Diversity and Distribution of Ant Communities in Puerto Rico[1]

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ABSTRACT

I studied ants in upland tropical forest, grassland and agricultural land in San Lorenzo, Puerto Rico, to uncover factors responsible for the distribution and number of species in these communities. Observations, laboratory studies and field experiments were used. Microclimate influenced the distributions of *Pheidole fallax, Solenopsis geminata* and *Monomorium ebeninum*; forest ants had lower tolerance to high temperatures than ants from non-forested areas. In addition, Ponerinae ants did not tolerate high temperatures as well as ants in the Formicinae, Myrmicinae and Dolichoderinae. The larger number of species in non-forested areas is correlated with larger food overlaps, tighter guilds, a more variable microclimate, and higher levels of aggressiveness.

RESUMEN

Estudié las hormigas en áreas adyacentes de bosque tropical, pradera y zonas agrícolas en San Lorenzo, Puerto Rico. Observaciones, estudios en el laboratorio y experimentos de campo fueron realizados para tratar de descubrir los factores responsables de la distribución y el número de especies en estas comunidades. Encontré que las distribuciones de *Pheidole fallax, Solenopsis geminata* y *Monomorium ebeninum* son altamente influenciadas por el microclima. Las hormigas del bosque toleran altas temperaturas menos que las hormigas de áreas no forestales. Además, las hormigas de la subfamilia Ponerinae toleran altas temperaturas menos que las que pertenecen a las subfamilias Formicinae, Myrmicinae y Dolichoderinae. El número mayor de especies de hormigas en áreas no forestales está relacionado al mayor solapamiento alimenticio, gremios más compactos, un microclima más variable y niveles más altos de agresividad.

Two problems that ecologists address are the identification of those factors that determine the distribution and number of species in a community. Species distributions have been found to be affected by climate, nutritional requirements, predators, competitors and dispersal barriers (Andrewartha and Birch 1954, Krebs 1972). Several factors have been found to account for differences in species numbers. Paine (1966) and Harper (1969) found that predation on superior competitors increases diversity by keeping the weak competitor on the system. Connell (1978) suggested that disturbances intermediate in frequency and intensity should account for high diversity in coral reefs and tropical rain forest trees. Increase in area results in higher diversity due to its effect in reducing extinction rates (MacArthur and Wilson 1967). Greater resource diversity, smaller niche breadth, greater mean niche overlap, compact guilds, through their influence on species packing (Inger and Colwell 1977) and stochastic phenomena (Sale 1977, 1982; Caswell 1978) have been found to be related to diversity patterns.

Through a series of experimental field studies, I tried to determine the influence of food competition and microclimate on the distribution of *Pheidole fallax, Monomorium ebeninum* and *Solenopsis geminata.* In addition, I conducted analyses of food diversity, food breadth and overlap, and microclimate diversity to determine the contribution of these factors to the number of species in three adjacent ant communities. Also, ant tolerance to high temperature is analyzed to assess its contribution to ant species numbers. A companion paper discusses the subject of ant coexistence in these communities (Torres 1984).

HABITATS AND ANTS

From July 1978 to September 1980, I studied ants in a subtropical wet forest, grassland dominated by *Chloris radiata* and agricultural crops in San Lorenzo, Puerto Rico. Crops consisted of coffee (*Coffea arabica*), plantains (*Musa paradisiaca*), and yams (*Dioscorea alata*). These habitats were located near Route 7740 (forest: Km 4.4; grassland and crops: Km 1.1–2.5). The tight forest canopy produced a microclimate cooler and wetter than in the grassland and plantain-yams crops. Coffee groves and forest had similar microclimates. The forest contained 20 ant species, the grassland 37, and agricultural land 38 (see accompanying paper for a list of species). Thirty-four species were shared by grassland and agricultural land, and ten were found in all three habitats. The same ants tended to be found in coffee groves and forest. Excluding the coffee-groves species, agricultural land species were similar to those found in grassland. *Iridomyrmex melleus* and *Myrmelachista ramulorum* were found once on grass-

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land and might have been transient members of this community since they were usually found in shaded areas.

