la representación faunística y la latitud, pero su representación fue mayor en los trópicos. En cultivos **fructícolos** se detectó un porcentaje mayor de especies de ***Pheidole*** que en otros tipos de hábitat. Adicionalmente, el porcentaje de especies de ***Pheidole*** relacionó negativamente **con** el porcentaje de especies de ***Formicinae.*** Este efecto fue mayor que la influencia de la latitud sobre ***Fomicinae.*** No se encontró una relación negativa significativa entre ***Pheidole*** y otros grupos **taxonómicos.** Este resultado sugiere que las especies de ***Pheidole*** pueden competir **con** las especies de ***Formicinae,*** o que estos dos grupos están ubicados en los extremos opuestos de un gradiente de estrés ambiental.

Palabras clave: **Comunidad,** hormiga, latitud, hábitat, patrón, diversidad, ***Pheidole.***

SUMMARY

Using 195 published ground ant wmmunity **surveys** from the Amencas, the **faunal** representation of ***Pheidole*** was **greater** than any other genus. No significant relationship between the **percent faunal representation with latitude** was found, although their representation was much richer in the **tropics.** Tree crops had **significantly** higher **percentages** of species of ***Pheidole*** than did other habitat **types.** Furthermore, a **significant** negative relationship was found **between** the **percent** representation of ***Pheidole*** and **all** formicines. This effect was stronger than the relationship **between** formicines and latitude. No significant negative relations were found for other **subfamilies.** This **suggests** that ***Pheidole*** may compete strongly **with** formicines, or that these groups are **placed** on opposite ends of an enviromental stress gradient.

Key words: Community, ant, latitude, habitat, pattem, **diversity,** ***Pheidole.***

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INTRODUCTION

The cosmopolitan ant genus ***Pheidole*** has apparently evolved and diversified since the Oligocene. It has replaced members of the Dolichoderinae in the temperate regions and has diversified at high rates in the tropics (BROWN, 1973). In the Americas, the ant genus ***Pheidole*** is the most species rich (CREIGHTON, 1950; KEMPF, 1972; WILSON, 1976), and may have 700 or more valid species (E. O. WILSON, personal communication). Although it is at present impossible to place a name on the majority of the taxa, especially in South America, species have clear morphological differences and can be fairly easily separated into morphospecies. Complete worker dimorphism is a characteristic of ***Pheidole,*** and behavioral specializations of the major caste may be inversely proportional to their representation within the worker population of the colony (WILSON, 1984), although other researchers have not obtained this pattern (ARAB *ef al.*, 1989; PATEL, 1990; TSUJI, 1990; LACHAUD *et al.*, 1992). Species of ***Pheidole*** have diversified ecologies, including seed harvesters, general omnivores and predators, as well as mutualists in associations with many plants and Homoptera (KUSNEZOV, 1956; BRIAN, 1983; HOLLDOBLER & WILSON, 1990). Because of this, members of ***Pheidole*** are found in nearly all types of terrestrial habitats (WILSON, 1987).

Recent efforts have been made to use species of ***Pheidole*** as an indicator group for comparative diversity studies (BENSON & BRANDAO, 1987; MOUTINHO, 1991). Here, I examine the relative contribution of ***Pheidole*** species in 195 local ground ant assemblages of the Americas.

DATA BASE

Data are derived from a survey of literature, and a complete listing, as well as criteria used for classifying major habitat types, can be found elsewhere (FOWLER, in press). Because ant assemblage size varied from a dozen to more than 100 species per assemblage, I standardized local assemblages by taking the percentage of ***Pheidole*** of the total assemblage species richness. Comparisons with other taxonomic levels were also performed likewise. Taxonomy follows CREIGHTON (1950), KEMPF (1972) and BROWN (1973).

