COMPARATIVE STRUCTURE OF HARVESTER ANT COMMUNITIES IN ARID AUSTRALIA AND NORTH AMERICA[1]

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Abstract. In the Australian arid zone, the species richness of ants is greater and that of mammalian granivores is less than in North American deserts. This study aimed to determine if the structure of harvester ant communities differs from that seen in North American deserts, focussing on differences related to the paucity of rodents. We tested three hypotheses: (1) because there are fewer rodents, Australian harvester ants should be more abundant and diverse in local habitats than in North American deserts of similar productivity; (2) because the absence of rodents would allow ants to use larger seeds that are preferred by rodents in North America, Australian ant communities should include a larger size range and contain larger workers; and (3) that apart from differences resulting from a paucity of rodents, Australian and North American communities would be convergent in characteristics of community structure resulting from competition. We sampled 19 communities across a climatic gradient in the Australian arid zone and compared the results with data previously obtained for 10 North American communities.

Australian harvester ants exhibited similar alpha (within-habitat) diversity but higher beta (between-habitat) diversity between communities. Australian and North American communities were similar in species richness, species diversity, numbers of common species, and abundance of ants, although Australian communities tended to be richer and more diverse at sites with lower precipitation. North American communities increased in species richness, diversity, numbers of common species, and proportions of column-foraging species with increasing precipitation. In contrast, Australian communities did not change regularly across a gradient in precipitation. Thus, the first hypothesis was rejected. The second hypothesis was also rejected because Australian harvester ants were smaller, covered a smaller size range, and tended to be more tightly distributed along the size gradient. Dietary data indicated a lack of correspondence between resource use and availability, suggesting that Australian communities may not generally be in equilibrium with their resource environment. However, neither of the first two hypotheses could be tested unequivocally because it remains possible that evolutionary interaction between seeds and ants in the absence of rodents has allowed seeds to adopt defenses minimizing consumption by ants, or that other granivores (particularly birds) compensate in part for the paucity of rodents. Tests of the third hypothesis were ambiguous. Some results suggest basic similarities between the effects of competition on the communities, such as the similar maximum values for abundance, richness, and species diversity. However, several attributes of Australian communities differed from those in North America: foraging occurred over a wider range of soil temperatures; temporal displacement of foraging among coexisting species was prominent; and individually foraging species occurred with equal frequency across climatic gradients. We discuss various biotic and abiotic features that may explain differences in community structure between continents.

We conclude that the paucity of rodents, a potentially competing group of granivores, has not led to predictable changes in harvester ant communities of arid Australia.

Key words: ants; Australian arid zone; community structure; convergence; diversity; ecological release; granivores; North American deserts; size distributions; species richness.

TABLE 1. Descriptions of the North American study sites, and characteristics of their ant faunas (recalculated from Davidson 1977*a*).

Study site	Mean annual precipitation (mm)	Ant species			
		Species richness	Common species*	Diversity (H)	No. occupied baits†
1. Baker, 8.5 km SE, San Bernardino County, California	76	3	2	0.93	57
2. Barstow, 11 km NE, San Bernardino County, California	88	2	2	0.68	68
3. Mojave, 1 km SE, Kern County, California	121	3	2	0.58	39
4. Wellton, 15 km E, Yuma County, Arizona	91	6	6	1.58	190
5. Gila Bend, 5 km SW, Maricopa County, Arizona	142	3	3	1.05	37
6. Ajo, 8 km N, Pima County, Arizona	216	7	4	1.81	20
7. Casa Grande, 8 km SW, Pinal County, Arizona	215	6	2	1.12	61
8. Rodeo (A), 10 km NW, Cochise County, New Mexico	276	7	7	1.74	251
9. Rodeo (B), 9 km NW, Cochise County, New Mexico	276	8	8	2.00	260
10. Deming, 9 km SE, Luna County, New Mexico	224	7	6	1.49	174

* Those species occuring at 10% or more of baits.
† Defined in Materials and Methods: Censusing and Analysis of Community Structure.

INTRODUCTION

Many authors conclude that convergence between communities and ecosystems can occur, although it is difficult to demonstrate conclusively (Cody 1975, Karr and James 1975, Mooney 1977, Orians and Solbrig 1977, Cody and Mooney 1978, Brown et al. 1979*b*, Mares 1980, Orians and Paine 1983). Others argue against the phenomenon on the grounds that unique histories or subtle environmental differences inevitably produce differences in ecosystem organization (Pianka 1973, 1975, Schall and Pianka 1978). The problem has pragmatic as well as theoretical importance, for ecologists rely largely on research conducted in North America and Europe for data and insights. Comparisons with other ecosystems are essential to identify which functional units have truly general attributes.

One ecosystem unit that has attracted much attention is that comprising seeds and their consumers in arid ecosystems (Brown et al. 1979*b*). The seeds of ephemeral plants constitute a relatively dependable resource for a diverse array of ants, rodents, and birds, but deserts on different continents show marked differences in the abundances of granivores in these taxa. For example, whereas ants and rodents appear to be the most important granivores of North American and Israeli deserts (Mares and Rosenzweig 1978, Brown et al. 1979*b*, Abramsky 1983), mammalian seed eaters are insignificant in the Australian arid zone where ant and avian granivores predominate (Morton 1979, 1985), and Argentina's Monte Desert has few granivorous ants or rodents (Mares and Rosenzweig 1978).

Both historical and ecological factors have probably contributed to disparities in the proportional representation of the three granivorous classes between Australia and North America (Morton 1979). For example, although the most prominent family of North American seed-eating rodents, the Heteromyidae, originated when the desert flora was developing in the Oligocene (Axelrod 1950), rodents probably were absent from Australia until the Pliocene (Lee et al. 1981). Thus, development of the vegetation in the Oligocene or Miocene (Truswell and Harris 1982) would have long preceded the occupation of Australian deserts by rodents, and food niches for granivores might have been preempted by ants and birds. Greater variability in precipitation and primary productivity in Australian deserts (Leeper 1970, Gentilli 1971) may have accentuated the advantages of ants and birds over granivorous rodents. Bipedal rodents, morphologically convergent with the North American heteromyids, exist in arid Australia (Watts and Aslin 1981) but are not generally significant in seed removal (Morton 1985).

Although the literature on Australian ants is relatively sparse, it confirms that ants are unusually diverse in parts of the arid zone, and that a significant proportion of these species are seed harvesters (Greenslade and Greenslade 1973, Briese and Macauley 1977, Greenslade 1978, 1979, 1982, Andersen 1982, 1983, Briese 1982, Davison 1982). In contrast to North American deserts, where most seed-eating birds are seasonal migrants that breed outside deserts and feed on insects while breeding, at least some habitats in arid Australia contain specialized avian granivores that are year-long residents (Morton and Davies 1983). Presently, there exist no carefully controlled comparisons over broad climatic gradients to document whether the within-habitat (alpha), between-habitat (beta), or regional (gamma) component of diversity contributes most to the higher richness of granivorous ants and birds in arid Australia.

Australian and North American granivorous faunas clearly are not convergent in proportional contributions of the three major taxa, but the processes regulating the abundance and diversity of granivores may yet be similar in the two deserts. For example, like their North American counterparts, populations of seed consumers in Australia may be limited by food. In North American deserts, the abundance and diversity

of granivores in all three taxa increase with mean an-
nual precipitation, an index of productivity in these
arid regions (Brown 1975, Davidson 1977*a,* Dunning
and Brown 1982). The composition of communities of
both harvester ants and seed-eating rodents suggests
that strong resource competitors cannot coexist in the
same local habitats (Brown 1975, Davidson 1977*a, b*).
Manipulative experiments also demonstrate compe-
tition among and between rodents and ants (Brown et
al. 1979*a,* Brown and Munger 1985, Davidson 1985).
Despite evidence that competition influences the abun-
dance and diversity of granivores in North American
deserts, however, the generality of these conclusions
for granivores in other deserts is untested.

In this study, we focus on geographic patterns of
abundance, diversity, and community organization of
Australian harvester ants in an attempt to test three
hypotheses. These hypotheses are based on the as-
sumption that resource limitation and competition have
been as important in molding communities of seed-
eating ants in arid Australia as they have been in North
America. Our first hypothesis was that Australian hab-
itats similar in precipitation and productivity to those
in North American deserts would contain a greater
abundance and diversity of seed-eating ants coexisting
in local habitats, because rodent competitors are largely
absent from arid Australia. Our second hypothesis was
that, in Australia, release from competition with ro-
dents would result in greater numbers of large harvester
ants, because rodents eat larger seeds on average than
do ants (Inouye et al. 1980, Davidson et al. 1984) and
worker body sizes are closely correlated with the sizes
of seeds used by North American ants (Davidson 1977*a,*
Hansen 1978, Bernstein 1979*b*). Our third hypothesis
was that competitive structuring of communities would
result in similar patterns in community composition
of harvester ants in North American and Australian
deserts.

Our study depends on data that are directly com-
parable for ants on the two continents. In general, we
followed sampling procedures employed in studies in
North American deserts (Davidson 1977*a, b*) and shown
to be equally useful in Australia (Morton 1982). We
re-analyzed Davidson's (1977*a, b*) data to allow com-
parison with the simplified sampling procedures used
in our Australian work.