Due to the insular effect, the fauna in these habitats is depauperate, and ants are an example. Ants found on the island are generally small. Representatives of larger Camponoti of the *maculatus* and *abdominalis* groups are absent (Wheeler 1908). Neotropical genera such as *Atta, Azteca* and *Eciton* are also absent and *Crematogaster, Pseudomyrmex* and *Pheidole,* well developed in tropical mainland, are scarce in Puerto Rico (Wheeler 1908).

METHODS

FIELD EXPERIMENTS.—*Monomorium ebeninum, Solenopsis geminata* and *Pheidole fallax* are grassland and agricultural land ants found in forest grass-covered dirt roads but not within the forest. I conducted experiments to determine the factors that barred these species from the forest.

On July 3, 1980 I introduced to the forest nine logs containing *Monomorium ebeninum* colonies to which I fed honey and tuna fish every other day. Six other nests were introduced but not fed. I transferred six nests from grassland to another grassland 200 m from the forest as control for moving effects. I fed tuna fish and honey to six additional nests in the grassland to determine their nutritional adequacy as ant food. I isolated all fed nests from interspecific interference by hanging these from trees or fence posts and applying automotive grease to the strings. Grease was applied to unfed nests but in a manner that allowed ants to leave and re-enter. I observed nests every three days and placed food near unfed nests to check for ant presence and removed it when activity was observed. The experiment ended on September 25, 1980 when logs were split open to search for ants. Presence or absence of ant colonies and their conditions were recorded. If microclimate is the factor barring these species from the forest, fed and unfed nests in the forest would disappear; on the other hand, if competition for food is the limiting factor fed nests should remain and prosper while unfed nests should die, disappear or not prosper.

Finally, four *M. ebeninum* nests were introduced to the forest and fed but not isolated to study interspecific interactions. I brought three *Solenopsis* B (mainly a forest species) nests to the grassland on a sunny day and put them next to three *M. ebeninum* nests. Food was placed between the nests to study interspecific aggression.

On March 23, 1980 I introduced to the forest ten coconut fruits containing *Solenopsis geminata* nests. Five were fed with *Chloris radiata* seeds, tuna fish and honey every other day. *S. geminata* nests were not isolated from ant interference due to this species' aggressiveness. *S. geminata* is able to defeat the majority of Puerto Rican ant species under all environmental conditions (Torres 1981). I transferred five additional nests from grassland to grassland approximately 250 m from the forest to control for moving effects. Observations were made as in *Monomorium ebeninum*'s experiments. The experiment ended on April 27, 1980 when the fruits were opened to check for live ants. The experiment was repeated from April 3 to April 27, 1980. The reasoning behind these experiments was the same as for the *M. ebeninum* experiments.

The ground-nesting *Pheidole fallax* was almost impossible to transplant. I constructed a shade *in situ* over *P. fallax* nests simulating the forest canopy. The shade produced a cooler and wetter microclimate compared to control unshaded nests. I drove four wooden stakes at a distance of 18 cm from nest openings and fixed a 28 × 50 cm wire net covered with cloth to the stakes. Rain water percolation was normal through the shade and light intensity was approximately 50 percent of unshaded areas and approximately 25 percent higher than in the forest. Controls had four wooden stakes driven at the same distance from the nest with clothless wire nets. The experiments were performed three times involving four nests as experimental units and four as controls, and were conducted in 1980 on 9 Feb–22 March, 19 Feb–27 April, and 5 July–26 Sept. Observations were made weekly.

TOLERANCE TO 45°C.—Surface temperatures of 45°C and higher were experienced by ants that foraged during midday, and few ant species foraged in these temperatures. Since 45°C represents a realistic, but potentially limiting temperature, I studied ant tolerance to 45°C in an environmental chamber (Environator Model WL221). The chamber's cover was replaced with glass to enable observation of ants. I placed a minimum of ten ants at 45°C in vials with perforated caps to allow air circulation. The time it took 50 percent of the ants to assume a crouched position was taken as a measure of tolerance to 45°C. I replicated each experiment with individuals from ten colonies for most species.

