

Comparative analysis of harvester ant assemblages of Argentinian and Chilean arid zones

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In this paper we compare several attributes of a number of harvester ant assemblages of Argentinian Monte desert and Chilean arid zones, two South American arid regions separated by the Andes Mountain Range. Our data indicate that Monte desert assemblages have a higher species richness and diversity than Chilean assemblages. However, other attributes such as foraging distance, type of foraging, and community body size do not differ between the two regions. Argentinian ants presented a wider temporal activity breadth than Chilean ants, which may be due to the absence of species resistant to high temperatures in the Chilean myrmecofauna. Seed removal rate by harvester ants was markedly different in the two regions, being four times higher in the Argentinian biota than in the Chilean. Despite the geographical proximity of the two regions, biogeographical and historical processes such as the uplift of the Andes Mountain Range, the radiation of granivorous genera in Argentina, and the dispersal of granivorous species from the tropic toward the Monte must have contributed to the ant community dissimilarity between the two deserts. Judging by the genera participating in the seed removal, the species that compose the South American seed-eater myrmecofauna present a more generalized trophic behaviour than that observed in granivorous ant species of North American deserts.

Introduction

One of the most important taxa inhabiting deserts are harvester ants (Brown *et al.*, 1979; Davidson *et al.*, 1980). Studies conducted at a local spatial scale in Australian and North American deserts have revealed that granivorous ants exert an important effect on the vegetation (e.g. Reichman, 1979; Inouye *et al.*, 1980; Davison, 1982; Andersen, 1987). Despite the apparent simplicity of granivore communities, it has been demonstrated that harvester ants interact in complex and often subtle ways with their resources, and with other seed predator taxa (see review in Brown *et al.*, 1986). Granivore communities are characterized by a high spatial variability in diversity and species composition (Andersen, 1982; Brown, 1987), thus precluding to make inter-regional or inter-continental comparisons based on a few local study sites.

The importance of granivory by ants in South American deserts is little known, reflecting the scarcity of research. Mares & Rosenzweig (1978) estimated seed removal rates in one locality of the Monte desert (Andalgalá, Argentina), and concluded that the

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low intensity of granivory in the Monte reflected the low species richness of seed-eater ants in South America as compared to North America (see also Orians *et al.*, 1977). However, South American arid and semi-arid regions vary greatly in climate and topography, and a proper comparison should include a number of local communities so that spatial variability of assemblages may be explicitly taken into account. Despite the critical importance of community variation to our understanding of the factors affecting organization of harvester ant communities, this variable has been usually dismissed in comparative studies.

The development of arid zones in the western margin of southern South America (Chile) began in the Pleistocene, and the present level of aridity was reached very recently in Holocene times (Arroyo *et al.*, 1988). Actual arid and semi-arid climates in the Chilean margin extend from 18°S to around 34°S (Di Castri & Hajek, 1976). On the other hand, the formation of arid zones in the eastern margin of the Andes Mountain Range (Argentina) began in the Pliocene but the actual Argentinian Monte desert originated in Pleistocene times around 1–1.5 million years ago (Vuilleumier, 1971; Solbrig *et al.*, 1977; Mares *et al.*, 1985). The Monte desert presently extends from 25°S to around 41°S (Mares *et al.*, 1985). In this paper, we shall compare the community structure of several harvester ant assemblages inhabiting the arid and semi-arid region of Chile and the Monte desert of Argentina in an attempt to evaluate the effect of historical and biogeographical processes on the community attributes of seed-eating ants in both regions.

Materials and methods

We censused five granivorous ant assemblages of the Argentinian Monte desert (Morello, 1958) and five assemblages belonging to the Chilean arid zones (Fig. 1). Since a proper comparison should be made between localities with similar abiotic characteristics, we selected study sites in both deserts with similar mean annual precipitation (Table 1). Precipitation data were obtained from the Ministerio de Obras Públicas in Chile and from the Servicio Meteorológico Nacional in Argentina.