STUDY AREAS

North America

Ten sites in desert scrub on sandy soils were sampled
in the Chihuahuan, Sonoran, and Mojave deserts of
the southwestern United States (Table 1). A range of
climatic regimes from 70 to 280 mm mean annual
precipitation was chosen, but characteristics such as
slope and soil were held as constant as possible. The
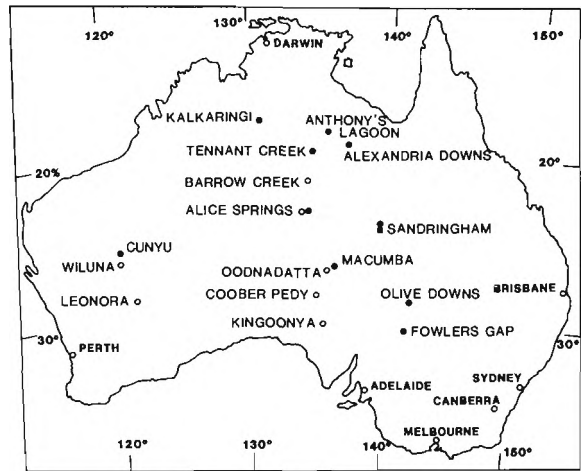sites were sampled either in July or August 1974 or in

FIG. 1.   Location of study sites in Australia. ● hummock
grasslands, O acacia shrublands, ■ miscellaneous vegetation
types.

August 1975. Elevation of the sites varied from 219
to 1320 m.

Australia

The Australian arid zone has two major vegetation
formations, which cover about two-thirds of the region.
Acacia shrublands are usually dominated by *Acacia
aneura,* occur principally on sands and earths, and have
a diverse understory that usually contains grasses. The
second formation consists of hummock grasslands and
contains the perennial grasses *Triodia* and *Plectrachne.*
These occur on nutrient-poor lithosols, sands, and
earthy sands, and generally contain a less diverse ground
flora than acacia shrublands (Williams 1982). We chose
to examine communities of harvester ants in these for-
mations because they make up such a large proportion
of the arid zone and thus should provide representative
answers to our questions. Further, acacia shrubland is
the closest equivalent among Australian vegetation for-
mations to the desert scrub in which harvester ants
were sampled in North America.

Fifteen study sites were chosen in hummock grass-
lands and acacia shrublands so as to span as great a
range as possible of the rainfall regimes in the arid zone
(Fig. 1, Table 2), and four other sites of diverse vege-
tation were included also (see Morton 1982 for details).
Elevation of the sites ranged from 100 to 600 m. We
conducted censuses at sites 1 and 3–15 in September
and October 1981, and at sites 2 and 16–19 in January
and February 1980. Data on precipitation at the sites
were obtained from the Bureau of Meteorology (1977)
(sites 3–7, 9–15), from unpublished data provided by
the Bureau (1, 8, 18), and from local station records
(2, 16, 17, 19). No areas of the arid zone receive less
than ≈110 mm mean annual precipitation; conse-
quently, we could not duplicate in Australia the North
American sites where precipitation was <100 mm.

TABLE 2. Descriptions of the Australian study sites, and characteristics of their ant faunas.

	Mean annual precip-itation (mm)	Ant species			
Study site		Species rich-ness	Com-mon spe-cies*	Diversity (H)	No. occupied baits†
Hummock grasslands					
1. Macumba, 20 km NE of Homestead, South Australia	124	9	3	1.52	104
2. Sandringham, 20 km W of Homestead, Queensland	160	11	5	2.09	88
3. Cunyu, 5 km N of Homestead, Western Australia	202	9	2	1.81	34
4. Alice Springs, 20 km SE, Northern Territory	278	9	3	1.55	85
5. Alexandria Downs, 17 km NW of Homestead, Northern Territory	338	8	4	1.64	111
6. Tennant Creek, 11 km N, Northern Territory	365	12	5	1.81	170
7. Anthony's Lagoon, 5 km SE of Homestead, Northern Territory	482	10	4	1.80	93
8. Kalkaringi, 40 km W, Northern Territory	568	10	3	1.77	62
Acacia shrublands					
9. Oodnadatta, 5 km SE, South Australia	119	9	6	1.81	205
10. Coober Pedy, 50 km S, South Australia	154	12	6	1.97	129
11. Kingoonya, 5 km E, South Australia	172	8	1	1.12	93
12. Leonora, 11 km N, Western Australia	217	6	2	1.11	65
13. Wiluna, 11 km N, Western Australia	241	7	1	0.79	54
14. Alice Springs, 15 km SE, Northern Territory	278	8	6	1.66	183
15. Barrow Creek, 5 km N, Northern Territory	312	13	8	2.08	188
Other sites					
16. Sandringham, 2 km NW of Homestead, Queensland (tussock grassland)	160	6	3	1.52	62
17. Sandringham, 10 km N of Homestead, Queensland (sandridge)	160	8	5	1.50	108
18. Olive Downs, 10 km S of Homestead, New South Wales (tussock grassland)	190	7	4	1.62	58
19. Fowlers Gap, 5 km NE of Homestead, New South Wales (chenopod shrubland)	205	6	2	0.88	130

* Those species occurring at 10% or more of baits.
† Defined in Materials and Methods: Censusing and Analysis of Community Structure.

MATERIALS AND METHODS

Censusing and analysis of community structure

A standard census procedure was used in North America and Australia. At each site, 80 shallow glass dishes were placed in an 8×10 bait grid with ≈ 5 m intervals between dishes. The dishes were buried so that their edges were flush with the ground, and strips of masking tape were attached to each dish to facilitate access by ants. Wire netting or hardware cloth was stretched over each dish to discourage interference by birds or rodents. Bait consisted of ground barley or cracked wheat, in a variety of sizes, and was placed in the dishes at least 3 h before censusing began. Ants were sampled by recording each presence of an ant species at a bait during a 60-s observation period. All baits were inspected five times during each 24-h census; one census was conducted per site. The relationship between soil temperature and activity of different species of harvester ants is well known (e.g., Whitford and Ettershank 1975, Bernstein 1979a, Briese and Macauley 1980), so we chose to sample when surface soil temperatures were $\approx 25°$, $35°$, $45°$, and $50°C$ during the day, and also 1–2 h after sunset to sample any purely nocturnal species. The precise method of sampling used for this study differed from that described by Davidson

(1977a) and Morton (1982) in that we considered only five censuses over 24 h and in most cases recorded only the species presence at baits rather than their numerical abundance. Recalculation of Davidson's (1977a, b) data has confirmed the attributes that she described (see Results: Species Richness and Species Diversity and Results: Foraging Behavior), thus supporting our simplification of the method.

Species richness at each site was quantified both by the total number of species occurring at baits and by the number of common species. Common species were defined as those occurring at 10% or more of baits during the 24-h census. Species diversity was calculated according to the formula

$$H = -\sum p_i \ln p_i,$$

where p_i is the number of baits occupied by the ith species as a proportion of the number of baits occupied by all species. An occupied bait is a record of a species at any one of the 80 baits when all five observation periods are considered together. An occupied bait is in fact usually a record of one colony of ants, but this measure gives weight to large colonies, which may visit several baits. The number of occupied baits was the best measure of abundance available to us.

To examine potential relationships between species richness or diversity and measures of productivity, we calculated regressions between these attributes and mean annual precipitation or precipitation minus its standard deviation. Further, we tested relationships between measures of diversity in Australia and Nix's (1982) growth index, to examine the possibility that the seasonality of productivity may interact with precipitation in correlating with species richness and diversity of harvester ants. The growth index transforms the nonlinear responses of plants to major environmental regimes into dimensionless indices; the functions are response to light, temperature, and water. H. A. Nix (*personal communication*) calculated for our sites the mean weekly growth index, a measure of productivity, and the coefficient of variation around the weekly mean, a measure of seasonality.

Specimens of each species recorded at baits were collected, preserved in 70% ethanol, and returned to the laboratory where their head widths were measured under a binocular microscope using an ocular micrometer. We attempted to measure at least 6 individuals of each monomorphic species and 10 of each polymorphic species, but did not achieve this for many uncommon Australian species. We used head width rather than body length because it seems likely that head width is a more direct measure of the capacity of harvester ants to carry seeds of different sizes and because it can be measured more accurately than body length.

North American species were identified by D. W. Davidson or R. R. Snelling. Application of specific names to many Australian ants is impossible; consequently, ants were identified by R. W. Taylor and P. J. M. Greenslade using specific codes unique to our collection. The codes are used throughout this paper, and specimens labelled with these codes are deposited in the Australian National Insect Collection, Division of Entomology, Commonwealth Scientific and Industrial Research Organization (CSIRO), Canberra. The identifications are taxonomically conservative; for example, *Chelaner* A (the *Chelaner rothsteini* species group; see Table 4) is probably composed of several species with particular edaphic or vegetational preferences.

The similarity between communities at different sites was quantified with the formula

$$\text{coefficient of similarity} = \frac{2w}{a + b},$$

where w is the number of species common to both communities, and a and b are the numbers of species in each of the two communities.

Foraging behavior

At all North American sites and approximately half of the Australian sites, we recorded the distances from baits visited by workers to the entrances of their nests. The maximum sample size for a species was 20 distances. For a few uncommon Australian species we were unable to record any distances. Because most of these were individually foraging species of the genera *Meranoplus* and *Tetramorium* that we knew foraged over short distances, we arbitrarily assigned to them a distance of 0.5 m; all were rare, and contributed little to the subsequent calculation. We computed mean distances for each species and weighted these means by abundance to calculate an index of community foraging distance,

$$D = \sum d_i p_i,$$

where d_i is the mean foraging distance of the ith species and p_i is abundance as defined previously.