FIELD TEMPERATURES AND NICHE METRICS.—I measured ground and vegetation temperatures under shade and sunlight at randomly chosen times of day for the three habitats using YSI telethermometers and with the help of two assistants. Information on food habits was obtained by observing ant nests for five minutes each hour. Food that ants were carrying was removed with forceps or a piece of adhesive tape and later identified in the laboratory. In addition, gastric distention, which occurred when liquid food was brought, was recorded. To study microhabitat utilization, I put baits simultaneously on ground, rock, litter and vegetation (at randomly chosen times) at a distance of 5–15 m from each other. This was done in sunny, shady, wet and dry areas, during night and day. Species found on the bait and inside a 25 cm^2 quadrat put around the bait were recorded. In addition,

TABLE 1. *Fates of* Monomorium ebeninum *nests subjected to different experimental treatments.*

	Forest		Grassland		
	Fed	Unfed	Unfed	Fed	Total
Remained	6	1	4	4	15
Died or disappeared	3	5	2	2	12
Total	9	6	6	6	27

TABLE 3. *Fates of* Pheidole fallax *nests subjected to different experimental treatments.*

	Shaded	Unshaded	Total
Remained	1	8	9
Moved	11	4	15
Total	12	12	24

I recorded interspecific aggressive interactions at baits. I calculated noncircular niche metrics using the Colwell-Futuyma (1971) measures with absolute weighting factors.

RESULTS

FIELD EXPERIMENTS.—Fisher's exact test (one-tailed) was used to analyze frequencies of fates of nests (Tables 1–3). Fed nests of *Monomorium ebeninum* did not survive better than unfed ones in the forest (Table 1, $P = 0.08$) suggesting that lack of food did not bar the species from the forest. There was no difference in survival between fed nests in the forest and relocated fed nests in the grassland ($P = 0.71$), nor between unfed nests in the forest and relocated unfed nests in the grassland ($P = 0.12$). Fed and unfed grassland nests did not differ in survivorship ($P = 0.73$), indicating that food offered was nutritionally adequate. Although I did not find differences in nest survivorship, *M. ebeninum*'s activity was different in the forest. This species was active in grassland nests and inactive in the forest most of the time. *M. ebeninum* was diurnal in agricultural land and grassland; on cloudy days its activity was reduced. Only during unusually warm days was this species active in the forest. On these days smaller drops in night temperature occurred and *M. ebeninum* continued foraging during the night. This suggests that warm temperatures, which were rarely experienced in the forest, were needed for foraging in this species.

The four fed nests of *Monomorium ebeninum* in the forest (not isolated with grease) were attacked by *Solenopsis* B and within days the latter moved its nests into the logs previously occupied by *M. ebeninum. Solenopsis* B killed most *M. ebeninum* that surfaced to feed. These species were similar in size and had complementary distributions: *M. ebeninum* was found in sunny areas whereas *Solenopsis* B was found in shaded ones. The three *Solenopsis* B nests brought from the forest and put near nests of *M. ebeninum* in sunny grassland were easily defeated by the latter at tuna fish baits. This alternating superiority was related to differences in tolerances to temperature (see Torres 1984), and indicates an effect of microclimate on the distribution of these species. Thus, aggression by *Solenopsis* B and *M. ebeninum*'s sensitivity to low temperatures prevented the latter from entering the forest.

TABLE 2. *Fates of* Solenopsis geminata *nests subjected to different experimental treatments.*

	Forest		Grassland	
	Fed	Unfed	Unfed	Total
Remained	0	0	7	7
Died or disappeared	10	10	3	23
Total	10	10	10	30

All *Solenopsis geminata* nests (fed or unfed) disappeared from the forest within two to three weeks (Table 2). Grassland, unfed, control ants remained in their nests in contrast to the unfed, forest-introduced ants ($P < 0.001$), ruling out the possibility that forest results were caused by moving effects. Grassland, unfed, control ants remained longer in their nests than those in fed nests in the forest ($P < 0.001$). These results suggest that food limitation was not responsible for the distribution of *S. geminata* and that microclimate was, most likely, the decisive factor. In the *Pheidole fallax* experiments (Table 3), ants in shade moved their nests 60 to 90 cm to sunny areas within a week, while control nests usually were not moved ($P = 0.004$), suggesting that microclimate prevented this species from entering the forest.