RESULTS AND DISCUSSION

The mean percent contribution of species of ***Pheidole*** in local ground ant communities, and the mean species richness of the Formicinae and the assemblage as a whole (Fig. 1), reveal higher assemblage species richness from 0 - 9 ° N latitude, and a higher relative contribution of ***Pheidole*** in local assemblages from 0 - 9 ° S. When examined with respect to latitude without reference to hemisphere, the relative contribution of species of ***Pheidole*** in local ground ant assemblages declined significantly with increasing latitude (F = 26.255; P 0.001) as did mean generic (F = 9.685, P 0.001) and mean species richness (F = 18.364; P 0.001) of the assemblages did (Table 1). These results are in accord with previous studies (KUSNEZOV, 1957).

Likewise, the relative contribution of ***Pheidole*** in local ground ant assemblages remained constant, irrespective of habitat examined (F = 3.437; P 0.05), but not with respect to the type of sampling method employed (F = 10.745; P 0.05) (Table 2). Species of ***Pheidole*** were significantly more abundant on baits than any other sampling methodology. This was probably due to their efficient mass recruitment capabilities (WILSON, 1987), which allows them to dominate food resources and effectively exclude other competitors. Both habitat and sampling method influenced generic and species richness patterns of entire assemblages (Table 2). Soil and litter samples always had higher generic and species richnesses, while nest counts had the lowest (Table 2). Thus sampling method resulted in significant heterogenity of sampled habitats for both species and generic richness (Table 2). Forests and closed habitats always had higher generic and species richnesses, while grasslands and other open habitats had reduced richnesses, resulting in significant heterogenity of the sampled communities (Table 2). However, both habitat and sampling methods were not independent of latitude (FOWLER, in

TABLE 1. The latitudinal distribution of ground ant assembly species and generic richness, and the respective participation of species of ***Pheidole*** in local ant assemblages of the Americas.

La distribución latitudinal de riqueza de especies y géneros en comunidades **locales** de hormigas de suelo, y la participación **relativa** de especies de Pheidole **m** comunidades locales de **hormigas en** las **Américas.**

Latitude	% *Pheidole*	Mean Genera	Mean Species Richness	N
0 - 9	28.8 ± 12.9	23.0 ± 19.2	77.8 ± 62.8	9
10 - 19	20.7 ± 14.0	13.7 ± 11.0	29.7 ± 27.3	37
20 - 29	20.9 ± 12.3	16.8 ± 9.3	37.3 ± 25.7	52
30 - 39	12.1 ± 9.8	11.2 ± 5.9	17.1 ± 11.6	56
⇒ 40	2.2 ± 6.2	7.7 ± 5.1	13.9 ± 13.3	41

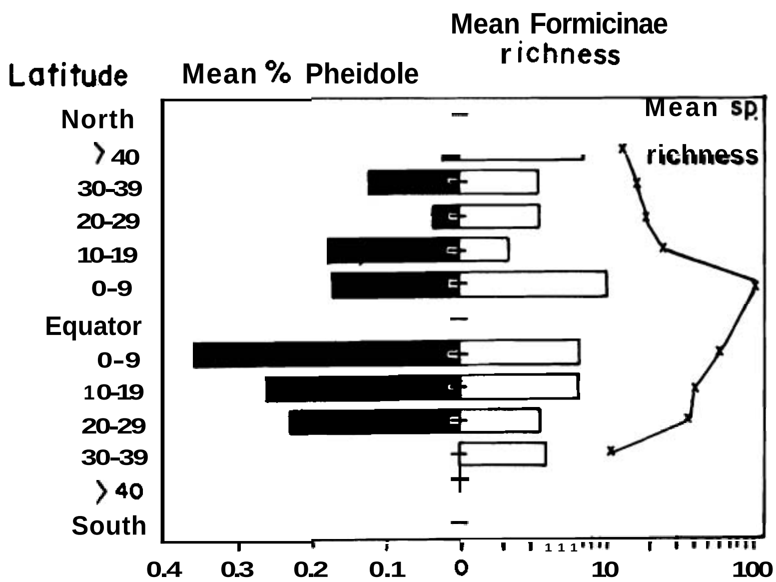


FIGURE **1.** The reiative contribution of species of ***Pheidole*** to local ground ant communities, and **corresponding** species richness of Formicine ants and the empire **ant** assemblage **with respect** to latitude. Data derived from **195** studies (**FOWLER**, in press)

La contribución relativa de especies de Pheidole en comunidades **locales** de hormigas de suelo, y la **correspondiente riqueza** de especies de hormigas Formicinae y de la comunidad total con respecto a la latitud. **Los** datos se han extraído de 195 estudios.