Ant species were categorized as either individual or column foragers, based primarily on their behavior at baits. Individual foragers are those species that were never observed to form columns while foraging, whereas column foragers usually form definite lines while gathering seeds (Whitford 1976, Davidson 1977*a, b*). (We use the terms "column" and "individual" forager to characterize gross differences in the manner in which workers of different species customarily search for seeds; we do not imply that individual foragers are unable to communicate the location of food.) Then, we created a community foraging score to quantify the relative contribution of individual foragers to each community. Individual foragers were given a score of one, column foragers zero, and one North American species (*Messor pergandei*) known to switch between individual and column foraging was given a score of 0.5. The community foraging score was calculated as

$$F = \sum f_i p_i,$$

where f_i is the foraging score for the ith species and p_i is abundance as defined previously.

To determine whether foraging territories of workers overlapped, we counted joint occurrences of pairs of species on baits and using chi-square tests compared them with numbers of overlaps expected if species occurred on baits independently of one another. Expected overlaps were calculated as

$$o_i \cdot o_j \cdot 80,$$

where o_i and o_j are the proportions of the 80 baits on which occurred species i and j respectively (Davidson 1977*a*). Data were analyzed only for pairs of species whose expected overlaps exceeded 5% of the baits; this criterion was met at only nine Australian sites.

Size distributions of ants and utilization of resources

Size relationships were investigated in two ways. First, to determine if mean worker size differed between the

two continents, we calculated a size index in which the head widths were weighted by the relative abundances of species. The community size index was defined as

$$S = \sum h_i p_i,$$

where h_i is the mean head width of the ith species and p_i is abundance as defined previously. Second, we wished to determine whether Australian and North American species were distributed differently along the size gradient. For each community, we calculated size ratios by dividing the head width of each species into that of the next largest species. We then calculated a community size ratio,

$$R = \frac{\displaystyle\sum \text{ ratios of head widths stepwise through the community}}{n - 1},$$

where n is species richness in the community. R was also calculated for common species only.

We also wished to compare the degree to which ants on the two continents select seeds on the basis of size. Fluctuations in resource availability can affect both the diversity of seed types included in the diet and interspecific overlap in the diets of harvester ants (e.g., Briese and Macauley 1981, Davison 1982). We attempted to counter this problem by sampling seeds in both deserts during peak resource availability and ant activity. Thirty returning ants of each of six species at our North American site 8 were robbed of their forage in September and October 1974 (Davidson 1977a, 1980). Seeds were analyzed for size by passing them through a series of Tyler sieves. For each ant colony, we calculated a seed size index in which the mean size of each seed species was weighted by its abundance in the diet. At the same time as forage was collected, 75 soil samples (volume $10 \times 10 \times 1$ cm deep) were taken at random from the study site; seeds were extracted from the soil by flotation (Goodall et al. 1972) and then were counted and identified. Data on diets of the ants and availability of seeds were incorporated into a matrix of exploitative interactions using an index of overlap from Hurlbert (1978)

$$a_{ij} = \sum_k (p_{ik}p_{jk}/f_k)/\sum_k (p_{ik}^2/f_k),$$

where p_{ik} and p_{jk} are the proportionate numerical representations of the kth food type in the diets of the ith and j^{th} species, respectively, and f_k is the relative abundance of food type k in the soil. The matrix allows assessment of the degree of dietary overlap between species in the community.

At our Australian site 19, we collected from 4 to 42 food items from returning workers of five species in November 1979 and four species in October 1980. Reference collections of seeds were weighed, and a seed size index was calculated for each colony in the same way as described above; because the index was based on mass rather than size, however, direct comparisons with data from the North American collections must be made with caution. During each dietary sampling, we took 20 soil samples ($10 \times 10 \times 2$ cm deep) from the study site and extracted seeds as described above. Data on diets and availability of seeds were used to calculate a_{ij} as for North American data.

RESULTS

Species richness and species diversity

To determine how effectively each of the communities was sampled by our censuses, we examined the change in species richness at each site as the number of occupied baits increased; i.e., we determined the species-area relationship. Because the most frequent species-area relationship is a power function (Connor and McCoy 1979), we calculated for each site the correlation coefficients for a power relationship and a linear relationship between species richness and numbers of occupied baits. We reasoned that a better fit to a power relationship, where the exponent is <1, would provide evidence that richness was approaching an asymptote. In contrast, if a linear relationship provided a better fit and richness showed less sign of levelling off, then communities had been sampled incompletely. At eight of the North American sites, the correlation coefficient for a power relationship was higher than for a linear relationship, and at the other two, maximum species richness was reached in the first 10 occupied baits. Thus, we concluded that all sampling had been effective. At 17 of the Australian sites, power relationships had higher correlation coefficients, but at the other two (Cunyu and Wiluna) linear relationships provided the better fit. We are unsure why these two sites were less effectively sampled; possibly the vegetation was more heterogeneous, or nearby there may have been a habitat boundary not apparent to us at the time. Consequently, data from Cunyu and Wiluna have been excluded from the following analyses unless the contrary is stated.

The species richness of harvester ant communities in North American deserts rose from 2 at lower rainfalls to a maximum of 8 at higher rainfalls (Tables 1 and 3). In Australia, species richness ranged from 6 to 12 (Tables 2 and 4). Richness was significantly and positively correlated with mean annual precipitation in North America, but not in Australia (Fig. 2, Table 5). Similarly, both the numbers of common species and species diversity (H) were significantly correlated with precipitation in North America, but were not in Australia (Table 5).

Relationships between precipitation and estimates of richness and diversity in Australia may be obscured because we considered a greater range of precipitation than in North America. Thus, we calculated regressions for these parameters at Australian sites where precip-

itation was <300 mm. No significant relationships emerged between precipitation and richness, number of common species, or H in acacia shrublands or at all sites (r between -0.38 and 0.21, $P > .25$). We were unable to test relationships within hummock grassland alone because too few sites were available within this range of precipitation.

One clear difference between measures of diversity in communities on the two continents is that at low rainfall sites, species richness in Australia was not reduced significantly below higher rainfall sites, whereas it was in North America. Consequently, at sites with mean annual precipitation <300 mm, species richness was significantly greater in Australia (Mann-Whitney U test, one-tailed, $P < .001$). However, H and the number of common species at these sites did not differ significantly between the two continents ($.1 > P > .05$). Our measure of abundance (the number of occupied baits) did not differ significantly between North America and Australia, whether we considered hummock grasslands, acacia shrublands, or sites with mean annual precipitation <300 mm (Mann-Whitney U tests, $P > .1$ in all cases).

Other climatic indices failed to reveal relationships between productivity in Australia and measures of diversity. For all regressions between precipitation minus its standard deviation and species richness, diversity, and number of common species in hummock grasslands, acacia shrublands, all sites, and sites with precipitation <300 mm, correlation coefficients were <0.30, and none was significant. Nix's (1982) growth index was not significantly correlated with species richness, species diversity, or the number of common species in hummock grasslands, acacia shrublands, or at all sites (r between -0.27 and 0.67, $P > .05$). Nix's seasonality index was not significantly correlated with
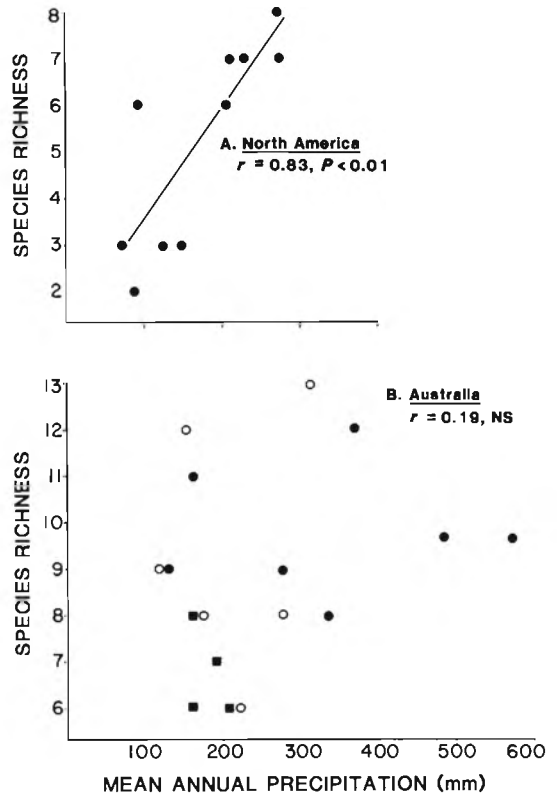
FIG. 2. Species richness of harvester ants plotted against mean annual precipitation for North America (A) and Australia (B). Data in A based on Davidson (1977a); symbols for B as in Fig. 1.

species richness or number of common species in hummock grasslands, acacia shrublands, or at all sites (r between 0.25 and 0.32, $P > .2$); nor was it significantly correlated with species diversity in hummock grass-

TABLE 3. Specific composition of harvester ant communities at 10 study sites in North America (based on Davidson 1977a).