FOOD (DIVERSITY, BREADTH AND OVERLAP).—This study followed the analyses done by Inger and Colwell (1977) in their study of amphibian and reptile associations in Thailand. They proposed that to evaluate the contribution of food diversity to species-number determination, the resource matrices should be reduced to the resources common to the three habitats. If, after doing so, similar number of species are left in each of the reduced resource matrices then differences in species diversity are the result of the extra resources. After reducing the matrices (see Torres 1981) to the 15 food resources common to the three habitats, the number of ant species was the same in the reduced and in the nonreduced matrices. This indicates that differences in ant species diversity were not the result of the extra food resources.

TABLE 4. *Food niche breadths computed for 15 resources in all three habitats.*

Species	Agricultural land	Grassland	Forest
Brachymyrmex heeri	—	.1374[b]	—
Brachymyrmex minutus	.0963	—	—
Camponotus ustus	.0914	—	—
Cardiocondyla emeryi	.1288[a]	.1509	—
Cardiocondyla nuda	.0860	.2059	—
Cyphomyrmex rimosus	.0464	.1502	—
Iridomyrmex melleus	.1060	—	.1035
Monomorium ebeninum	.2079	.1340	—
Monomorium floricola	.1240	.1190	—
Mycocepurus smithi	.0889	.0262	—
Myrmelachista ramulorum	—	—	.0648[c]
Odontomachus brunneus	.1436	.0715	—
Paratrechina longicornis	.1328	.1281	—
Paratrechina steinheili	.1735	.1746	.0609
Platythyrea punctata	.0681	—	—
Pheidole exigua	.1733	.1875	—
Pheidole fallax	.0777	.1196	—
Pheidole moerens	—	—	.0335
Pheidole subarmata	.2113	.1537	—
Solenopsis A	.1357	—	—
Solenopsis B	—	—	.0709
Solenopsis geminata	.1641	.0483	—
Strumigenys louisianae	.0530	.1114	—
Tetramorium bicarinatum	.1978	.1814	—
Wasmannia auropunctata	.2271	.1682	—

[a,b,c] median niche breadth for agricultural land, grassland and forest species, respectively.

Niche breadth and overlap were also computed for the 15 resources in common. This is the only way in which niche metrics can be compared across habitats (Inger and Colwell 1977), assuming the 15 food resources were equally abundant in the three habitats. Food niche breadths differed (Kruskal-Wallis, $P < 0.05$) but niche breadth tended to be smaller in the forest (Table 4) which does not explain the higher species numbers in non-forested areas.

Since not all niche overlaps are of equal biological importance (Inger and Colwell 1977), it is best to analyze overlaps with the notion of nearest neighbor. Figure 1 shows mean overlaps with the first, second, . . . , ith nearest neighbor for the species in the three habitats. Mean food overlaps were higher in the agricultural land and grassland communities at all orders of nearness. The standard deviations of overlaps (Fig. 1) show that communities consisted of tighter guilds in the non-forested areas. This is indicated by the peak of the distributions, which occurs when the order of nearness begins to exceed the average guild size (because at this point overlaps are within guilds and between members of different guilds). The peaks show that guilds were of approximately the same size in the agricultural land and grassland communities. Similarity in community organization in grassland and agricultural land as compared to forest is also indicated by the distribution of mean food overlap (Fig. 1).

MICROHABITAT (DIVERSITY AND OVERLAP).—Temperatures on the ground and vegetation are summarized for days and nights in Figure 2. Analyses concentrate on forest and agricultural land data (grassland and agricultural land data were similar). Mean temperature was lower in the forest than in non-forested areas (t-test, correction for unequal variances, $t = 18.91$; df = 1022, 400; $P < 0.05$). I made conservative tests of equality of variances selecting the 0.01 significance level. Total variances (Fig. 2) in the three habitats were heterogeneous ($F_{max} = 2.17$; df = 3, 400; $P < 0.01$) pointing to more variance in temperature in non-forested areas. Temperature was more variable in sunny agricultural land ground than in sunny forest ground ($F = 2.56$; df = 53, 48; $P < 0.01$), while shaded agricultural land and shaded forest ground did not differ in temperature variance ($F = 1.56$; df = 52, 51; $P > 0.05$). Temperature variability in sunny forest ground was no different from that of shaded forest ground ($F = 1.55$; df = 48, 51; $P > 0.05$). Statistical analyses for vegetation microhabitats gave similar results (see Torres 1981 for details).