TABLE 2. Mean relative representation of Pheidole species in local ground ant communities of the Americas, and the respective mean number of genera and species in these communities with respect to the habitat sampled and the type of sampling method employed.

La representación media relativa de especies de Pheidole en comunidades locales de hormigas de suelo en las Américas, y el número medio respectivo de géneros y especies en estas comunidades con relación al habitat de la muestra y el tipo de método de muestra empleado.

Habitat	% Pheidole	Total Genera	Total Species
row crop	14.6 ± 10.2	14.1 ± 9.1	24.7 ± 16.7
grass/open	12.5 ± 11.3	9.1 ± 5.2	17.1 ± 14.7
tree crop	23.5 ± 14.5	12.1 ± 9.5	21.6 ± 22.0
forest/closed	14.7 ± 14.5	16.4 ± 11.3	36.8 ± 34.7
F value	3.437	8.907*	7.781*
Type of sample			
Litter/soil	13.9 ± 11.3	18.2 ± 15.2	38.4 ± 41.7
Baits	22.1 ± 16.0	12.2 ± 8.7	31.1 ± 31.5
Pit-fall trap	9.2 ± 8.5	16.2 ± 9.7	26.8 ± 23.3
Nest counts	14.3 ± 11.1	8.0 ± 3.2	12.6 ± 7.4
General	6.6 ± 7.8	14.9 ± 8.0	29.4 ± 20.0
F value	10.745*	9.932*	12.664*

$P < 0.05$

press). In the Americas, nest counts are used extensively in temperate areas, while baits are used more intensively in the tropics (FOWLER, in press), probably due to the difficulty of locating nests. Likewise, most studies in the temperate regions of the Americas have been conducted in open arid regions, while in the tropics attention has focused upon crops and forests (FOWLER, in press).

The percent contribution of Formicinae in local ant assemblages demonstrated a positive relation with increasing latitude (Fig. 2). However, no significant relation was found between Pheidole relative assembly participation and latitude (Fig. 3).

The Formicinae also presented a significant inverse relationship with relative *Pheidole* species richness in local communities (Fig. 4; Table 3). Furthermore, significant latitude X Pheidole interactions were also found, with the later having a larger contribution in local assemblage contributions: % Formicinae = 0.267 (° Latitude) - 0.396 (% Pheidole) -0.315 (° Latitude X % *Pheido-*

TABLE 3. The relation of the percent taxonomic representation to the percent of ***Pheidole*** in local ground ant assemblages in the Americas. Regression model is % subfamily representation = intercept + slope **(% *Pheidole*).**

La relación del porcentaje de representación taxonómica con el porcentaje de ***Pheidole*** en comunidades locales de hormigas de suelo en las Américas. El modelo de regresión es % de representación de la subfamilia = intercección + pendiente **(% *Pheidole*).**

Subfamily	intercept	Slope	F value	r^2
Ponerinae	0.061*	0.171*	8.882*	0.046
Ecitoninae	0.016*	-0.016	0.419	0.274
Pseudomyrmecinae	0.005	0.039*	4.626*	0.025
Dolichoderinae	0.086*	0.027	0.264	0.001
Formicinae	0.383*	-0.859*	75.615*	0.290
Myrmicinae	0.457	0.562*	39.227*	0.176