Following Morton & Davidson (1988), at each study site we established a grid of 80 Petri dishes at ground level in a configuration 8×10 with a distance of 5 m between dishes. Each plate was filled with cracked millet seeds and four strips of masking tape were applied to facilitate the access of ants to seeds. Seeds were offered to ants 2 h prior to census. In order to minimize the error associated with presumable different activity temperatures of species, we made four censuses corresponding to 25, 35, 45 and 50°C at different times of day in each locality. In addition, since it is well known that some species may modify their activity time periods depending on the seed availability (Whitford & Ettershank, 1975; Hölldobler & Moglich, 1985), thus displacing its foraging activities toward more nocturnal hours, we made a fifth census 2 h after sunset in each locality. Each of the five censuses involved of a visual inspection of the species consuming seeds in each Petri dish during 60 s. We considered an ant to be a seed-eater when it was present at the seed baits and transported seeds to the nest. Species were characterized according to their abundance as common or uncommon. We considered a species to be common when the number of Petri dishes in which it was observed exceeded the 10% of the total of plates occupied by the total of species in the community. All censuses were carried out during the austral summer season, January and February of 1990 and 1991. Identification of species was carried out according to Kusnezov (1978) for Argentinian ants and Snelling & Hunt (1975) for Chilean ants.

We considered the following measures of community structure: (1) Species richness (S), estimated as the number of species present in a locality. (2) Species α -diversity, estimated by the Shannon diversity index, $H' = -\sum p_i \ln p_i$, where p_i corresponds to the number of Petri dishes occupied by species i as a proportion of the total number of plates occupied by all species in the grid. A plate was considered occupied by species i when that species was

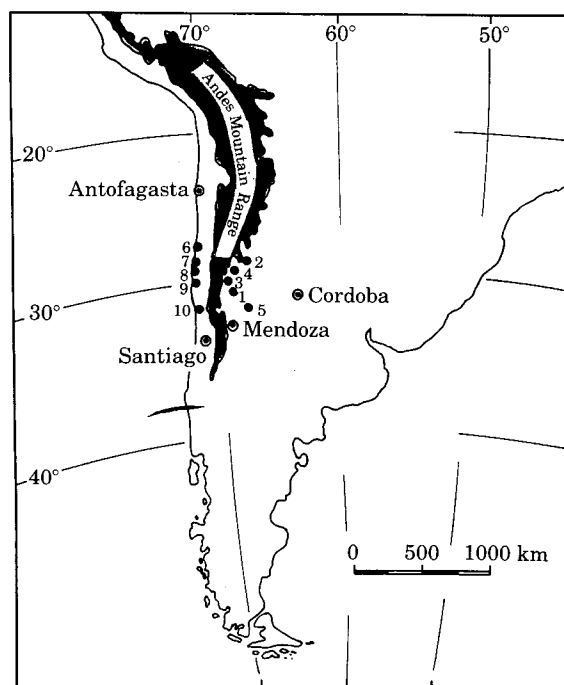


Figure 1. Map of southern South America indicating the geographical locations of the study sites. The shaded region indicates elevations above 3000 m in the Andes Mountain Range. Numbers indicate locality codes as in Table 1.

found at any census period. (3) Community body size structure, estimated from the mean size of each species belonging to a community. Since polymorphism due to geographic variability may exist depending upon the coexisting species (Davidson, 1978; Oster & Wilson, 1978), we evaluated the size structure for all species present in a locality. The size

Table 1. Community measures of species richness (S), species diversity (H'), foraging distance (D), foraging type (T) and body size structure (BS) for each granivorous ant assemblage. For each locality, mean annual precipitation (pp) is indicated

Country/locality	pp (mm)	S	H'	D	T	BS
Argentina						
1. El Balde (30°40'S, 68°30'W)	66	9	1.80	1.72	0.39	0.81
2. Villa Mazán (28°40'S, 66°30'W)	80	11	2.02	2.89	0.73	0.75
3. Jáchal (30°10'S, 68°40'W)	128	11	2.06	0.70	0.70	0.97
4. Villa Unión (29°39'S, 68°10'W)	194	10	2.08	1.34	0.33	0.81
5. Mascasín (31°30'S, 67°10'W)	270	10	1.65	1.21	0.19	0.83
Chile						
6. Caldera (27°10'S, 70°50'W)	43	2	0.57	3.57	0.74	0.98
7. Castilla (27°50'S, 70°35'W)	84	3	0.80	3.18	0.45	0.83
8. Cachiyuyo (29°04'S, 70°50'W)	123	3	0.75	3.25	0.58	0.89
9. La Serena (29°52'S, 71°15'W)	162	3	1.01	1.94	0.50	0.71
10. Aucó (31°45'S, 71°00'W)	297	3	0.98	0.37	0.46	0.51