Species	HW† (mm)	FB‡	Study sites*									
			1	2	3	4	5	6	7	8	9	10
Novomessor cockerelli	1.62	I						c		c	c	c
Messor pergandei	1.25	C/I	c	c	c	c	c	u	u			
Solenopsis xyloni	0.72	C			u	c		c	c	c	c	c
Pogonomyrmex rugosus	2.34	C						c		c		c
P. barbatus	2.29	C									c	
P. maricopa	1.43	I					c				c	
P. desertorum	1.65	I								c	c	c
P. californicus	1.54	I		c	c	c		u	c			
P. magnacanthus	1.42	I	c									
P. pima	1.10	I						c	u			
Pheidole militicida	0.83	C										c
P. desertorum	0.66	I				c				c	c	c
P. xerophila	0.57	C							u	c	c	
P. gilvescens	0.41	C				c			u			
P. rugulosa§	0.47	C			c	c	u			c	c	u
P. sp.	0.55	?	u									

* Numbered as in Table 1; c indicates a common species (occurring at 10% or more of baits) and u an uncommon species.
† Mean head width of workers.
‡ Foraging behavior: C indicates a column forager and I an individual forager.
§ Identified in Davidson (1977a) as *Pheidole sitarches*.

TABLE 4. Specific composition of harvester ant communities at 19 study sites in Australia during January and February 1980. Species are identified by codes referring to specimens deposited in the Australian National Insect Collection.

Species	HW† (mm)	FB‡	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Chelaner A	0.84	C		c	c	c		c	u	c		c		c	u	c	c	c	c	c	c
C. B	0.49	C	c		u	u					c	c			u	c					
C. C	0.90	C		u								u							c		
C. E	0.62	C								u								u			
C. F	0.50	C					u														
C. H	0.64	C											u								
Pheidole A	0.75	C																c		u	u
P. C	0.44	C		u																	
P. D	0.67	C		c															c		
P. F	0.41	C?																	u		
P. G	0.58	C																	u		
P. H	0.64	C																u			
P. L	0.68	C									c				u						
P. M	0.59	C										u									
P. N	0.66	C										u									
P. O	0.47	C								c											
P. P	0.44	C	u																		
P. Q	0.89	C				u															
P. R	0.46	C										u									
P. S	0.78	C														u					
P. T	0.54	C														c					
P. U	0.42	C						u													
P. V	0.51	C?															u				
P. W	0.51	C?															u				
P. X	0.61	C															c				
P. Y	0.43	C															c				
P. Z	0.52	C						u					•				u				
P. AA	0.63	C						c													
P. unidentified	?	C	u																		
Monomorium A	0.37	C	u		u					c		u								c	u
M. B	0.36	C	u			u	c					c			c	c		c			
M. C	0.38	C							u	u											
M. D	0.37	C								u								u			
M. E	0.40	C																			u
M. F	0.35	C					c			u											
M. G	0.36	C						c	c												
M. H	0.38	C											u								
M. I	0.44	C						c									c				
Meranoplus A	0.92	I		u						u											
M. B	0.56	I											u								
M. E	1.64	I								u							c				
M. F	0.65	I			u																
M. G	0.89	I													u						
M. H	0.55	I											u								
M. I	0.78	I											u								
M. J	0.71	I											u								
M. K	1.06	I										u									
M. L	0.62	I									u										
M. M	0.73	I					u														
M. N	0.69	I					u														
M. unidentified	?	I			u																
Tetramorium A	1.12	I		u	u		u		u										u		
T. B	0.61	I	u	u								u									
T. C	0.59	I		c																	
T. D	0.94	I	u								u										u
T. E	0.60	I																	u		
T. F	0.89	I					u	u	c								u				
T. G	1.33	I											c								
T. H	0.65	I								u											
T. I	0.62	I															u				
T. J	0.57	I							u												
T. unidentified	?	I									u										
Melophorus A	0.96	I					c				c					c					
M. B	0.80	I		c							c										
M. C	1.54	I		c																	
M. E	0.95	I	c	u	c						c										
M. H	1.02	I																	u		
M. I	1.42	I																		c	

TABLE 4. Continued.

Species	HW† (mm)	FB‡	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
M. J	1.31	I																	c		
M. K	0.82	I							c												
M. L	1.10	I						u													
M. M	1.08	I				u	c									u					
M. N	1.17	I			u																
M. O	1.54	I				u					c										
M. P	1.41	I							u												
M. Q	1.71	I				u															
M. R	1.24	I			u																
M. S	0.83	I						c	c												
M. T	0.73	I												u							
M. U	1.36	I											u								
M. V	1.03	I																		c	
M. W	1.03	I																c			
M. X	1.03	I																			c
M. Y	1.07	I						u		c							c				
M. Z	1.05	I	c			c															
M. AA	0.99	I										c	c								
M. BB	1.05	I				c							u			c	c				
M. CC	0.98	I												c							
M. DD	0.95	I													c						
M. EE	?	I								u											
M. unidentified	?	I					u				c		u								

* Study sites numbered as in Table 2; c indicates a common species (occurring at 10% or more of baits) and u an uncommon species.
† Mean head width of workers.
‡ Foraging behavior: C indicates a column forager and I an individual forager.

lands or acacia shrublands (Table 5). However, the seasonality index was significantly correlated with species diversity at all sites (Table 5). It is difficult to determine the importance of this significant relationship, because it may result from Type 1 error due to the large numbers of regressions we have calculated.

We conclude that no simple relationship is evident between gross estimates of productivity in the Australian arid zone and measures of richness and diversity of harvester ants. This conclusion is strengthened by a similar lack of correlations between precipitation and other community measures.

Foraging behavior

There was a significant inverse relationship between mean annual precipitation and F (community foraging score) in North America, but not in Australia, either for hummock grasslands, acacia shrublands, or all sites (Table 5). Similarly, no significant relationships existed between F and mean annual precipitation minus its standard deviation, or between F and Nix's (1982) growth or seasonality indices. These results suggest that, in Australia, column foragers occur equally frequently at sites of low and high precipitation.

The index of community foraging distance D was significantly inversely related to mean annual precipitation in North America (Fig. 3). In Australia, significant inverse relationships were evident in hummock grasslands between D and both mean annual precipitation (Fig. 3) and Nix's growth index ($r = -0.91$,

$P < .05$), but not in acacia shrublands or at all sites (Fig. 3). Again, the apparently significant trend could reflect Type 1 error.

Communities in Australia differed from those in North America in the temporal spread of foraging activity (Table 6). All sites except North American site 9 and Australian sites 3, 8, 11, 12, and 13, where soil temperatures did not rise to 50°C, were considered. North American species richness and proportions of occupied baits peaked at 25° (Table 6). In Australia, activity peaked at higher temperatures, when both measures of activity were significantly greater than in North America. Overall, foraging behavior was spread over a wider range of soil temperatures in Australia.

The increased spread of foraging temperatures in Australia could have occurred either because there was a greater degree of temporal separation between species than in North America, or because each Australian species foraged over a greater range of temperatures. In an attempt to determine the best explanation, we counted the number of sampling periods in which each common species visited baits. The mean numbers did not differ significantly between Australia (mean = 2.3 sampling periods, $n = 36$ species) and North America (mean = 3.0 periods, $n = 14$ species) (Mann-Whitney U test, $P > .2$), showing that Australian species did not forage over a greater range of temperatures. Thus, it seems likely that greater spreading of foraging occurs in Australia because of greater temporal separation between species, but our test is not conclusive.
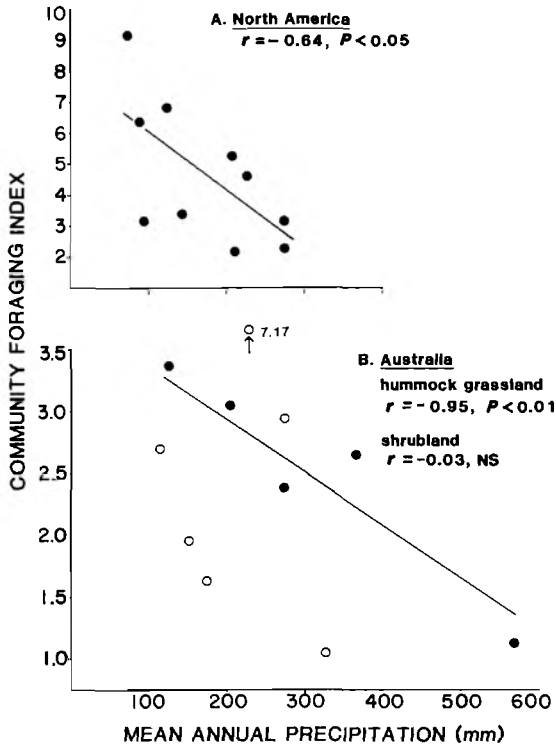
FIG. 3. Index of community foraging distance (D) plotted against mean annual precipitation for North America (A) and Australia (B). Data in A based on Davidson (1977a); symbols for B as in Fig. 1. Regression line in B is for data from hummock grasslands. A regression of data from all Australian sites was not significant ($r = -0.32$).

We examined temporal separation between genera in Australia by determining the five sampling periods in which each common species occurred at the greatest number of baits. When a species occupied the same peak number of baits in two sampling periods, it was scored as having its greatest abundance in both of those periods. The records of peak abundance were summed for each genus, and temporal activity quantified as proportions of the records occurring within each of the five sampling periods (Table 7). *Monomorium* spp. tended to be nocturnal, *Pheidole* spp. tended to forage at lower temperatures than *Chelaner* spp., and *Melophorus* spp. foraged at higher temperatures when other species were inactive. *Melophorus* workers are active, rapid, individual foragers that discover baits quickly, and their presence caused baits to be consistently occupied despite reduced species richness at 45° and 50° (Table 6).