* $P < 0.05$

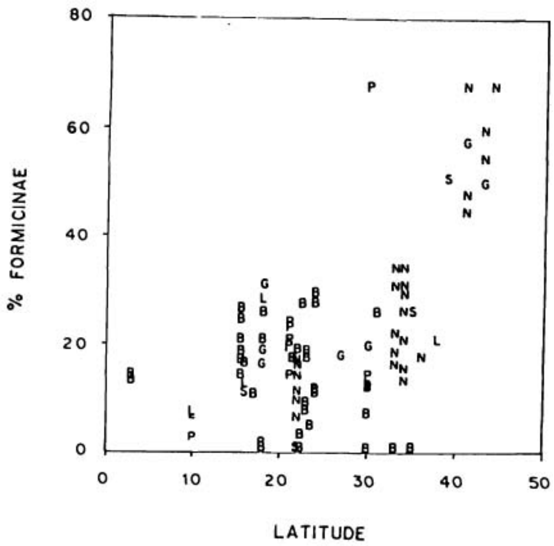
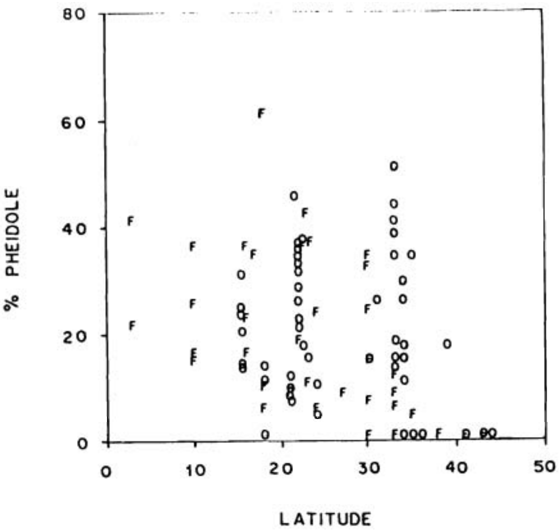


FIGURE 2. The relative contribution of Formicine ants in local ground ant assemblages of the Americas as a function of latitude [% Formicine = -0.036 + 0.011 ° latitude; r^2 = 0.439; F = 144.677, P < 0.00011. Letters refer to the type of sampling method employed: N = nest countes; S = soil samples; L = litter samples; P = pit-fall samples; B = bait samples; and G = general collection techniques.

La contribución relativa de Formicinae en comunidades locales de hormigas de suelo en las Américas en función de la latitud [% Formicinae = -0.036 + 0.011 ° latitud r^2 = 0.439; F = 144.677, P < 0.00011. Las letras representan el tipo de método de muestra usado: N = censos de nidos; S = muestras de suelo; L = muestras de hojarasca; P = muestras de pit-fall; B = muestras con cebos; G = técnicas generales de recolección.

FIGURE 3. The relative contribution of species of *Pheidole* in local ground ant assemblages of the Americas as a function of latitude [% *Pheidole* = 30.585 - 0.481 ° latitude; r^2 = 0.095; F = 10.115, P = 0.0021. Letters refer to the type of habitat sampled: *O* = open; F = closed.

La contribución relativa de especies de *Pheidole* en comunidades locales de hormigas de suelo en las Américas en función de la latitud [% *Pheidole* = 30.585 - 0.481 ° latitud; r^2 = 0.095; F = 10.115, P = 0.002]. Las letras representan el tipo de hábitat de la muestra: O = abierto; F = cerrado.



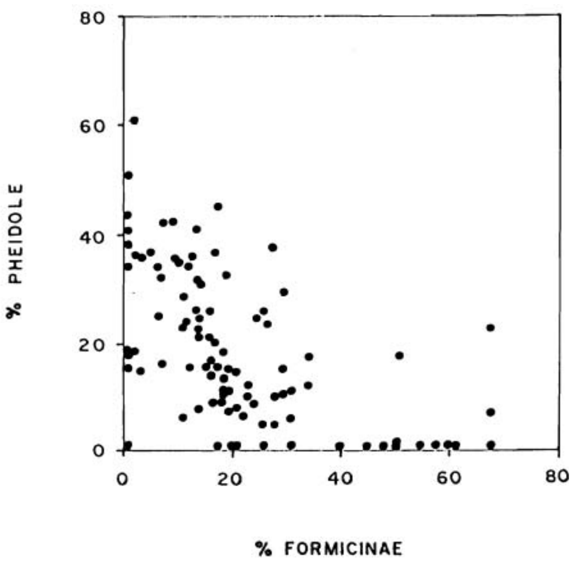


FIGURE 4. The relationship between the percentage representation of species of Formicine and *Pheidole* in ground ant assemblages of the Americas.