of ants was estimated indirectly by measuring its head width with a graduated binocular microscope (precision 0.05 mm). An average number of 13 workers of each species were measured, and the lowest number of measured workers was six for *Brachymyrmex giardii* in Castilla. It was possible to calculate an index of community size as, $BS = \sum t_i p_i$, where t_i is the mean body size of the species i and p_i represents its population abundance as previously defined. (4) Community foraging distance, measured as the distance from the nest entrance to the dishes actually used by workers, standardized by the relative abundance of each species. We calculated the index of community foraging distance as, $D = \sum d_i p_i$, where d_i is the foraging average distance of the species i and p_i as above. (5) Community foraging score, as the type of foraging used by each species at collecting seeds. Individual foraging was assigned a score of 1 and columnar foraging was assigned a score of 0. Species showing a mixed type of foraging were assigned a score of 0.5. This assignment allowed us to calculate a weighted index of community foraging type as, $T = \sum f_i p_i$, where f_i is the foraging score of the species i and p_i as previously defined. (6) Temporal activity breadth, estimated by the index proposed by Simpson (1949), $B = (\sum p_i^2)^{-1}$, where p_i indicates the proportion of active species at temperature i with respect to the total of species of the community. (7) Seed removal rate, estimated by offering 16 Petri dishes with 10 g of cracked wheat during 48 h to ants, excluding birds and rodents by covering every dish with wire mesh. Seed dishes were placed along linear transects every 10 m. In addition, we set two control dishes (all granivores excluded) to determine presumable effects of water loss on seed masses. Remaining seeds were weighed in the lab and corrected for water loss by comparison with controls. All comparisons were made by using a non-parametric two-tailed Wilcoxon–Mann–Whitney test (Siegel & Castellan, 1988). Two seed removal experiments were made, corresponding to Villa Unión (29°39'S, 68°10'W) in Argentina and one locality of central Chile (Fundo El Pangué, 33°18'S, 71°11'W). Seed removal experiments were carried out during the peak activity season of ants in each region, that is, summer (January) for Chilean arid zones (R. A. Vásquez, unpub. data), and fall (April) for the Monte desert (Mares & Rosenzweig, 1978).

Results

Comparison of species richness and diversity indicated that both attributes were lower in the Chilean communities [species richness (S): mean \pm S.E., 2.8 ± 0.2 for Chile versus 10.2 ± 0.37 for Argentina; α -diversity (H'): 0.82 ± 0.08 for Chile versus 1.92 ± 0.08 for Argentina, $z = 2.61$, $p < 0.01$, in both cases, Table 1]. Chilean ant species exhibited a similar mean foraging distance to their Argentinian counterpart (mean \pm S.E., 2.46 ± 0.59 versus 1.57 ± 0.37 , respectively, $z = 1.36$, $p > 0.1$, Table 1). This indicates that despite the low number of species in the Chilean biota, ants move a relatively similar distance when searching for seeds in the two biotas. Similarly, mean community foraging type (T) did not differ between Chilean and Argentinian ant assemblages (mean \pm S.E., 0.55 ± 0.05 versus 0.47 ± 0.11 , respectively, $z = 0.94$, $p > 0.3$) thus indicating that the proportion of columnar and individual foraging behaviour are about the same in both regions. Community body size structure (BS) did not show differences between regions (mean \pm S.E., 0.78 ± 0.08 versus 0.83 ± 0.04 , for Chilean and Argentinian assemblages, respectively, $z = 0$, $p > 0.5$, Table 1). Community temporal activity breadth (B) differed between the two regions (mean \pm S.E., 3.7 ± 0.06 versus 4.13 ± 0.13 , for Chilean and Argentinian assemblages, respectively, $z = 2.61$, $p < 0.01$). This result may be associated with the nil activity exhibited by Chilean ants at 50°C (Table 2). Finally, the rate of granivory by Chilean ants was lower than that exhibited by Monte desert ants (mean \pm S.E. [g/(tray \times 24 h)], 2.0 ± 0.22 versus 8.5 ± 0.34 , respectively, $z = 4.82$, $p < 0.001$), thus indicating the high variability in granivory by ants in nearby South American arid ecosystems.