TOLERANCE TO 45°C.—Species' tolerance to 45°C is presented in Torres (1984). I performed a two-way ANOVA with species and habitats as factors on the data of temperature tolerance for the species shared by the three habitats (forest, grassland and agricultural land). Interaction between factors was significant and for that reason I plotted the mean value for each species (Fig. 3). Interaction was produced because some samples from the agricultural land belong to species found mostly in closed canopy crops, the latter having a microclimate similar to the forest. A one-way ANOVA using the mean value for each species showed that species differed in temperature tolerance across habitats ($F = 4.13$; df = 2, 21; $P = 0.03$). The Student-Newman-Keuls (SNK) ($\alpha = 0.05$) procedure showed that organisms in non-forested areas tolerated high temperatures better than forest organisms and that there was no difference in tolerance to temperature between grassland and agricultural land organisms.

I performed a two-way ANOVA (habitats and subfamilies) on tolerance to 45°C for all the species for which I have data on these variables (Table 5). Subfamilies in non-forested areas tolerated high temperatures better (SNK, $\alpha = 0.05$). The subfamily Ponerinae withstood high temperatures less well than the Formicinae, Myrmicinae and Dolichoderinae subfamilies (SNK, $\alpha = 0.05$). These higher temperature tolerances in non-forested areas correlate with the higher temperatures experienced in these