La relación entre el porcentaje de especies de Formicinae con *Pheidole* en comunidades locales de hormigas de suelo en las Américas.

le) [r^2 =0.455, F = 26.202, P 0.0011 (Fig. 4). Relative species richness of the Pseudomyrmecinae, Ponerinae and Myrmicmae increased with increasing representation of *Pheidole* in local assemblages (Table 3), although these effects were less than the inverse relationship found between Formicinae and *Pheidole.* These results suggest that *Pheidole* contributes proportionally more to tropical ground ant assemblages as species richness increases as evidenced by the positive slopes of *Pheidole* contribution for the Pseudomyrmecinae, Ponerinae and Myrmicinae (Table 3), with a corresponding strong reduction of the Formicinae.

The negative relationship between *Pheidole* and formicines suggests that these may be involved in interference or diffuse competition, as found by VESPALAINEN & SAVOLAINEN (1990) for other myrmice species in boreal European ant communities. Another possible explanation is that species richness patterns of both groups are linked through a stress gradient, with formicines dominating more stressed environments, while *Pheidole* is more abundant in more favorable sections of the gradient. P. R. S. MOUTINHO (personal communication) has found an increasing faunal representation of *Pheidole* and a corresponding decline of formicines in successional seres in the eastem Amazon of Brazil, and suggests that this is due to micro-climatic effects, thus reforcing the stress gradient hypothesis. However, only experimental studies can separate these conflicting hypotheses. Pattems in contemporary ground ant assemblages do not indicate Dolichoderinae displacement by *Pheidole,* as suggested by BROWN (1973) in evolutionary time. However, in ecological time local exceptions may occur, especially with exotic species, such as *Linepithema humile* (Mayr) displacing *Pheidole megacephala* to an eventual spatial equilibnum in Bermuda (LIEBERBURG *et al.,* 1975), but these cases are exceptional in the Americas (FOWLER, 1992; FOWLER *et al.,* in press). Because the effect of *Pheidole* participation in local communities was even more intense than latitude on the reduction of formicines, these results suggest that in ground ant communities of the Americas species of *Pheidole* limit the formicines (KUSNEZOV, 1956), and not the inverse displacement of the related myrmicine genus *Myrmica* as found in boreal Europe (VESPALAINEN & SAVOLAINEN, 1990). Interspecific territoriality could reduce the number of ecologically distinct species to values smaller than the number of taxonomic species in the assemblage (CODY, 1974; PONTIN, 1982), and the use of higher taxonomic levels in this paper are justified by the results.

Biogeographic pattems are products of historical and ecological factors (ENDLER, 1982), and an understanding of the causes and consequences of the relative contributions of each is a major task of biogeographers. However, these unexpected but robust results suggest that our knowledge of the nutritional ecology of American ants is,at best, fragmentary and incomplete. Furthermore, due to poor fossil records of New World ants, it is at present impossible to try to separate histoncal from ecological factors. Nevertheless, the formicines are much more important in the higher North American latitudes, which may be due to their inferred Northem Hemisphere diversification (KUSNEZOV, 1953; BROWN, 1973). However, given the general dominance of *Pheidole* in ground ant communities of the Americas (WILSON, 1987; BENSON & BRANDAO, 1987; MOUTINHO, 1991), in species rich communities, especially in the tropics, *Pheidole* may regulate ant diversity (SAMWAYS, 1990; ANDERSEN, 1992), apparently by reducing formicine abundance. Although the foraging ecologies and nesting and nutritional demands of most ant species are still unknown, these results suggest that species of *Pheidole* and formicines may be using the same resources, and open further questions which must be necessarily resolved in carefully designed field experiments.

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