Although seed removal estimates have been used extensively to infer the relative

Table 2. Proportion of active species of each community at different surface soil temperatures. B indicates the community temporal activity breadth (see Materials and methods for details)

Country/locality*	Surface soil temperatures					B
	25°C	35°C	45°C	50°C	Nocturnal	
Argentina						
1.	0.78	0.89	0.67	0	0.55	3.88
2.	0.70	0.90	0.30	0.10	0.70	3.86
3.	0.54	0.64	0.45	0.27	0.82	4.49
4.	0.90	0.70	0.60	0.20	0.80	4.38
5.	0.62	0.87	0.37	0.12	0.62	4.03
Chile						
6.	1.0	1.0	0.50	0	1.0	3.77
7.	0.67	0.67	0.33	0	1.0	3.55
8.	0.67	0.67	0.67	0	0.67	3.76
9.	1.0	0.67	0.33	0	0.67	3.55
10.	0.67	1.0	1.0	0	0.67	3.85

* See Table 1 for explanation.

importance of different granivore taxa or species richness (e.g. Mares & Rosenzweig, 1978; Abramsky, 1983; Morton, 1985; Kerley, 1991), comparisons have usually involved different seed types. This may lead to error since not all seeds are similarly palatable for ants (Vásquez, unpubl. data). Since we have used an identical experimental design in the two regions, we can be sure that differences are due only to ant granivory rather than to a technique bias (see also Kelrick *et al.*, 1986).

Discussion

Our data indicate that species richness and species diversity are higher in the Argentinian Monte desert than in the Chilean arid zones. It is possible to visualize two historical and biogeographical processes that may help to explain dissimilarities between the two regions. On one hand, it has been suggested that the high diversification of some granivore genus (e.g., *Pogonomyrmex*) in Argentinian arid zones may reflect centres of radiation (Kusnezov, 1951a). On the other hand, beside native species, the ant fauna of Argentinian arid zones is composed of immigrants from more mesophilic tropical and subtropical areas (Kusnezov, 1963). Colonization from tropical areas towards arid zones is a process that began during the formation of the Monte desert and is presently in course. Species of the genera *Pheidole* and *Elasmopheidole* are the most important tropical immigrant granivorous species (Kusnezov, 1951b). Regarding the cosmopolitan genus *Solenopsis*, some species are represented in Chilean arid zones (Snelling & Hunt, 1975), suggesting its presence in the western margin of southern South America prior to the emergence of the Andes Mountain Range. The uplift of the Andes began 65 million years ago (Paskoff, 1977) and subsequent Pleistocene glaciations must have affected dispersal of species from Argentina to Chile. Judging by checklists of Snelling & Hunt (1975) and Kusnezov (1978), species of the genera *Pogonomyrmex*, *Pheidole* and *Elasmopheidole* are poorly or not at all represented in Chilean arid zones, with species of the genera *Pogonomyrmex* and *Pheidole* representing 8.0 and 0.1% of the total Chilean myrmecofauna, respectively. Snelling & Hunt (1975) suggested that Chilean *Pogonomyrmex* may have colonized the northern arid zones by migrating from the more mesic southern areas. On the other hand, the only

Pheidole species found in Chilean territory may have migrated from Perú through the Chilean-Peruvian coastal desert. Although the effectiveness of the Andes Mountain Range as a barrier to dispersal of ants from Argentina to Chile has been questioned on the base of the high motility exhibited by winged reproductives (Hunt, 1973), colonization by granivorous ant species from tropical areas toward arid zones during the Pleistocene must have produced a gradual accumulation of granivore ant species in the Argentinian deserts. Consequently, the adaptive radiation of ants in the eastern margin after the uplift of the Andes Mountain Range, colonization from the tropics toward the Monte desert, as well as the effects of subsequent aridity and geomorphological barriers to dispersal, must have been important factors in determining the actual depauperated granivorous ant assemblages of Chilean arid zones as compared to the Argentinian Monte desert.