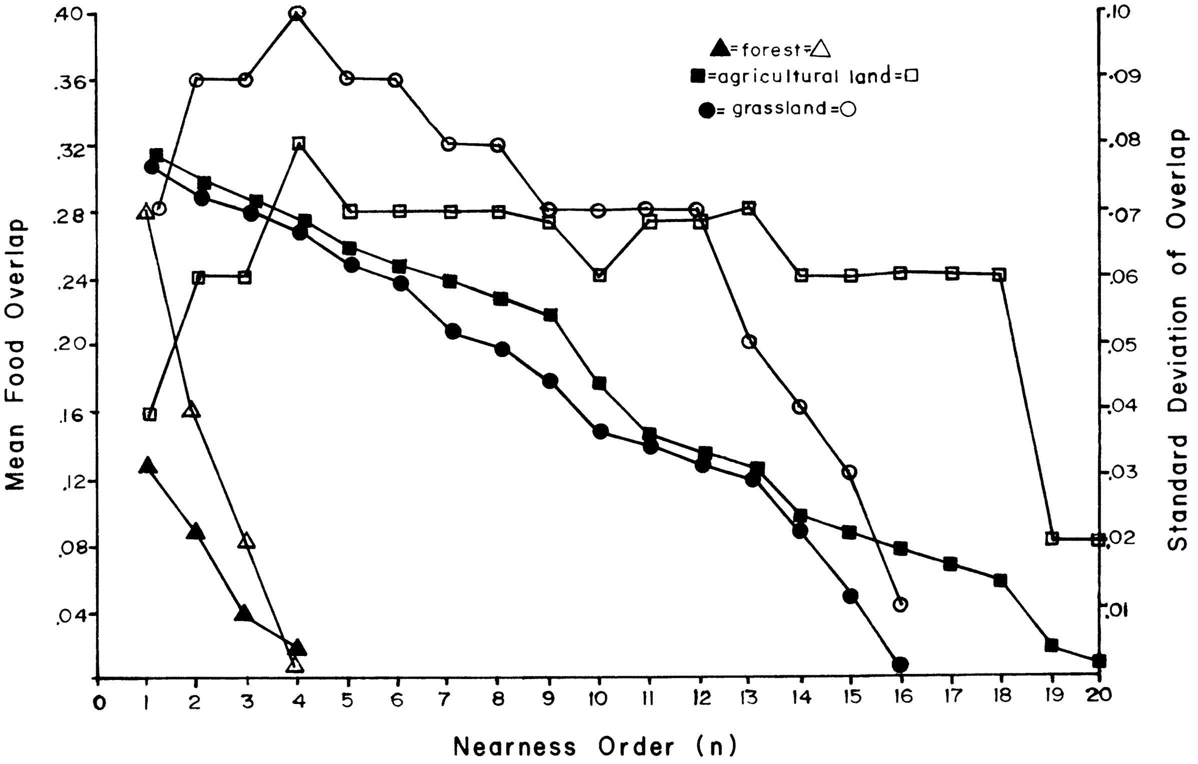

FIGURE 1. Mean food overlap and standard deviation of food overlap of first through nth nearest neighbors. Dark symbols indicate mean and open symbols indicate standard deviation.

areas. Variances in tolerance to 45°C did not differ across habitats in the Ponerinae (F_{max} = 2.07; df = 3, 3; $P >$ 0.05). The Myrmicinae exhibited almost no variability in the forest but they did exhibit a huge variability in non-forested areas (F_{max} = 137.2; df = 3, 5; $P <$ 0.01).

DISCUSSION

Field experiments demonstrated that microclimate played an important role in ant species distribution in the communities studied. Microclimate is important to ants in terms of their foraging activities and nesting places (Gösswald 1951, Brian 1956, Brown 1973, Hunt 1973, Levins *et al.* 1973, Lieberburg *et al.* 1975, Trempler 1976, Taylor and Adedoyin 1978, Smallwood and Culver 1979, Whitford *et al.* 1981). Temperature is very important in the development of larvae and pupae in ants (Wilson 1971). *Solenopsis geminata* larvae and pupae seem to need high temperatures for their development because they were kept at the top of the mound where maximal temperatures were recorded (pers. obs.), and this is probably one reason for its absence in the forest.

Experiments with *Monomorium ebeninum* showed that temperature affected this species in two different ways: by reducing colony activity and by modifying its fighting abilities. *Monomorium ebeninum*'s sensitivity to relatively low temperatures will continue to bar it from the forest regardless of the removal of *Solenopsis* B from the forest. *M. ebeninum* switched to night foraging when nocturnal forest temperatures were high to try to compensate for those days in which temperatures were not high enough to allow foraging. Whitford and Ettershank (1975) found that *Novomessor cockerelli* switch their pattern of foraging according to the temperature, cloudiness or degree of ground humidity. Sanders (1972) suggested that shifts to crepuscularity or nocturnality in *Camponotus* spp. were temperature adaptations. In addition, Hunt (1973) was able to produce shifting in activity patterns by shading the nests of *Dorymyrmex antarcticus* and *Tapinoma antarcticum* in Chile. Nonetheless, Hodgson (1955) did not find compensation through increases in night activity in *Atta cephalotes,* even when this species loses a great part of its day-foraging time due to rain.

In the case of *Pheidole fallax,* microclimate also af-

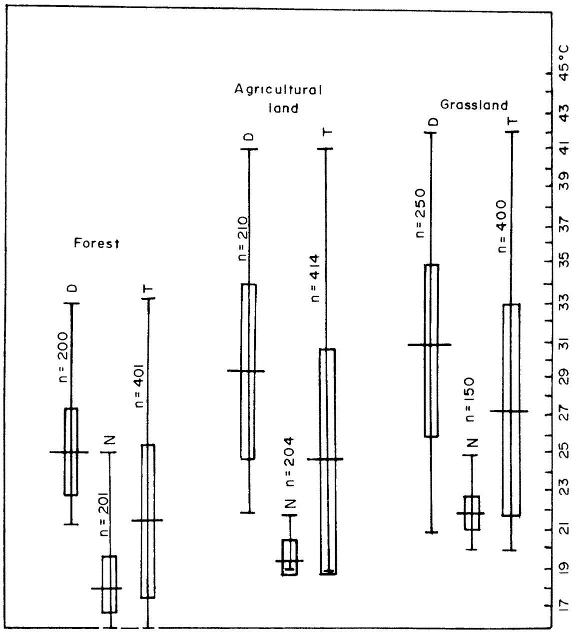

FIGURE 2. Temperature summaries for day (D) and night (N) on vegetation and ground. T = total. Mean (vertical bar), range (horizontal bar) and one standard deviation (rectangle) are indicated.