Each sympatric *Melophorus* sp. tended to forage at particular temperatures. Two or more species of *Melophorus* were present at 12 sites (excluding sites where soil temperature did not rise to 50°), and at nine of these the two most common *Melophorus* spp. had peak abundances in different sampling periods. In general, dark species foraged most intensively during the 45° sampling period, whereas red-headed or yellow species were most abundant at 50°. For example, three *Melophorus* spp. were common at site 9 (Fig. 4). Here we used actual counts of individuals on the baits to provide a vivid picture of differential activity, and we analyzed only the first 40 baits in each census so that soil temperatures were close to those actually specified in the

TABLE 5. Results of linear regressions between various attributes of communities and climatic parameters. Nix's seasonality index and the coefficients H, F, and D are defined in Materials and Methods: Censusing and Analysis of Community Structure, and Foraging Behavior.

Components of regression	Australia			North America	
	Sites†	r	P*	r	P*
Species richness vs.	a	0.19	NS	0.83	*
mean annual precipitation	b	0.01	NS		
	c	0.03	NS		
Number of common species vs.	a	0.04	NS	0.65	*
mean annual precipitation	b	0.08	NS		
	c	0.21	NS		
Diversity (H) vs.	a	0.24	NS	0.73	*
mean annual precipitation	b	0.07	NS		
	c	0.18	NS		
Diversity (H) vs. Nix's	a	0.50	*	...	...
seasonality index	b	0.08	NS		
	c	0.29	NS		
Community foraging score (F) vs.	a	0.18	NS	−0.68	*
mean annual precipitation	b	−0.51	NS		
	c	0.36	NS		
Community foraging index (D) vs.	a	−0.32	NS	−0.64	*
mean annual precipitation	b	−0.95	*		
	c	0.03	NS		

* $P < .05$; NS $= P > .05$.
† a = all sites; b = hummock grasslands; c = acacia shrublands.

TABLE 6. Comparison of the temporal spread of activity over five sampling periods (surface soil temperatures) within 14 communities in Australia and nine in North America. Mean soil temperatures during the nocturnal censuses were 25°C on both continents.

	Sampling period				
	Nocturnal	25°	35°	45°	50°
A) Fraction of species present†					
Australia	0.49	0.48	0.49	0.36	0.25
North America	0.45	0.67	0.57	0.21	0.00
Significance	NS	Australia less*	NS	Australia greater*	Australia greater**
B) Fraction of baits occupied‡					
Australia	0.18	0.17	0.21	0.25	0.18
North America	0.19	0.46	0.28	0.07	0.00
Significance	NS	Australia less*	NS	Australia greater**	Australia greater**

* $P < .05$; ** $P < .01$; NS = $P > .05$ (Mann-Whitney U test).
† Mean of numbers of species present at baits in each sampling period calculated as a proportion of total species richness.
‡ Mean of numbers of occupied baits (see Materials and Methods: Censusing and Analysis of Community Structure) in each sampling period calculated as a proportion of the sum of such occupied baits over all five periods.

graph (temperatures increased considerably during the time taken to sample all 80 baits). The three species foraged predominantly at different soil temperatures (Fig. 4; chi-square test, $P < .001$). Thus, temporal separation appears widespread among sympatric, seed-harvesting *Melophorus* spp. In contrast to the temporal separation described here, North American communities contain no harvester species that prefer to forage at temperatures greater than ≈40°.

Finally, we examined the possibility that species foraged in distinct, nonoverlapping territories. Nine comparisons of observed and expected overlaps of 61 pairs of species on baits in Australia showed no significant chi-square values (at all nine sites, $P > .1$). In North America, only two pairs of species (*Pogonomyrmex desertorum* with *P. rugosus* or *P. barbatus*) appeared to subdivide space (Davidson 1977a).

Size distributions and foraging modes

Head widths and foraging modes on the two continents showed one similarity and several differences. With one possible exception (*Pheidole* F at Australian site 17), all North American and Australian species <0.5 mm in head width were column foragers. Other relationships were disparate for the two continents (Fig. 5). First, Australian communities frequently contained species in which the head width was <0.4 mm, whereas

in North American communities, only one such species occurred (*Pheidole gilvescens* at site 7). Second, North American communities at sites receiving >200 mm mean annual precipitation frequently contained large *Pogonomyrmex* spp. whose head widths exceeded 2.0 mm. Such large harvester ants were never observed at our Australian sites. Finally, Australian communities appeared to be more crowded along the size gradient because of the slightly greater richness described earlier.

The community size index S was significantly smaller in Australian communities (Table 8), showing that Australian harvester ants are generally smaller than North American species. The community size ratio R was similarly significantly smaller in Australia than in North America (Table 8); thus, species are distributed along a narrower gradient of worker body size in Australia as suggested by Fig. 5. However, R did not differ significantly between continents when only common species were considered. This result indicates that the species probably having greatest impact on the seed resource are no more closely packed in Australia than in North America.

Utilization of resources

Seeds collected by Australian harvester ants at Fowlers Gap (site 19) are listed in Table 9. We collected

TABLE 7. Comparison of the temporal spread of activity within genera of Australian harvester ants, based on the sampling periods (surface soil temperatures) of greatest abundance for common species at the 14 sites examined in Table 6.

Genus	No. of species	No. of records	Proportions having greatest abundance in each sampling period*				
			Nocturnal	25°	35°	45°	50°
Monomorium	5	11	0.73	0.18	0.09	· · ·	· · ·
Tetramorium	2	2	0.50	0.50	· · ·	· · ·	· · ·
Meranoplus	1	1	· · ·	1.00	· · ·	· · ·	· · ·
Pheidole	8	9	0.22	0.67	0.11	· · ·	· · ·
Chelaner	3	17	· · ·	0.35	0.47	0.18	· · ·
Melophorus	17	26	· · ·	· · ·	0.19	0.42	0.39

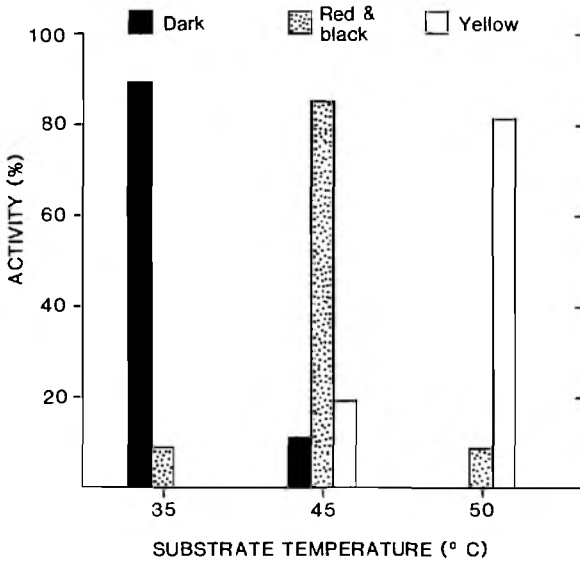* Calculated from all records for each species.

FIG. 4. Differences in preferred foraging periods (surface soil temperatures) between three *Melophorus* spp. at Oodnadatta (Australian site 9). The histogram shows the percentage of workers observed at baits during censuses when soil temperatures were approximately 35°, 45°, and 50°C. Total numbers of workers were: 9 *Melophorus* A (dark), 39 *Melophorus* unidentified (red and black), and 115 *Melophorus* B (yellow).

forage from species that were common during each sampling period, and included *Chelaner* C, a species common near our site but absent from it. Some insect parts were collected from *Melophorus* X and *Chelaner* A, and collections from most species included some flowers; nevertheless, the bulk of food was seeds. Reanalysis of Davidson's (1977a) North American data on sizes of ants and of seeds collected confirmed a significant relationship between head widths of ants and their food (Fig. 6). Australian ants also showed a significant relationship between head width and the size of food items, although the correlation was poorer than in North America. Direct comparison cannot be taken too far, because the indices were based on seed dimensions (passage through specified sieves) in North America but on seed mass in Australia. Further, the dietary data came from the only chenopod shrubland

sampled in our study; thus, the results should be generalized only with caution.

We next determined whether the smaller size of Australian ants led to a different relationship between seeds collected and seed availability. Davidson (1980: Table 1) studied this relationship at North American site 8 and found in two samples that 16 seed types were taken in proportion to their availability. Equivalent data from two sampling periods during spring at Australian site 19 revealed several cases of poor relationships between usage and availability (Table 9), such as *Calotis hispidula* (0.77 mg; underutilized) and *Plantago drummondii* (0.99 mg; overutilized). We compared these relationships generally between the two continents by computing the difference between proportionate usage and proportionate availability for each seed species from Table 9 and from Table 1 of Davidson (1980). The analysis showed that Australia ($n = 43$) did not differ significantly from North America ($n = 32$) (Mann-Whitney U test, $P > .1$). This limited information suggests that correspondence of resource usage with availability was not altered in the Australian community despite the different size relationships on the two continents.

A second measure of resource utilization is Hurlbert's (1978) index a_{ij}, an asymmetric measure of dietary overlap that takes resource abundance into account. North American data were reported by Davidson (1980: Table 2); data for Australia are shown in Table 10. We tested the indices to determine if interspecific overlap in diet was greater in Australian communities because of reductions in size ratios of ants within them. All data in Table 10 were used, but we excluded overlaps for *Pogonomyrmex desertorum* and *P. rugosus* in Table 2 of Davidson (1980) because they were principally measures of interference competition. The mean value for a_{ij} in Australia (0.29, $n = 32$) was significantly higher than in North America (0.20, $n = 28$) (one-tailed Mann-Whitney U test, $.025 < P < .05$). This analysis does suggest that the reduced size range in the Australian community led to greater dietary overlap.