Similarity in foraging distance, type of foraging, and size structure between the two regions implies that despite the historical and biogeographical factors affecting diversity, other community attributes have not been affected, being roughly the same in the two regions. It is possible that the more generalist food habits of South American desert ants produces a lesser dependence on seeds as food items, thus diminishing the potential for food limitation. Although we cannot reject the possibility that ant assemblages are not in equilibrium with their resources, an alternative explanation may lie in other biotic factors related to the different levels of granivory exhibited by rodents in the two regions. Specialist granivorous rodents are absent in South American deserts (Brown & Ojeda, 1987); however, some rodents tend to be more granivorous in Chilean arid zones than in the Monte desert (Meserve, 1981). Since it is well known that granivorous rodents are strong competitors of ants in arid zones of other latitudes (Brown *et al.*, 1986), the low species diversity of ants in Chile may be compensated by a higher intensity of granivory by rodents. Consequently, all else being equal, it is possible that Chilean ants may be exposed to roughly similar levels of interspecific competition for seeds as Argentinian ants. Clearly more work is needed to test these hypotheses.

Table 3. Status [common (c) or uncommon (u)] of each species in Argentinian and Chilean localities. Numbers indicate the locality code as in Table 1

Species	Argentina					Chile				
	1	2	3	4	5	6	7	8	9	10
<i>Acromyrmex lobicornis</i>	c	c		u	c					
<i>Acromyrmex aspersus</i>			c							
<i>Araucomyrmex tener</i>			u							
<i>Araucomyrmex goetschi</i>						c	c	c	c	c
<i>Brachymyrmex giardii</i>							u	u	c	c
<i>Brachymyrmex laevis</i>	u	u	u	c	u					
<i>Brachymyrmex longicornis</i>		c	u		u					
<i>Dorymyrmex ensifer</i>		u	c	u	u					
<i>Dorymyrmex exsanguis</i>	u	c	c	u	u					
<i>Forelius grandis</i>	u	c	c	u	u					
<i>Pheidole</i> sp.	c	u		c	u					
<i>Pogonomyrmex breviparbis</i>	u	u	c	c						
<i>Pogonomyrmex inermis</i>			u							
<i>Prenolepis longicornis</i>	c	u		c	c					
<i>Pseudomyrmex denticollis</i>		u								
<i>Solenopsis gayi</i>						c	c	c	c	c
<i>Solenopsis granivora</i>	u	u		u	c					
<i>Solenopsis saevissima</i>	c		u	c	c					
<i>Solenopsis</i> sp.			u							

Our results indicate that the intensity of granivory by ants was higher in Argentina than in Chile as expected from differences in species diversity between the two regions. Interestingly, seed removal rate by Argentinian ants was higher than that reported by Mares & Rosenzweig (1978) in the same season for one Argentinian locality. They observed a low seed removal rate in comparison to North American arid zones and suggested that the Monte desert myrmecofauna is depauperated compared to that observed in the Sonoran desert. Nevertheless, although our data indicate that the intensity of granivory by ants in the Monte is still much lower than in North America (see also Morton, 1985), species richness is higher than previously suggested, thus contradicting Mares & Rosenzweig's assertion. In fact, comparing our data with Davidson's (1977), it is clear that both species richness and species diversity are higher in the Monte desert. Perhaps differences in species richness of harvester ants between the Monte desert and North American deserts are due to a more generalist trophic behaviour of South American ants. This fact is indirectly corroborated when comparing the genera actually involved in seed consumption in the two biotas. Harvester ant species of North American deserts belong to the typical specialist granivorous genera such as *Pheidole* and *Pogonomyrmex*. In South America, besides these granivorous groups, we have detected seed removal by the fungus-growing genus *Acromyrmex*, and the more generalist genera *Araucomyrmex*, *Brachymyrmex*, *Dorymyrmex*, *Forelius*, *Prenolepis*, and *Solenopsis* (Table 3). Mares & Rosenzweig (1978) pictured an evolutionary scenario regarding the evolution of granivore communities in the Argentina Monte desert in an attempt to explain the apparent lower intensity of granivory by ants. They suggested that the extinction of granivorous marsupials (Family Argyrolagidae) in South America during the Pliocene allowed the release of large-seeded plants from predation, increasing the extinction probability of competing small-seeded plants and their consumers, the specialist harvester ants. If their hypothesis is correct, it is possible that the higher occurrence of granivory by generalist rather than by specialist granivorous ants observed in South American arid regions as compared to North America may be the result of a higher extinction rate experienced by specialist South American harvester ants.

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