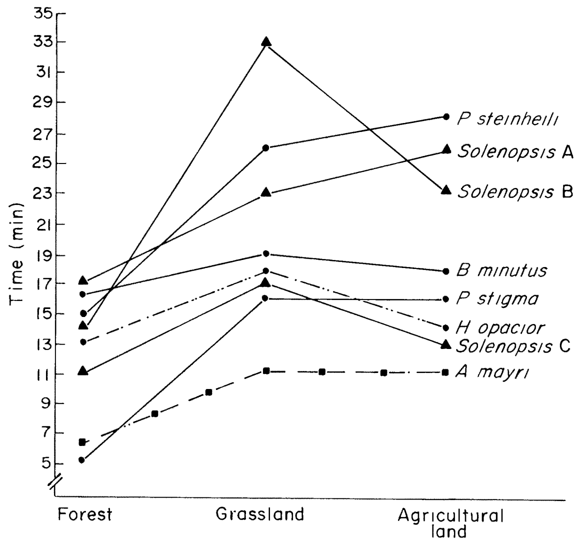

FIGURE 3. Mean tolerance at 45°C for the species in the three habitats. Tolerance is indicated by the time required for 50 percent of exposed ants to assume a crouched position.

fected the outcome of combats with *Pheidole subarmata* (see Torres 1984). *P. fallax* won daily combats in sunlight but lost night and shade combats. *P. fallax*'s poor fighting abilities in shade and during the night could be a reason for its absence from the forest. Tolerance to 45°C was correlated with these species' fighting abilities (*P. subarmata* tolerated high temperatures less well than *P. fallax*).

The effect of shade on ants has been documented in other ant communities. Brian (1956) found that increases in shade due to the gradual growth of trees reduced the number of warm, dry nest sites resulting in a reduction in the number of ant colonies. Taylor and Adedoyin (1978) found that the distribution of ants in Nigerian cocoa farms depended on the degree of shadiness. Ants are absent 2300 meters above sea level in closed-canopy forests everywhere, especially in the tropics (Brown 1973). On treeless slopes at higher elevations (3500–4000 m) ants may be abundant suggesting that radiant heat controls distribution (Brown 1973). Working with Chilean ants, Hunt (1973) found that artificially shaded *Tapinoma antarcticum* move their nests to unshaded locations. Wheeler (1910) discusses several examples where he found that ants are more abundant in eastern and southern slopes among temperate zone ants. The distribution of *Iridomyrmex humilis* is also highly influenced by climatic conditions (Brown 1973, Trempler 1976). These studies, together with my findings, suggest that temperature is one of the most important factors regulating ant distributions in all regions of the world.

TABLE 5. *Two-way ANOVA for temperature tolerance to 45°C. Factors are ant subfamilies and habitats. A logarithmic transformation of the data was performed to reduce heterogeneity of the variances.*

Source of variation	df	MS	*F*	*P*
Habitats	2	.731	8.38	.001
Subfamilies	3	.535	6.12	.001
Interaction	6	.028	0.32	.924
Explained	11	.322	3.69	.001
Error	67	.087		
Total	78	.120		

The Ponerinae did not withstand high temperatures well. This could be the reason this subfamily's species were found mostly in wet-shaded places. In terms of tolerance to high temperatures, the Ponerinae were close to the Myrmicinae in the forest but closer to the Formicinae in agricultural land. This occurred because the Myrmicinae that entered the forest were those that tolerated or preferred low temperatures, whereas in agricultural land members of this subfamily that tolerated high temperatures were found together with low tolerance species. The high variability in temperature tolerance in the Myrmicinae has contributed to their exploitation of more climatically variable habitats like those present in non-forested areas.