Between-site comparisons of communities

We found previously unrecorded species in Australia every time we sampled a new site. This was not the

TABLE 8. Analysis of two aspects of morphological packing within communities in Australia and North America.

Statistic[†]	Australia		North America		Significance
	$\bar{X} \pm$ SD	(n)	$\bar{X} \pm$ SD	(n)	
Community size index S	0.80 ± 0.12	(17)	1.21 ± 0.18	(10)	***
Community size ratio R					
All species	1.20 ± 0.05	(17)	1.46 ± 0.21	(10)	***
Common species only[‡]	1.37 ± 0.21	(16)	1.46 ± 0.31	(10)	NS

*** $P < .001$; NS $= P > .05$ (one-tailed Mann-Whitney U test).
† See Materials and Methods: Size Distribution of Ants and Utilization of Resources.
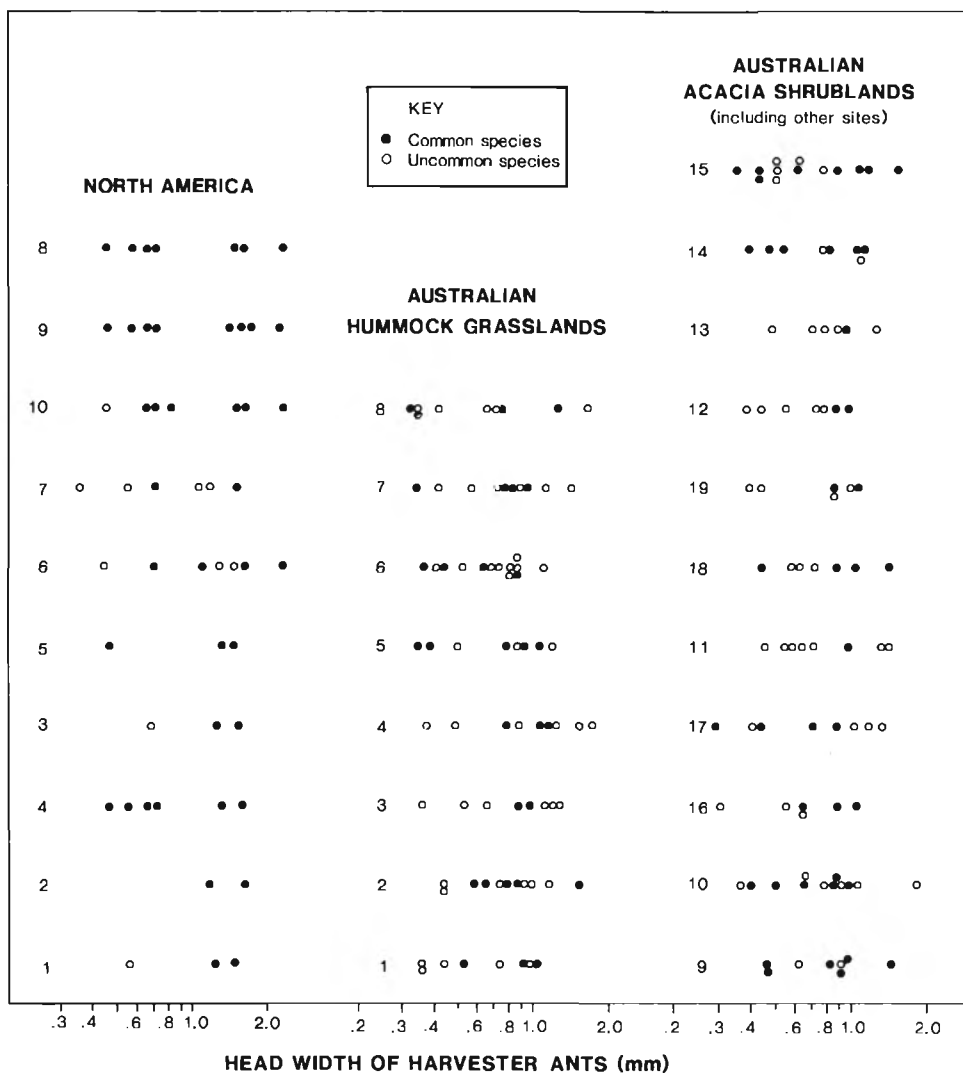‡ Those species occurring at 10% or more of baits.

FIG. 5. Mean worker head widths of harvester ants at North American and Australian study sites. The sites are numbered as in Tables 1 and 2 and are arranged from highest to lowest annual precipitation. Data for North America based on Davidson (1977a).

case in North America (Fig. 7), where the total species pool in desert scrub (≈20 species) is considerably less than in arid Australia. Our experiences, together with those of P. J. M. Greenslade (*personal communication*), lead us to suggest that there are several hundred species of harvester ants in arid Australia.

We quantified beta diversity as the coefficient of similarity (Appendix and Table 11). To allow testing of the possibility that sites in the same vegetation formation shared more species than sites in different formations, we divided the Australian coefficients into five groups: hummock grasslands, acacia shrublands, hummock grasslands vs. acacia shrublands, hummock grasslands vs. other sites, and acacia shrublands vs. other sites. North American coefficients were significantly greater than each of the five groups of Australian coefficients (Table 11), confirming that beta diversity

is higher in Australia. No group of Australian coefficients differed significantly from any other, indicating that no vegetation formation contained a unique suite of species. Thus, higher beta diversity in Australia results both from species turnover between vegetation formations and from differences between sites within the same formations.

Species turnover may be higher in Australia because we sampled over a greater geographic area than in North America. Thus, we restricted comparisons of Australian coefficients to sites closer than 1100 km (the range in North America), a legitimate test because the distributions of distances between sites did not differ significantly between North American sites and Australian hummock grasslands and acacia shrublands (Mann-Whitney U tests, $P > .05$). The coefficients differed between North America and the two Australian

TABLE 9. Relative abundances of seeds in the diets of harvester ants at Fowlers Gap (Australian site 19) during two sampling periods, proportionate usage of seeds by the total ant community, and estimates of relative abundance of seeds in the soil. The numbers of colonies of ants sampled for forage are shown in Table 10. + indicates that the seed was present at a frequency <0.005, and − indicates that the seed was not observed to be present.

	Pheidole G (Nov 1979)	Pheidole A (Nov 1979)	Pheidole A (Oct 1980)	Pheidole I (Nov 1979)	Chelaner A (Nov 1979)	Chelaner A (Oct 1980)	Chelaner C (Nov 1979)	Chelaner C (Oct 1980)	Melophorus X (Oct 1980)	Total usage by ants (Nov 1979)	Total usage by ants (Oct 1980)	In soil (Nov 1979)	In soil (Oct 1980)
Seed species													
Aristida sp.				0.02						+	−	+	−
Atriplex angulata				0.02			0.57	0.11	0.18	0.12	0.07	+	0.01
A. lindleyi								0.01		0.02	+	0.03	0.01
Boerhavia diffusa									0.04	−	0.01	−	0.01
Brachycome heterodonta				0.01	0.08					0.02	−	+	−
B. sp.				0.03						0.01	−	0.01	−
Calotis hispidula				0.08				0.02	0.06	0.02	0.02	0.55	0.56
Chloris truncata						0.01				−	+	−	+
Dactyloctenium radulans	0.20			0.02	0.01					0.05	−	0.09	−
Daucus glochidiatus									0.01	−	+	−	+
Dichanthium sericeum				0.01	0.01		0.07			0.02	−	+	−
Enneapogon sp.			0.03	0.02		0.03				+	0.02	0.03	0.01
Erodium sp.				0.01						+	−	0	−
Gnephosis foliata				0.06						0.01	−	0.01	−
Helipterum spp.	0.30		0.38	0.06	0.07	0.14	0.04	0.54	0.02	0.09	0.27	0.11	0.07
Lepidium sp.								0.02	0.32	−	0.09	−	0.01
Lotus cruentus									0.02	−	0.01	−	0.02
Plantago drummondii	0.30	0.96	0.59	0.57	0.51	0.73	0.25	0.27	0.23	0.51	0.46	0.09	0.12
Portulaca abracea		0.04								0.01	−	0.01	−
Sclerolaena brachyptera									0.02	−	0.01	−	0
S. diacantha									0.02	−	0.01	−	0.01
S. divaricata				0.02				0.01		+	+	0.01	0.06
S. ventricosa									0.06	−	0.02	−	0.09
S. sp.				0.01	0.02					0.01	−	0.03	−
Wahlenbergia stricta	0.10									0.02	−	0	−
Seed #2									0.02	−	0.01	−	+
#4				0.03	0.02		0.04			0.02	−	+	−
#5									0.01	−	+	−	0.01
#7				0.02						+	−	+	−
#15					0.29	0.01	0.04			0.07	+	0	0
#22					0.01					+	−	0	−
#24	0.10									0.02	−	0	−
#25				0.03						0.01	−	0	−
#27				0.01						+	−	0	−
#30						0.08				−	0.02	−	0

TABLE 10. Matrix of similarity indices a_{ij} for diets of harvester ants at Fowlers Gap (Australian site 19) during two sampling periods.

		November 1979				
		P. G	*P. A*	*P. I*	*C. A*	*C. C*
Pheidole G	(2)*	⋯	0.14	0.09	0.09	0.04
Pheidole A	(2)	0.31	⋯	0.59	0.53	0.26
Pheidole I	(7)	0.31	0.91	⋯	0.65	0.69
Chelaner A	(4)	0.02	0.06	0.05	⋯	0.16
Chelaner C	(1)	0.02	0.06	0.11	0.35	⋯

		October 1980			
		M. X	*P. I*	*C. A*	*C. C*
Melophorus X	(5)	⋯	0.12	0.18	0.15
Pheidole A	(5)	0.56	⋯	0.42	0.43
Chelaner A	(4)	0.65	0.34	⋯	0.27
Chelaner C	(5)	0.05	0.41	0.34	⋯

* Numbers of colonies sampled.

habitats ($P < .001$), but not between the Australian habitats ($P > .5$). Thus, higher species turnover in Australia is a result of greater beta diversity, and not simply greater gamma (regional) diversity.

DISCUSSION

Consideration of the hypotheses

Our results suggest that density compensation and ecological release from competition by granivorous rodents have not occurred in Australian harvester ants. Species richness was higher in arid Australia than in North American deserts of comparable precipitation, but this was primarily due to greater numbers of rare species and perhaps the greater beta diversity of the Australian ant fauna. In contrast to species richness, diversity and numbers of common species did not dif-
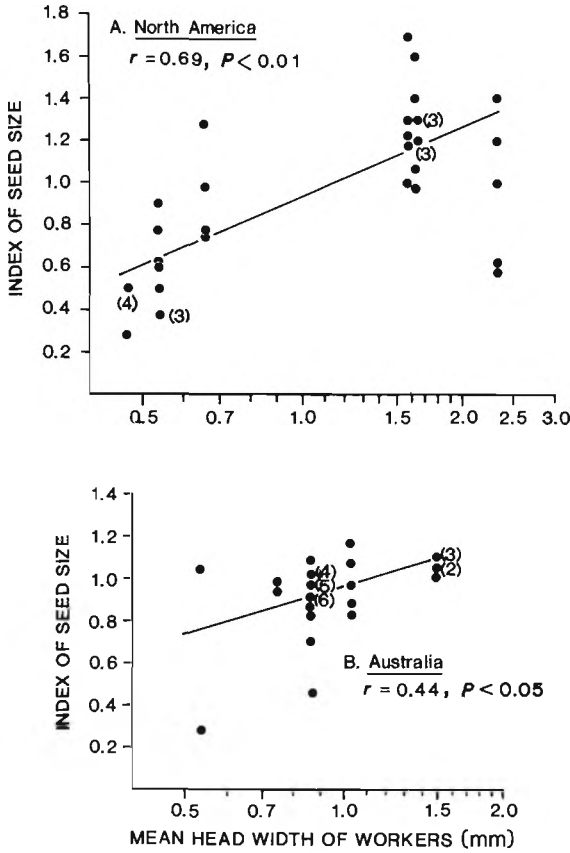
FIG. 6. Indices of seed size plotted against the mean head width of harvester ants at Rodeo, North America (A) and Fowlers Gap, Australia (B). In A, each point represents the seed component of 30 forage items from one colony; the seeds were sized in sieves to produce the index of size (based on Davidson 1977a). In B, each point represents the seed component of from 4 to 42 forage items; the seeds were weighed to produce the index. Because indices from the two continents were calculated differently, the regressions for each cannot be compared quantitatively.

fer significantly between continents. Communities in both deserts had approximately the same upper alpha diversity as measured both by H (≈ 2.0) and by numbers of common species (6–8).

Two additional forms of evidence also suggest that Australian harvester ants have not undergone release from competition by mammalian granivores. First, directly contrary to our initial prediction, these ants were on average smaller than their North American counterparts and spanned a smaller range of worker body sizes. This was true despite evidence that worker body sizes were positively correlated with seed sizes used, as in North American species. Also, the head widths of many Australian species were <0.4 mm, whereas only one such species was encountered in North America. At sites receiving >200 mm mean annual precipitation, North American communities frequently contained large *Pogonomyrmex* spp. whose head widths

exceeded 2.0 mm, and workers of similar size were present in size-polymorphic *Messor pergandei* at all other sites. Such large harvester ants were never observed in our Australian censuses. Some large *Pheidole* spp. do occur uncommonly in the Australian arid zone (P. J. M. Greenslade, *personal communication*), but it is clear that such ants are markedly less important than in North America.

Second, our best measure of harvester ant abundance, the number of occupied baits, suggests that densities are also similar on the two continents. This result is supported by the similarity of rates of seed removal from baits by ants in Australian and North American deserts (Morton 1985). Thus, available evidence argues against density compensation by Australian harvester ants as a response to the reduced importance of seed-eating rodents.

We found no patterns in Australia in abundance, species richness, numbers of common species, species diversity, or proportions of column foragers as a function of any index of productivity. These results were independent of vegetation formation and of the range of mean annual precipitation considered. Regressions of species richness as a function of sample size showed that inadequate sampling marred only two censuses and probably was not a general explanation for the lack of pattern.

Two significant trends did appear in our Australian data. First, the mean foraging distance to baits was inversely correlated with mean annual precipitation for our hummock grassland sites, suggesting that species with smaller foraging territories may be less likely to persist in relatively unproductive habitats (Davidson 1977a). Second, the species diversity of Australian harvester ants increased significantly with Nix's (1982) estimate of the seasonality of plant growth. Because of the possibility of Type 1 statistical error, we are unsure of the significance of these results.

Several other attributes of communities differed between the two continents. Australian ants foraged over a wider range of temperatures, possibly because of
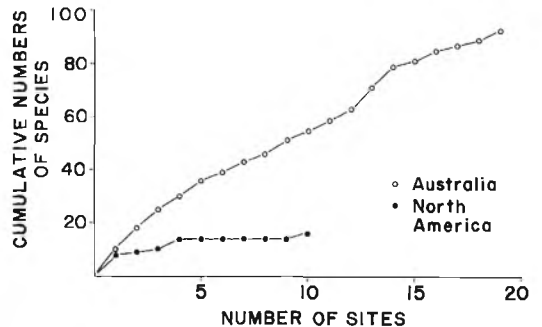

FIG. 7. Cumulative numbers of species as one moves from wetter to drier sites in Australia and North America. The Cunyu and Wiluna sites are included in this analysis.

TABLE 11. Comparison of coefficients of similarity for harvester ant communities in Australia and North America. Australian coefficients are summarized from the Appendix into five groupings (B–F) to allow detailed testing against North American coefficients.

Similarity comparison	n	Coefficient[†] ($\bar{X} \pm$ SD)	Comparisons of coefficients				
			A	B	C	D	E
A) Between sites within North America	45	0.38 ± 0.24	· · ·				
B) Between sites within hummock grasslands	28	0.16 ± 0.09	***	· · ·			
C) Between sites within acacia shrublands	21	0.13 ± 0.12	***	NS	· · ·		
D) Between hummock grasslands and acacia shrublands	56	0.16 ± 0.13	***	NS	NS	· · ·	
E) Between hummock grasslands and other sites	32	0.16 ± 0.11	***	NS	NS	NS	· · ·
F) Between acacia shrublands and other sites	28	0.12 ± 0.08	***	NS	NS	NS	NS

*** = $P < .001$; NS = $P > .05$ (Mann-Whitney U tests).

† The coefficient of similarity = $2w/(a + b)$, where w = number of species common to the two communities and a and b are the numbers of species in each of the two communities.

greater temporal partitioning between species. Narrow activity periods were most obvious among size-polymorphic species of *Melophorus,* a genus comprising 50% of common species in Australian communities. Furthermore, with only three exceptions (*Tetramorium* C and F and *Meranoplus* E), all common individually foraging species in Australia belonged to this genus.

Further, the smaller size range and slightly greater species richness of Australian species appears to lead to tighter distribution along the size axis, and this packing would be even greater if we could include individual morphs of *Melophorus* spp. We attempted to determine the importance of this size difference by examining resource utilization at one site on each continent. Because worker sizes are significantly correlated with seed-size preferences, we expected dietary overlap to be greater in the Australian communities. Our limited sampling partially confirmed this prediction. In addition, in two consecutive years, we found a relatively poor match between seed use by the community as a whole and the relative abundances of seed types in the environment. This contrasted with the close match between seed use and availability at one site in North America.

In summary, the results do not support our first two hypotheses that ants have expanded their ecological roles in the relative absence of rodents. Further, many aspects of community composition are dissimilar between the two continents, casting doubt on our third hypothesis. We turn now to the abiotic and biotic factors that may account for these differences.

Potential abiotic causes of intercontinental differences

To the extent that resources influence harvester ant communities, two distinctive abiotic features of arid Australia may help to explain the considerable scatter in our data: edaphic variability and climatic uncertainty. First, because of edaphic variability among our study sites, mean annual precipitation may be a relatively poor indicator of productivity. In comparison with soils in North American deserts, the ancient soils

of arid Australia are infertile (Jackson 1957, Wild 1958, Charley and Cowling 1968). Consequently, nutrient limitation probably plays a greater role in governing productivity than in North America. In addition, greater variability in soil types, from sands to clays, occurs across short distances in arid Australia. In any particular area, soils may vary in the way they redistribute rainfall, in moisture storage capacity, and in fertility, thereby altering the translation of precipitation into productivity. Diverse plant associations occur in response to the relatively discrete soil types of the arid Australian landscape (Moore and Perry 1970, Williams 1982), making precipitation an inadequate indicator of productivity within general vegetation formations as well. Because we sampled mainly in two formations, our Australian sites covered a small range of the major soils of the arid zone, but they nevertheless encompassed sands, earths, and crusty duplex soils. Our North American sites were all situated on coarse sands, and the confounding effects of soil were thereby reduced.