There are several factors associated with the higher numbers of species in non-forested areas. First, the occurrence of open and closed-canopy crops allowed for the highest number of species in the agricultural land (correcting for transient species found in the grassland). The presence of closed-canopy crops permitted several forest ant species to enter the agricultural land. Second, higher food overlaps and tighter guilds are associated with a greater number of species in non-forested areas. Microhabitat diversity affected the degree of overlap in the food niche dimension. Its effects were greater in non-forested areas due to greater variability in microclimate, as indicated by the field temperature data. The presence of a more variable environment affects the distribution of resources through its influence on ants' daily activities, patch utilization (in time) and outcome of aggressive interactions (see Torres 1984).

There were more interspecific combats at tuna fish baits in non-forested than forested areas. I observed combats in 6 percent ($N = 464$) of the baits put in the forest compared to 38 percent ($N = 1056$) of those in non-forested areas. This agrees with Culver's (1974) finding of more prevalent aggression in structurally simple habitats, but is in disagreement with his conclusion of lower species packing in communities where aggressions are more common. This suggests that interspecific aggression, which is climatically influenced, plays a greater role in the allocation of resources in the non-forested areas.

MacArthur's (1972) suggestion that habitats with greater structural diversity should have greater numbers of species was not supported by this study. The forest's greater structural diversity, acting as a buffer, reduced the number of climatic microhabitats for ants, thus reducing the number of ant species. Food overlaps were larger in the non-forested areas, contrary to the expectation of larger overlap in more predictable environments (Levins 1968, MacArthur 1972, May 1973). It is possible that overall overlaps were smaller in the non-forested areas when food overlaps are combined with microhabitat overlaps. The difficulties of comparing microhabitats across habitats and the non-independence of these niche dimensions impeded the analyses of overall overlaps.

Although I did not carry out experiments to determine the contribution of area, predation and disturbance to the number of species in these communities, it seems that these factors are not responsible for the number of species. Greater area could be a factor permitting more species due to its influence in lowering extinction rates (MacArthur and Wilson 1967). However, forested areas were large enough (in terms of ant biology) to nullify this effect. In a study of the biogeography of ants in the Puerto Rican bank (Torres, unpublished), I have found islands with smaller areas than the forest which, nevertheless, contained more ant species; this makes unlikely an area effect for these diversity patterns. These islands were homogeneous in vegetation, eliminating the possibility that greater numbers of species were due to greater macrohabitat complexity.

Ox-plowing was carried out once or twice a year in agricultural areas disturbing the ant community, but it recovered quickly. The fact that grassland ant numbers were similar to those of the agricultural land (when species restricted to coffee groves were not taken into account) points to a minimal effect of plowing in determining species number. Also, the fact that overlaps and the tightness of guilds were almost identical in the grassland and agricultural land ant communities also supports the contention that plowing did not affect the organization in these communities. Ant recovery after disturbance is facilitated by the facts that ants do not build elaborate nests like many other social insects (Wheeler 1910), they eat the brood when starvation threatens, and that workers, larvae and queens can often endure long periods without food or water (Brown 1973, Carroll and Janzen 1973). Stability in ant communities is also enhanced by the longevity of their members and the fact that the total number of ants can vary without altering the number of colonies (Pickles 1940, Wilson 1971). When conditions improve colonies serve as nuclei in the rapid restoration of the populations of individuals (Wilson 1971).

Predation did not appear to be the cause of the difference in species numbers and distribution. Ants have few natural enemies (Wheeler 1910, Skaife 1974, Wilson 1971). The effect of predators on worker ants is best described as a parasitic relationship (at the colony level) due to the sterility of worker ants. Worker losses through foraging mortality are usually compensated by the amount of food taken in exchange (Carroll and Janzen 1973). Ants are the worst enemies of other ants (Wilson 1971), but the Cerapachyinae, Dorylinae and some Ponerinae that are specialized predators on other ant species are absent from Puerto Rico.

In summary, the greater number of species in non-forested areas is related to greater food overlaps, tighter guilds, a more variable microclimate and higher levels of aggressiveness.

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