Variability in soil is probably a major factor underlying the high beta diversity in Australia, which seems to occur in most groups of ants and not just in harvesters (Greenslade 1978, 1982, Andersen 1983). More variable soils and consequent subtle vegetational changes could result in a larger regional species pool than is present in North America and may explain the presence of more rare species in Australian communities. The presence of many closely related species of harvester ants in apparent parapatry may parallel patterns seen in other speciose groups such as *Acacia* (Hopper and Maslin 1978) and lizards (Pianka 1986). It is possible, therefore, that poorly understood historical factors leading to rapid speciation contribute to extensive change in Australian harvester ant communities across edaphic and climatic gradients. It is also possible that historical factors and extensive speciation have affected the structure of Australian communities (see Ricklefs 1987). For instance, the mismatch we observed between resource availability and usage and the compressed size range of Australian ants may be attributes of historically young communities that have not yet passed through an intensive selective

filter, as suggested by Diamond (1986) for certain New Guinean birds.

Second, rainfall is more variable in arid Australia than in North American deserts of comparable mean annual precipitation (Leeper 1970, Gentilli 1971, Low 1978, Milewski 1981). Infrequent large-scale incursions of cyclonic rainfall can lead to productivity of a magnitude rarely seen in North American deserts, but these peaks are often separated by periods of low rainfall and lack of production. This variability could mean that Australian ant communities are less likely than North American ones to be in equilibrium with their resources. Although this nonequilibrium hypothesis could explain the observed mismatch between resource use and availability in Australia, at least one alternative hypothesis (see below) is equally plausible.

Extensive productivity after heavy rain in Australia also has indirect effects on consumers because it frequently leads to fire (Griffin and Friedel 1985), and postburning succession alters plant species composition and, presumably, rates of seed production (Griffin 1984). Fire can occur as frequently as every 10 yr in hummock grasslands, but even in acacia shrublands the rare fires affect vegetation composition (Griffin and Friedel 1985). Fires have immediate (Andersen and Yen 1985) and long-term effects (Greenslade 1985) on ants in arid Australia. We could not describe the fire history of each Australian site, and so may have introduced scatter into our data by sampling across successional as well as climatic gradients.

Further, more variable rainfall in Australia and the associated fire-driven succession almost certainly lead to more unpredictable seed production, because semiperennial plants may establish during periods of high rainfall and subsequently dominate the flora. After a succession of years with low rainfall, or after fire, ephemeral plants may be more abundant. Thus, the plant communities and the supply of seeds may change through time more dramatically than in North American deserts, where the flora is always dominated by annuals. Clearly, peculiarities of the physical environment of arid Australia may have substantial effects on consumers, but separating such influences from biotic interactions will be a difficult task.

Potential biotic causes of intercontinental differences

Biotic differences between the two continents have probably interacted with physical factors to determine differences in harvester ant communities. In the first place, our initial predictions based on differences in the relative importance of the three major taxa of granivores were almost certainly oversimplified, because continuing studies in North American deserts are demonstrating complex interactions among granivores and seeds. For example, although rodents and ants are short-term competitors, specialization by these taxa on different classes of seeds affects long-term interactions between plants (Davidson et al. 1984). It seems that although ants are both short-term and long-term competitors of rodents for shared resources, rodents actually facilitate ants over the longer term in some environments by suppressing competitors of the plants providing most resources for ants.

If the mismatch between seed production and use by Australian ants turns out to be a general phenomenon, rather than an artifact of our limited sampling, it might be a consequence of reduced interaction between seeds, rodents, and ants. In the absence of rodents, Australian plants may have evolved defenses (e.g., larger seed size, harder seed testae, chemical toxins, etc.) against seed predation by ants. Among chenopods, for example, the spongy bractioles surrounding some *Atriplex* seeds and the hard woody utricles enclosing seeds of *Sclerolaena* protect them from most harvester ants (Davison 1982).

Predators or interference competitors unique to Australia may have influenced the behavior of harvester ants as well as their abundance and diversity. The diverse and abundant lizard fauna in arid Australia (Pianka 1986) may have favored less energetically costly and, therefore, smaller foragers as a means of reducing a colony's loss to predators. Second, temporal displacement of foraging, especially in individually foraging *Melophorus* spp., may be a response minimizing contact with the ubiquitous and abundant Australian ants in the genus *Iridomyrmex*. Although these ants do not compete with harvesters for food, their extraordinary numbers and inquisitive behavior probably allow them to dominate assemblages of ants and to influence the composition of the ant fauna over most of inland Australia (Greenslade 1976, 1979, Greenslade and Halliday 1983). Whereas harvester ants with relatively populous colonies and dense foraging columns (e.g., *Chelaner* A) are capable of foraging when *Iridomyrmex* are active, higher rates of contact with these aggressive intruders in individually foraging workers may be a strong selective pressure favoring displacement of foraging by *Melophorus* (see also Carothers and Jaksic 1984).

Finally, and perhaps most importantly, birds may compensate in part for missing rodents (Morton and Davies 1983, Morton 1985). Particularly in relatively productive areas, rapid depletion of seed crops by the diverse and abundant fauna of specialized avian granivores may prevent use of these resources by ants. It is impossible at present to determine whether Australian birds consume quantities of seeds similar to North American rodents (Morton 1985). However, we cannot rule out the possibility that birds have compensated for rodents, and consequently that the resource base for ants has not expanded.

CONCLUSION

We asked whether harvester ants compensate numerically and ecologically in arid Australia for a pau-

city of mammalian granivores that may be their pri-
mary competitors in North American deserts. No
difference between faunas on the two continents could
be interpreted unequivocally as a response to the re-
duction in rodent competitors. Second, we asked
whether harvester ant communities were convergent
in their diversity and structure, aside from the effects
of the predicted ecological release. Answers to this
question were ambiguous. On the one hand, there were
certain similarities between communities in Australian
and North American deserts. The close correspon-
dence between estimates of ant abundance and maxi-
mum values for numbers of common species and species
diversity on the two continents suggests the existence
of upper limits. On the other hand, many substantial
differences emerged. In the absence from Australia of
many of the strong patterns found in North American
harvester ant communities, we cannot argue in favor
of a single explanation for these differences. Some dif-
ferences may be due to resource limitation, but we are
unable to rule out the hypotheses that Australian ant
communities are not in equilibrium with their resource
environments or that they are not food limited in any
simple way. Thus, convergence does not appear to have
occurred in any but the most general sense, and our
studies support the conclusion (Pianka 1973, Schall
and Pianka 1978) that ecological differences between
the arid environments of Australia and North Amer-
ican deserts have had significantly divergent conse-
quences for the assembly of animal communities.

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APPENDIX

TABLE A1. Coefficients of similarity* for Australian communities (above the diagonal) and North American communities (below the diagonal). Code numbers for study sites are as in Tables 1 and 2.

Study sites	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	···	0.20	0.33	0.22	0.12	0	0	0.11	0.33	0.48	0	0	0.13	0.24	0.09	0	0.12	0.13	0.27
2	0.40	···	0.30	0.10	0.11	0.09	0.19	0.10	0.20	0.33	0	0.12	0.11	0.11	0.08	0.12	0.47	0.11	0.12
3	0.33	0.80	···	0.22	0.12	0.10	0.32	0.21	0.22	0.38	0.12	0.13	0.25	0.24	0.09	0.13	0.24	0.25	0.27
4	0.22	0.50	0.67	···	0.23	0.10	0.11	0.11	0.22	0.38	0	0.13	0.25	0.59	0.27	0.13	0.24	0.13	0.13
5	0.33	0.40	0.33	0.44	···	0.10	0.22	0.11	0.12	0.10	0	0	0.13	0.38	0.19	0	0.25	0	0
6	0.20	0.44	0.60	0.62	0.40	···	0.36	0.18	0	0.08	0	0.11	0.11	0.10	0.40	0.11	0.10	0.11	0.11
7	0.22	0.50	0.86	0.67	0.22	0.73	···	0.20	0	0.09	0.11	0.13	0.12	0.11	0.17	0.13	0.22	0.12	0.13
8	0	0	0.20	0.46	0.20	0.43	0.31	···	0	0.18	0	0.13	0.12	0.11	0.26	0.38	0.11	0.24	0.25
9	0	0	0.18	0.43	0.36	0.40	0.29	0.80	···	0.19	0	0	0.13	0.24	0	0	0	0	0.13
10	0	0	0.20	0.46	0.20	0.57	0.15	0.86	0.67	···	0.10	0.11	0.32	0.40	0.24	0.11	0.30	0.21	0.22
11											···	0	0	0	0	0	0	0	0
12												···	0.15	0.14	0.11	0.17	0.14	0.15	0.17
13													···	0.27	0.10	0.15	0.13	0.14	0.15
14														···	0.29	0.14	0.25	0.13	0.14
15															···	0.11	0.19	0.10	0.11
16																···	0.14	0.31	0.33
17																	···	0.13	0.14
18																		···	0.46

* The coefficient of similarity = $2w/(a + b)$, where w = number of species common to the two communities and a and b are the numbers of species in each of the two communities.